Herbivore-carrying capacity of grasslands in the Swiss National Park

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Zurich 1997
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The following chapters are based on papers with the same titles:
Chapter 4: Oikos, submitted.
1 Summary

The Swiss National Park (168 km²) is located in the eastern Central Alps within the subalpine and alpine zones. The density of ungulates is assumed to be very high in the Swiss National Park. Therefore, data on phytomass available for ungulates were needed to get a basis for further discussions of the herbivore-carrying capacity.

By means of a Geographic Information System the grasslands (20 km²) of the study area (106 km²) were classified into 41 categories by habitat factors. In 31 categories, covering 99% of the grasslands, 76 sample points were selected. In 1996, the green phytomass was assessed at each sample point with a radiometer. In addition, the accuracy of the radiometric technique was investigated. Using the data of the radiometric measurements, the phytomass was then modelled for the study area for three scenarios: (a) 'present', (b) 'maximum possible', and (c) 'no' grazing pressure. The differences (c) - (a) and (c) - (b) were assumed to be the phytomass offtake under present or maximum possible grazing pressure, respectively. The calculated offtake was compared to the requirements of ungulates, rodents and grasshoppers to evaluate the plausibility of the model and to calculate the herbivore-carrying capacity of the Swiss National Park.

In order to assess the energy balance as well as the impact of ungulates on fodder quality of subalpine grasslands, both a productive and a less productive grassland were studied by using a paired-sample design (grazed and ungrazed plots) between May and August 1995.

Accuracy of radiometric technique
The 95% confidence interval of prediction for calculating the dry weight of green and total above-ground phytomass (20 measurements) was ±28% and ±45%, respectively.

Fodder quality and energy balance
The productive grassland investigated showed a mosaic pattern of short turf and tall vegetation, which was caused by grazing. Steady grazing during the growing season resulted in a smaller increase of crude fibre and in a smaller decrease of crude protein content in the short turfs compared with (a) the taller vegetation areas of the productive grassland, as well as (b) the entire less productive grassland. This resulted in better fodder quality.
On both subalpine grasslands, ungulates consumed less than 56% of the energy available in phytomass. In May and July, the ungulates occurring in high density covered all their energy demands on the productive grassland; in June their energy intake on the same site was only 60%. On the less productive grassland, the ungulates occurring in low density covered their energy demands from May to July only to 40–74%, although phytomass was not limited. They grazed in the surrounding forests or in the nearby alpine grasslands instead.

Productivity and herbivore-carrying capacity

Under the actual grazing pressure of 1996 the net community productivity of the subalpine and alpine grasslands varied between 1.5–2.2 t ha\(^{-1}\) yr\(^{-1}\) and 0.8–1.2 t ha\(^{-1}\) yr\(^{-1}\), respectively. The green phytomass production of the 20 km\(^2\) grassland amounted to 1750 t yr\(^{-1}\), 642 t yr\(^{-1}\) and 2723 t yr\(^{-1}\) for the scenarios of 'present', 'maximum possible' and 'no' grazing pressure. The calculated offtake was 973 t yr\(^{-1}\) (36% of the highest possible green phytomass production) under 'present' and 2081 t yr\(^{-1}\) (76%) under 'maximum possible' grazing pressure.

The requirements of all considered consumer groups accounted in 1996 for 85% of the calculated offtake under present grazing pressure. Because this is within the confidence interval of the radiometric measurements (±28%), the model applied seems to be plausible.

The number of herbivores present in 1996 used only 40% of the maximum available phytomass. Therefore, it could be concluded that the herbivore-carrying capacity of the Swiss National Park is about 2.5 times the present number. This conclusion must be treated with caution, because heavy grazing pressure is known to reduce productivity, and production as well as herbivore density are subjected to annual variations. In addition, data of only one summer were available. Thus, it is probably more appropriate to say that the present number of herbivores attained the summertime herbivore-carrying capacity of the Swiss National Park to two thirds.
2 Zusammenfassung

Der Schweizerische Nationalpark (168 km²) liegt in den östlichen Zentralalpen in der subalpinen und alpinen Zone. Weil die Huftierdichte des Nationalparks im allgemeinen eher als zu hoch betrachtet wird, sind Daten über die für Huftiere verfügbare Phytomasse nötig. Diese sollen als Basis für weitergehende Diskussionen über die Tragfähigkeit des Nationalparks für Pflanzenfresser dienen.

Mit Hilfe eines Geographischen Informationssystems wurde das Grasland (20 km²) des Untersuchungsgebietes (106 km²) aufgrund von Standortsfaktoren in 41 Kategorien einteilt. Auf 31 Kategorien, welche 99% des untersuchten Graslandes deckten, wurden 76 Stichprobenpunkte verteilt. An jedem Stichprobenpunkt wurde 1996 auf 20 Flächen die vorhandene grüne Phytomasse mit einem Radiometer bestimmt. Zusätzlich wurde auch die Genauigkeit der Radiometermethode untersucht. Anhand der Radiometermessungen wurde die vorhandene Phytomasse des ganzen Untersuchungsgebietes für folgende drei Szenarien modelliert: (a) 'aktuelle', (b) 'maximale' und (c) 'keine' Beweidung. Für die Differenzen (c) - (a) und (c) - (b) wurde angenommen, dass sie die gefressene Phytomasse unter aktueller, resp. maximal möglicher Beweidung repräsentieren. Dann wurde die so berechnete gefressene Phytomasse mit dem totalen Bedarf von Huftieren, Nagetieren und Heuschrecken verglichen, um die Plausibilität des Modells zu beurteilen und die Tragfähigkeit des Nationalparks bezüglich Pflanzenfressern zu berechnen.

Um die Energiebilanz sowie den Einfluss von Huftieren auf die Nahrungsqualität von subalpinen Weiden zu messen, wurden zwischen Mai und August 1995 eine Fett- und eine Magerweide mit Hilfe einer gepaarten Stichprobenanordnung (beweidete und unbeweidete Flächen) untersucht.

Genauigkeit der Radiometermethode
Bei 20 Radiometermessungen pro Probefläche beträgt das 95% Vertrauensintervall für die Vorhersage der grünen und totalen oberirdischen Phytomasse ±28% bzw. 45%.

Futterqualität und Energiebilanz
Die untersuchte Fettweide wies ein Mosaik von Kurzrasen und hochgewachsenen Graslandflächen auf, das durch unterschiedliche Beweidungsintensität entstanden ist. Permanente Beweidung während der Vegetationsperiode führte zu einer verringerten Zunahme des Rohfaser- und einer geringeren Abnahme des
Rohproteingehalten im Vergleich zu (a) den hoch aufwachsenden Flächen der Fett- sowie (b) der gesamten Magerweide. Dies resultierte in einer erhöhten Nahrungsqualität.

Auf den beiden untersuchten subalpinen Weiden konsumierten Huftiere 1995 weniger als 56% der vorhandenen Energie. Im Mai und Juli konnten die Huftiere in der Fettweide bei hoher Dichte ihren Energiebedarf decken; im Juni jedoch nahmen sie hier nur 60% der benötigten Energie auf. In der Magerweide deckten die Huftiere bei geringer Dichte ihren Energiebedarf von Mai bis Juli nur zu 40-70%, trotz der ausreichend vorhandenen Phytomasse. Statt dessen ästten sie in den umliegenden Wäldern oder nahen alpinen Rasen.

**Produktivität und Tragfähigkeit bezüglich Pflanzenfresser**

1996 variierte unter der aktuell herrschenden Beweidung die Netto-Produktivität zwischen 1.5–2.2 t ha⁻¹ a⁻¹ für subalpine und 0.8–1.2 t ha⁻¹ a⁻¹ für alpine Rasengebüschaften. Die total produzierte Menge an grüner Phytomasse des Graslandes (20 km²) betrug 1750 t a⁻¹ für das Szenario ‘aktuelle’, 642 t a⁻¹ für ‘maximale’ und 2723 t a⁻¹ für ‘keine Beweidung’. Die berechnete gefressene Menge an grüner Phytomasse betrug für das Szenario ‘aktuelle Beweidung’ 973 t a⁻¹, was 36 % der maximalen Produktion entspricht. Beim Szenario ‘maximale Beweidung’ wurden 2081 t a⁻¹ als gefressen berechnet (76% der maximalen Produktion).


Dieselbe Anzahl Pflanzenfresser benötigte hingegen nur 40% der maximal zur Verfügung stehenden Phytomasse. Daher könnte man den Schluss ziehen, dass die Tragfähigkeit des Nationalparks bezüglich Pflanzenfressern etwa das 2.5-fache der gegenwärtigen Anzahl beträgt. Dieser Schluss sollte allerdings mit Vorsicht gezogen werden, weil einerseits ein hoher Beweidungsdruck die Produktivität erniedrigen und andererseits die pflanzliche Produktion sowie die Anzahl Pflanzenfresser von Jahr zu Jahr starken Schwankungen unterworfen sind. Zusätzlich sind in die Berechnungen Daten von nur einem Sommer eingeflossen. Daher erscheint die Schlussfolgerung, dass der gegenwärtige Bestand an Pflanzenfressern die Tragfähigkeit des Nationalparks im Sommer zu etwa zwei Drittel erreicht, angebracht.
3 General introduction

The Swiss National Park was founded in 1914 to protect nature from all human interference and influence which are not subservient to its purpose, which is to let nature develop according to its own rules and to enable long-term scientific research (Act of Parliament of October 7, 1959, art. 2). To minimize the influence of man on the ecosystem, visitors are restricted to the trails and some valleys are not accessible at all since they have been declared strictly off limits. The Swiss National Park is located in the eastern Central Alps and covers 168 km². It is situated in both the subalpine and alpine zones, with altitudes between 1500 m and 3160 m a.s.l.. Annual average of precipitation amounts to 1142 mm per year for the total Park area (Committee for scientific research in the National Park 1966). About one third of the area is covered by alpine and subalpine grasslands, one third by coniferous forests and one third by bare rock. Carbonate soils (outcrops of austro-alpine sedimentary formations; Middle Triassic to Cretaceous; Bündnerschiefer) dominate the area of the Park; only about 5% of the area are covered by silicate soils (outcrops of crystalline rocks; opholithic green-stones) (Committee for scientific research in the National Park 1966).

At the time of foundation, of the larger herbivores only roe deer (Capreolus capreolus L.) and chamois (Rupicapra rupicapra L.) were present in the Park itself and its surrounding areas. Red deer (Cervus elaphus L.) and alpine ibex (Capra ibex L.), and predators such as brown bear (Ursus arctos L.), wolf (Canis lupus L.) and lynx (Lynx lynx L.) have been extirpated in the past. The Park's population of roe deer reached its maximum of 300 animals in 1930 and decreased since then to about 50 animals (Voser 1987). The population of chamois fluctuates between 1000 and 1500 animals in the Park (Filli 1995a). At the beginning of the 20th century, red deer immigrated from Austria into the Engadine (Luchsinger 1962) and were observed in the Swiss National Park shortly after its foundation. Since then the population increased, reaching a maximum of 2400 in the late seventies (Voser 1987), and then declined to 1783 red deer in 1995 (Filli & Robin 1996). Ibex were introduced into the Swiss National Park in 1920 and developed into a colony of about 300 animals (Filli 1995b). In winter, ibex and chamois remain in the park, whereas red and roe deer migrate to their winter quarters at lower altitudes (Committee for scientific research in the National Park 1966).

To understand the spatio-temporal behaviour of the ungulates and their ef-
fects on vegetation, many studies have been carried out in the Swiss National Park. Hofmann & Nievergelt (1972) investigated the seasonal distribution patterns of ruminants in the valley of Trupchun. Voser (1987) determined the impact of red deer on cultivated meadows in the Lower Engadine and Münstertal, and Buchli (1979) investigated the condition and constitution of the red deer population. Stüssi (1970) described the succession of different types of grasslands in connection with increasing grazing pressure on Alp la Schera. Hemmi (1991) studied the grazing pressure of ibex, red deer and chamois on alpine grasslands in the valley of Trupchun. Zimmermann (1990) investigated in cooperation with Hemmi the small-scale pattern of vegetation use. Bonfils (1989) and Brandt (1993) studied the effects of ungulate trampling on the vegetation cover and the erosion of alpine grasslands. Newest results from long-term studies on permanent plots, established 80 years ago, indicate that the present impact of ungulates is too low rather than too high, if the goal were to preserve the percentage of grassland in the Swiss National Park (Krüsi et al. 1996; Krüsi et al. 1995).

Within this context it was the aim of this study to find answers to the following questions: How much phytomass is available for ungulates to graze and how many animals can be maintained in the Swiss National Park, i.e. what is the carrying capacity of the Swiss National Park for large herbivores? Above-ground plant biomass (referred to here as phytomass) was chosen as the object of study, because herbivore biomass and consumption are closely correlated with plant productivity, suggesting that the latter is a principal integrator and indicator of functional processes in food webs (McNaughton et al. 1989).

This thesis consists of three main chapters which deal with the following three central topics: (1) In chapter 4, the radiometer - i.e. a non-destructive method for measuring aboveground phytomass - is described and evaluated for use in an alpine region. Data on the accuracy of the method are given. (2) Chapter 5 deals, on a small scale, with the amount of grazed phytomass, using enclosures, and the influence of grazing on the fodder quality (crude fibre and protein content) in two subalpine grasslands. (3) Chapter 6 deals with the application of the radiometer on a regional scale for determining the phytomass available for ungulates. A Geographical Information System (ARC/INFO) was used for setting up the sampling design as well as for calculating available phytomass by modelling different scenarios.
4 Radiometric determination of above-ground phytomass in an alpine region

4.1 Summary

(1) Radiometric measurements to determine standing crop of plants are more commonly applied to agricultural than to natural ecosystems. In this study the above-ground phytomass of subalpine and alpine grasslands and dwarf shrub associations was assessed using this technique. The measurements were carried out at 808 nm and 677 nm with a hand-held radiometer. The simple ratio \((SR)\) was calculated by dividing the near-infrared measurements (808 nm) by the red one. Diurnal series were measured to examine the influence of time of day on \(SR\). 26 plots were harvested to calibrate \(SR\) against clipped green and total phytomass.

(2) \(SR\) varied with solar time and was lowest at noon. Therefore it is advisable to measure between 9:30 a.m. and 2:30 p.m. solar time.

(3) For calibration of \(SR\) against phytomass, vegetation structure was more important than floristic composition of a plant community. Therefore, the plots of different grassland and dwarf shrub associations were pooled and categorised as 'grazed', 'ungrazed' or 'dwarf scrubs'. The dry weight of green and total phytomass was calculated separately for every category.

(4) The 95% confidence interval of prediction for calculating the dry weight of green and total phytomass (20 measurements) was ±28 % and ±45 %, respectively.

(5) The advantage of this non-destructive method is that changes in above-ground phytomass can be monitored during successive years without disturbing the vegetation. The method is fast and allows high numbers of replicates. Hence, the phytomass could be monitored on a regional scale.

4.2 Introduction

Above-ground biomass is traditionally measured by clipping. This method is tedious and limits the number of samples that can be taken. In addition, it prevents remeasuring the same plot at a later date to estimate changes in biomass with time. By the use of radiometric measurements it is possible to overcome these drawbacks.

The radiometric method has been more commonly applied to agricultural than
to natural ecosystems and has been used for estimating leaf area index, standing crop, production and for indicating plant stress (e.g., Asrar et al. 1984; Daughtry et al. 1992; Holben, Tucker & Fan 1980; Kuusk 1991; Lord, Desjardins & Dubé 1985; Millard et al. 1980; Nilsson 1991).

Interaction of incident spectral irradiance with plant canopies results in spectral absorption or spectral reflection. Wavelength bands for radiometric measurements are selected according to the strong difference of reflectance between green vegetation and the natural background. Usually the following two bands are chosen: (1) 620 - 700 nm (red), where strong absorption by plant pigments occurs, and (2) 740 - 1100 nm (near infra-red), where minimal absorption occurs and the leaf scattering results in high levels of spectral reflectance, especially for dense canopies (Knipling 1970; Mayhew, Burns & Houston 1984; Scurlock & Prince 1993; Tucker 1977; Tucker 1979; Tucker & Sellers 1986). The ratio of near infra-red to red (simple ratio, SR) or other combinations of the two bands, such as the normalised difference vegetation index (NDVI), are used to estimate the photosynthetically active biomass. These ratios are usually based on estimates of reflectance (reflected radiance relative to incoming solar irradiance), but they may also be derived from absolute values of red and near infra-red reflected radiance, e.g. provided by satellites or aircraft sensors (Scurlock & Prince 1993; Tucker 1979).

The objectives of this study were to use radiometric measurements to determine the dry mass per area of different heterogeneous grasslands in the subalpine and alpine zone and to investigate the accuracy of the method. To give advice on when to take these measurements, the influence of time of day on the radiometric measurements of vegetation plots was investigated.

4.3 Methods
4.3.1 Site description
The study was performed mainly in the region of the Ofenpass in the Swiss National Park, which is located amongst the inner valleys of the Alps. The climate is characterised by a relatively low precipitation of about 1140 mm per year (Committee for scientific research in the National Park 1966).

The grasslands investigated are situated mostly on calcareous soils or on a mixture of calcareous and siliceous soils (1750 m - 2380 m a.s.l.). Two sites represent nutrient-rich subalpine grasslands (Trisetetum flavescentis and Crepido-
Festucetum nigrescentis; nomenclature of plant associations follows Zoller (1995)) which are heavily grazed by red deer (*Cervus elaphus* L.). The others are subalpine or alpine grasslands (Medicagin-Mesobrometum raeticum, Nardetum alpigenum typicum, Seslerio-Caricetum sempervirentis, Trifolio-Festucetum violaceae) or dwarf shrub associations (Juniper-Arctostaphyletum, Rhododendretum ferruginei, Rhododendretum hirsuti) which are moderately grazed.

A few measurements were made in an Arrhenatheretum elatioris in Riehen, two kilometres northeast of Basel (275 m a.s.l., 815 mm precipitation).

### 4.3.2 Radiometric measurement of standing crop

The main instrument used was a Tektronix J17 Photometer with a J1812 Irradiance sensor, which gives readings in W m⁻² (Tektronix Inc., Oregon); the measuring accuracy was ± 8% of readings. The sensor was mounted on a hand-held boom, 90 cm in length. During measuring, the sensor was held perpendicular to the measured surface.

*Table 4.1. Date of measuring and number of samples dependent on the purpose of the study. R, nutrient-rich subalpine grasslands; P, nutrient-poor subalpine grasslands; A, nutrient-poor alpine grasslands; C, nutrient-rich colline grassland.*

<table>
<thead>
<tr>
<th>Purpose</th>
<th>Date of measuring (<em>N</em> samples)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diurnal series (2 replicates, taken with radiometer)</td>
<td></td>
</tr>
<tr>
<td>with mask</td>
<td>R</td>
</tr>
<tr>
<td>with mask (Jul 95 (2))</td>
<td>R</td>
</tr>
<tr>
<td>Aug 95 (1)</td>
<td>P</td>
</tr>
<tr>
<td>Aug 95 (1)</td>
<td>Sep 95 (2)</td>
</tr>
<tr>
<td>without mask</td>
<td>A</td>
</tr>
<tr>
<td>Jul 95 (1)</td>
<td></td>
</tr>
<tr>
<td>Aug 95 (1)</td>
<td>C</td>
</tr>
<tr>
<td>May 96 (3)</td>
<td></td>
</tr>
<tr>
<td>without mask (May 96 (5))</td>
<td></td>
</tr>
<tr>
<td>Jul 95 (1)</td>
<td></td>
</tr>
<tr>
<td>Aug 95 (1)</td>
<td></td>
</tr>
<tr>
<td>Calibrate against phytomass (4 replicates, taken with radiometer)</td>
<td></td>
</tr>
<tr>
<td>grazed</td>
<td>R</td>
</tr>
<tr>
<td>Aug 95 (1)</td>
<td>A</td>
</tr>
<tr>
<td>Jul 96 (1)</td>
<td></td>
</tr>
<tr>
<td>Jul 96 (1)</td>
<td></td>
</tr>
<tr>
<td>ungrazed</td>
<td>P</td>
</tr>
<tr>
<td>Aug 95 (3)</td>
<td></td>
</tr>
<tr>
<td>Jul 96 (1)</td>
<td></td>
</tr>
<tr>
<td>Jul 96 (1)</td>
<td></td>
</tr>
<tr>
<td>ungrazed</td>
<td>A</td>
</tr>
<tr>
<td>Aug 95 (1)</td>
<td></td>
</tr>
<tr>
<td>Jul 96 (2)</td>
<td></td>
</tr>
<tr>
<td>Jul 96 (5)</td>
<td></td>
</tr>
<tr>
<td>dwarf scrubs</td>
<td>C</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
</tbody>
</table>
| Measurements were carried out at 807.5 ± 3.5 nm (near-infrared, *NIR*) and 676.8 ± 10 nm (red, *R*). The filters were produced by Balzers AG, Liechtenstein.
The filters were mounted on a rotatable disc and could be switched easily, with a delay of about two seconds. The readings were stored in a pocket calculator and later transferred to a computer.

For calibrating the radiometric measurements against phytomass it seemed important to measure a clearly defined section of the plot sampled, because alpine and grazed grasslands are quite heterogeneous. Since the sensor would cover from a distance of 68 cm nearly one square meter on the ground, a circular mask with a radius of 55.5 cm and a hole of 36 cm square in the middle was used to measure a 0.125 m² plot of vegetation. The wooden mask was painted matt black with a commercially available wrought-iron coating. The distance from surface to sensor was 68 cm. To standardise the measurements, I positioned myself so that the sun was always on my right side and no shadow was cast on the plot.

To investigate whether the black mask affected the SR, some plots were measured both with and without a mask. For measurements that were taken without a mask, the distance from surface to sensor was 101 cm and the angle of view was narrowed down with a tube to 20°. To standardise the measurements, I positioned myself opposite the sun.

It is important to notice that reflected radiance, as measured by satellite or aircraft sensors, and not reflectance was measured. Reflectance means the reflected radiance relative to a reference panel and is used in most studies. But with the use of a reference panel additional errors are introduced by the reflectance properties of the panel (Kimes, Smith & Ranson 1980).

For further calculations the simple ratio (SR) was used:

\[
SR = \frac{NIR}{R}
\]

The measurements were carried out under conditions ranging from cloudless, partially covered to overcast sky. The only restriction that was imposed was that the irradiance should not change between the successive measurements of NIR and R.

4.3.3 Calibration of radiometric measurement

4.3.3.1 Time of day dependence of SR

To examine the influence of time of day on the SR, diurnal series were measured in July, August and September 1995 in different grasslands in the Swiss National Park and on 30 May 1996 in Riehen (Table 4.1). In total 18 diurnal se-
ries were measured (9 with a mask, 9 without a mask). The measurements (2 replicates) were taken at approximately hourly intervals from 8 a.m. to 5 p.m. CET.

**Table 4.2. Dependence of SR on time of day: significance of the regressions of equation 2 for the models 'All SR values' and '9:30 - 14:30' where only SR values which were measured between 9:30 and 14:30 ST were included.***, P ≤ 0.001; **, P ≤ 0.01; *, P ≤ 0.05; ns, P > 0.05; N, number of hourly measurements.**

<table>
<thead>
<tr>
<th>Date</th>
<th>Plot</th>
<th>Mask</th>
<th>All SR values</th>
<th>9:30 - 14:30</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P-Value</td>
<td>N</td>
<td>P-Value</td>
<td>N</td>
</tr>
<tr>
<td>21.7.95</td>
<td>1</td>
<td>+</td>
<td>*</td>
<td>9 ns</td>
</tr>
<tr>
<td>24.7.95</td>
<td>2</td>
<td>+</td>
<td>**</td>
<td>10 ns</td>
</tr>
<tr>
<td>24.7.95</td>
<td>3</td>
<td>+</td>
<td>***</td>
<td>10 ns</td>
</tr>
<tr>
<td>24.8.95</td>
<td>4</td>
<td>+</td>
<td>***</td>
<td>10 ns</td>
</tr>
<tr>
<td>28.9.95</td>
<td>5</td>
<td>+</td>
<td>*</td>
<td>6 ns</td>
</tr>
<tr>
<td>28.9.95</td>
<td>6</td>
<td>+</td>
<td>*</td>
<td>6 ns</td>
</tr>
<tr>
<td>30.5.96</td>
<td>7</td>
<td>+</td>
<td>**</td>
<td>8 ns</td>
</tr>
<tr>
<td>30.5.96</td>
<td>8</td>
<td>+</td>
<td>***</td>
<td>8 *</td>
</tr>
<tr>
<td>30.5.96</td>
<td>9</td>
<td>+</td>
<td>**</td>
<td>8 ns</td>
</tr>
<tr>
<td>24.7.95</td>
<td>10</td>
<td>-</td>
<td>*</td>
<td>10 ns</td>
</tr>
<tr>
<td>24.8.95</td>
<td>11</td>
<td>-</td>
<td>ns</td>
<td>10 *</td>
</tr>
<tr>
<td>28.9.95</td>
<td>12</td>
<td>-</td>
<td>ns</td>
<td>6 ns</td>
</tr>
<tr>
<td>28.9.95</td>
<td>13</td>
<td>-</td>
<td>*</td>
<td>6 ns</td>
</tr>
<tr>
<td>30.5.96</td>
<td>14</td>
<td>-</td>
<td>**</td>
<td>8 *</td>
</tr>
<tr>
<td>30.5.96</td>
<td>15</td>
<td>-</td>
<td>ns</td>
<td>8 ns</td>
</tr>
<tr>
<td>30.5.96</td>
<td>16</td>
<td>-</td>
<td>ns</td>
<td>8 ns</td>
</tr>
<tr>
<td>30.5.96</td>
<td>17</td>
<td>-</td>
<td>**</td>
<td>8 ns</td>
</tr>
<tr>
<td>30.5.96</td>
<td>18</td>
<td>-</td>
<td>ns</td>
<td>8 ns</td>
</tr>
</tbody>
</table>

For further calculations the local apparent solar time (ST) was used. It is calculated as follows: for each degree of longitude the site is east (west) of the standard meridian, 4 minutes are added (subtracted) from the local standard time (here: CET) and then the equation of time correction is algebraically added (Oke 1990).

For each diurnal series of the 18 plots investigated the following model of time of day dependence was calculated:

\[ SR = a + b \text{(ST in minutes)} + c \text{(ST in minutes)}^2 \] eqn 2
4.3.3.2 Calibration of SR against phytomass

To determine the green and the total aboveground phytomass, the vegetation of 26 plots (0.125 m$^2$) was clipped at ground-level after the radiometric measurements had been taken (four replicates; Table 4.1). The samples were separated into dead and green plant material, and dry weight (80 °C) of the components was determined.

Every measured plot was categorised as 'ungrazed', 'grazed' or 'dwarf shrub'. 'Ungrazed' stands for either ungrazed or slightly grazed grassland vegetation where only the tips of grasses or forbs have been taken. 'Grazed' means heavily grazed grassland vegetation in which grazing pressure has caused a shift from taller grasslands to a short turf.

A general linear regression was calculated, in which the log of SR and the category were explanatory variables and the log of dry weight was the target variable:

$$\log(\text{dry weight}) = \alpha + \beta \log(SR) + (\gamma, \delta) \text{ category}$$  \text{eqn 3}

The resulting intercept $\alpha$ and coefficients $\beta, \gamma$ and $\delta$ were used to calculate the phytomass as follows:

$$\text{dry weight} = 10^{\alpha + \gamma \cdot SR^\delta}$$  \text{ (grazed) eqn 4}

$$\text{dry weight} = 10^{\alpha + \delta \cdot SR^\delta}$$  \text{ (ungrazed) eqn 5}

$$\text{dry weight} = 10^{\alpha - \gamma - \delta \cdot SR^\delta}$$  \text{ (dwarf shrub) eqn 6}

4.4 Results

4.4.1 Time of day dependence of SR

All diurnal series that were measured with a mask showed a significant ($P<0.05$) time of day dependence of the SR (Table 4.2). All series showed a similar pattern with the lowest values at about one hour after solar noon (Fig. 4.1). Of the diurnal series that were measured without a mask, only four of nine plots showed a significant dependence of SR on time of day (Table 4.2), though the trends are similar to those measured with a mask (Fig. 4.2).
Fig. 4.1. The daily course of the simple ratio (SR) for nine vegetation plots which were measured with a mask. ■, plot 1; ○, plot 2; Δ, plot 3; V, plot 4; <, plot 5; †, plot 6; □, plot 7; ◊, plot 8; ‡, plot 9.

If only values which were measured between 9:30 and 14:30 ST were taken, only three of 18 diurnal series showed a significant time of day dependence of SR.

Fig. 4.2. The daily course of the simple ratio (SR) for nine vegetation plots which were measured without a mask. ■, plot 10; ○, plot 11; Δ, plot 12; V, plot 13; <, plot 14; †, plot 15; □, plot 16; ◊, plot 17; ‡, plot 18.
4.4.2 Calibration of SR against phytomass

4.4.2.1 Dry weight of green plant material

All regressions showed with $R^2 > 0.896$ a good coefficient of determination (Table 4.3). For both regressions with and without a mask $R^2$ increased and the mean square of the error declined if only SR values which were measured between 9:30 and 14:30 were included in the regressions: the estimates of the regressions against the log of the clipped dry weight of the green phytomass are shown in Fig. 4.3.

The 95% confidence intervals for the prediction of the actual dry weight from a single SR value were ±76% and ±85% for measurements without and with a mask respectively. The confidence interval of prediction depends on the number of replicates and it reduces for 19 replicates to ±28% and ±30% for measurements without and with a mask respectively. Hence the prediction of the dry weight was almost independent of the use of a mask.

Table 4.3. Regression parameters and 95% confidence intervals of prediction (for 1, 10 and 20 measurements) of different models for calculating the dry weight of green and total phytomass. Mean square, mean square of error; $N$, number of plots included in regression; SEpred, mean standard error of prediction; †, only SR values which were measured between 9:30 and 14:30 ST were included in regression.

<table>
<thead>
<tr>
<th>Mask</th>
<th>$R^2$</th>
<th>$\alpha$</th>
<th>$\beta$</th>
<th>$\gamma$</th>
<th>$\delta$</th>
<th>Mean square</th>
<th>$N$</th>
<th>SEpred</th>
<th>1</th>
<th>10</th>
<th>20</th>
</tr>
</thead>
<tbody>
<tr>
<td>Green plant material</td>
<td>+</td>
<td>0.901</td>
<td>1.85</td>
<td>1.81</td>
<td>-0.343</td>
<td>0.085</td>
<td>0.0141</td>
<td>23</td>
<td>0.048</td>
<td>85</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>0.896</td>
<td>1.84</td>
<td>1.81</td>
<td>-0.372</td>
<td>0.099</td>
<td>0.0148</td>
<td>26</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>0.917</td>
<td>1.63</td>
<td>1.36</td>
<td>-0.384</td>
<td>0.105</td>
<td>0.0119</td>
<td>23</td>
<td>0.044</td>
<td>76</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>0.904</td>
<td>1.62</td>
<td>1.35</td>
<td>-0.412</td>
<td>0.115</td>
<td>0.0136</td>
<td>26</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total plant material</td>
<td>+</td>
<td>0.786</td>
<td>2.16</td>
<td>1.91</td>
<td>-0.288</td>
<td>-0.022</td>
<td>0.0353</td>
<td>23</td>
<td></td>
<td></td>
<td>†</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>0.794</td>
<td>2.15</td>
<td>1.93</td>
<td>-0.296</td>
<td>-0.020</td>
<td>0.0314</td>
<td>26</td>
<td>0.067</td>
<td>147</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>0.744</td>
<td>1.96</td>
<td>1.36</td>
<td>-0.327</td>
<td>-0.001</td>
<td>0.0423</td>
<td>23</td>
<td></td>
<td>†</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>0.749</td>
<td>1.94</td>
<td>1.37</td>
<td>-0.336</td>
<td>-0.003</td>
<td>0.0383</td>
<td>26</td>
<td>0.074</td>
<td>171</td>
<td>59</td>
</tr>
</tbody>
</table>
4.4.2.2 Dry weight of total plant material
All regressions showed an acceptable $R^2$ greater than 0.744 (Table 4.3). In contrast to the dry weight of green plant material, $R^2$ declined and the mean square
of the error increased if only SR values which were measured between 9:30 and 14:30 were included in the regression. Fig. 4.4 shows the estimates of the regressions against the log of the clipped dry weight of the total phytomass. The values of the three categories - ungrazed, grazed and dwarf shrub - are more scattered than in Fig. 4.3.

The 95% confidence intervals for the prediction of the actual dry weight from a single SR value were ±171% and ±147% for measurements without and with a mask respectively. The confidence interval of prediction reduces for 19 replicates to ±51% and ±45% for measurements without and with a mask respectively. Also in contrast to the phytomass of green plant material, the prediction of the dry weight was slightly more accurate if SR values were measured with a mask.

4.5 Discussion

4.5.1 Precision of radiometric measurements

The different diurnal series showed that the simple ratio (SR) depended on time of day and generally was lowest at noon. Kimes, Holben & Tucker (1984) and Duggin (1977) also reported an increasing spectral reflectance with increasing solar zenith angle, i.e. with increasing deviation of noon. The latter found changes in reflectance of wheat of 25-50% with a 30° change in solar zenith angle. Middleton (1991), too, reports increasing SR with increasing solar zenith angle for prairie sites with a LAI of 0.5 to 2, whereas taller or denser vegetation (LAI>2) exhibited either a maximum value at solar noon which decreased as solar zenith angle increased, or a moderate to high SR which remained approximately constant. Kimes et al. (1980) actually measured a decrease in reflectance for increasing solar zenith angle. Middleton (1991) concludes that a general "correction" to remove sun angle effects on spectral ratios is inappropriate because of the great variation of SR responses as a function of solar zenith angle. This corresponds with my results: diurnal series which were measured with a mask showed a clear pattern, whereas the ones which were measured without a mask did not show such uniform behaviour. Instead of looking for a correction it is recommended to measure around solar noon, because if only measurements of SR which were measured between 9:30 and 14:30 were used, only three of 18 diurnal series showed a significant dependence of SR on time of day.

This dependence of SR on time of day is likely caused by vegetation. Kimes
et al. (1980) found that in August the near-infrared (780-1400 nm) and red (620-700 nm) reflectances of a meadow were lower in the afternoon than in the morning at the same solar zenith angle, whereas in spring no difference could be detected. Plant turgor seems to play a crucial role, because the plant's water stress increases on a hot summer day. C₃ plants can reduce the loss of water by closing the stomata, by rolling up leaves or by changing the leaf orientation to avoid or at least reduce heating up. According to Tucker & Sellers (1986), the correlation of radiometric data with LAI depends on leaf orientation and solar elevation for canopies with non-horizontal leaf angle distribution functions. Kimes (1984) points out that the orientation distribution can change on a diurnal basis because of heliotropic leaf movements and other responses to environmental conditions. These small perturbations in leaf geometry may drastically alter the reflectance distribution.

Other factors such as clouding or dust can influence the spectrum of the incoming solar beams and thus change the recorded ratio of near-infrared to red. Between the hourly measurements the weather often fluctuated considerably from sunny, slightly overcast to dull conditions. The effect of clouds is found to be about 5% (Holmes & Smith 1977), resulting in a significant increase of the SR reading (Mayhew et al. 1984). A solution is to take measurements of the spectral reflectance of natural surfaces under conditions of uniform irradiation such as bright sunshine or a uniform overcast day (Milton 1981). However, random variations of at least 5-10% can occur, even on apparently clear days (Duggin & Philipson 1982), and high altitude cirrus clouds passing in front of the sun are difficult to detect with the human eye (Milton 1982). In alpine regions uniform irradiation conditions rarely persist for significant periods during a day.

It seems as if an error of about ±10–15% cannot be avoided, even if the measurements are taken under apparently uniform conditions.

### 4.5.2 Phytomass assessment with radiometric measurements

Many studies of phytomass using radiometric techniques are restricted to only one vegetation type (Das, Mishra & Kalra 1993; Kuusk 1991; Mayhew et al. 1984; Middleton 1991; Pearson, Tucker & Miller 1976). In the present study, however, plots of six different grassland and three different dwarf shrub associations were included. The analysis showed that the vegetation structure (e.g.
leaf angle or leaf transmittance) rather than the plant association is of importance for the calibration of \( SR \) (Kimes 1984; Kuusk 1991; Scurlock 1992; Scurlock & Prince 1993).

In the present study the vegetation plots were categorised as grazed, ungrazed or dwarf shrub. This resulted in a reliable \( R^2 > 0.90 \) and \( R^2 > 0.74 \) for the calibration of green and total phytomass, respectively. The distinction between ungrazed and grazed sites was not always clear, especially when the vegetation of the grazed plots was ungrazed for a period and grew taller than usual. But this was only the case for about 5% of the plots.

The 95% confidence interval for the prediction of the actual dry weight amounted for 20 measurements to ±28% and ±45% for the green and total phytomass respectively. A comparison of the accuracy of prediction with regressions described in literature is difficult, because this information is often lacking. The prediction for green phytomass is more accurate than for total phytomass, because the photosynthetically active tissue interacts with the red portion of the light spectrum which is measured and used as denominator for the calculation of the \( SR \) (Knipling 1970; Mayhew et al. 1984; Scurlock & Prince 1993; Tucker 1977). To have reliable values, at least 10-30% of the phytomass should be green vegetation (Mayhew et al. 1984; Pearson et al. 1976).

The use of a black mask did not increase the accuracy of determining the dry weight of green phytomass in heterogeneous vegetation, although the plots that were clipped for calibration were clearly defined. But for determining the dry weight of total phytomass the use of a black mask increased slightly the accuracy.

In conclusion, the method is useful for assessing biomass of subalpine and alpine grassland and dwarf shrub associations. Since the calibration of \( SR \) does not depend upon the plant association but on vegetation structure, the obtained regression could be used for measuring phytomass on a regional scale. It can also be used to monitor changes in aboveground phytomass of the same vegetation plot during successive years. It is recommended to measure between 9:30 a.m. and 2:30 p.m. solar time. To validate the measurements selected plots should be clipped. Because one measurement takes less than a minute, many readings can be taken. The method is of particular value in mountainous regions where satellite images are not appropriate because of the difficulty of correcting images.
5 Productivity and usage by red deer (Cervus elaphus) of two subalpine grasslands in the Swiss National Park

5.1 Summary

(1) Produced and by red deer (Cervus elaphus L.) consumed phytomass was studied on two subalpine grasslands of different productivity in the Swiss National Park. During three subsequent periods from May to August 1995, a productive ('Il Fuorn'; Trisetetum flavescentis; 3.7 ha; 1790 m a.s.l.) and a less productive grassland ('Stabelchod'; Crepido-Festucetum nigrescentis, Seslerio-Caricetum sempervirentis, Medicagini-Mesobrometum raeoticum; 2.6 ha; 1910 m a.s.l.) were compared using a paired-sample design with grazed and ungrazed plots (0.25 m²). The grassland of Il Fuorn was subdivided in a facies A (without litter) and a facies B (feltlike litter). Both sites were almost exclusively used by hinds and calves. Average densities of red deer were 8–14 individuals per ha on Il Fuorn and 1–4 individuals per ha on Stabelchod per night.

(2) During all periods red deer consumed on average 2 g m⁻² d⁻¹ dry matter on facies A of Il Fuorn. Thus, in May and June 85%, in July 67% of the produced phytomass were consumed. On facies B the animals consumed in May on average 5.3 g m⁻² d⁻¹ (41% of the produced phytomass), in June 0.7 g m⁻² d⁻¹ (16%) and in July 3.2 g m⁻² d⁻¹ (54%) of the plant production. On facies A, the intensive grazing during the growing season resulted in a smaller increase of crude fibre and a smaller decrease of crude protein content compared with facies B.

(3) Until mid June, red deer consumed on Stabelchod 0.6 g m⁻² d⁻¹ dry matter (46% of the produced phytomass). During the two subsequent periods until August, 0.3 g m⁻² d⁻¹ were consumed by red deer. The crude protein and crude fibre content of graminoids of the grazed plots differed after the second period from the ungrazed ones.

(4) On both grasslands red deer consumed less than 56% of the energy available in phytomass. In May and July, red deer covered their energy demands on Il Fuorn, in spite of their high density on this site; in June their energy intake on this site was only 60%. On Stabelchod they covered their demands only to 40–74%, although phytomass was not limited.

(5) The results show the differing use of subalpine grasslands in the Swiss Na-
tional Park by hinds. The productive grassland Il Fuorn led to a higher concentration of hinds on this site. Since the less productive grassland Stabelchod was only extensively used by red deer, they gathered about 60% of their energy from the surrounding forests and grasslands.

5.2 Introduction

When the Swiss National Park (SNP) was founded in 1914, only roe deer (Capreolus capreolus L.) and chamois (Rupicapra rupicapra L.) were present in the SNP and its surroundings. Red deer (Cervus elaphus L.) was extirpated in the 19th century. Close to the beginning of the 20th century, red deer immigrated from Austria via Prättigau into the Engadine (Luchsinger 1962) and were observed in the SNP shortly after its creation. Since that time the population in the SNP has increased, and 1476 red deer were counted in 1994 (Schweizerischer Nationalpark 1995). Therefore, the question of the impact of red deer on vegetation is of importance. In the SNP and its surroundings, several studies were done on this topic. Hofmann & Nievergelt (1972) investigated the seasonal distribution patterns of ruminants in the valley of Trupchun. Voser (1987) determined the impact of red deer on cultivated meadows in the Lower Engadine and Münstertal. Stüssi (1970) described the succession of different types of grasslands with increasing grazing pressure on Alp la Schera. Hemmi (1991) studied the grazing pressure of ibex (Capra ibex L.), red deer and chamois on alpine grasslands in the valley of Trupchun. In co-operation with the study of Hemmi, Zimmermann (1990) investigated the small-scale pattern of vegetation use. Bonfils (1989) studied the effects of ungulate trampling on vegetation cover and erosion of alpine grasslands. Results from long-term studies on permanent plots, established up-to 80 years ago, indicate that the present impact of red deer and chamois is too low, rather than too high, to preserve the percentage of grassland in the SNP (Krüsi et al. 1995).

In spring, during periods of unfavourable weather in summer, and in late autumn, red deer graze preferably on subalpine pastures. Within the SNP there are only few, small grasslands in the subalpine zone, and they are usually heavily grazed (Voser 1987). In the region of Il Fuorn these grasslands are Alp la Schera, Il Fuorn, Stabelchod, and three others.

In the present study, the above-ground productivity of the subalpine grasslands of Il Fuorn and Stabelchod and the grazing intensity of red deer are compared. For that purpose, phytomass production and its consumption by red
deer, as well as the seasonal variation of crude protein and crude fibre content were measured during one growing season. With these data the required and the consumed energy of the red deer as well as energy available in the grassland vegetation were calculated to judge the significance of the two subalpine grasslands as food resources for red deer.

5.3 Methods and study sites
5.3.1 Study sites
The study was carried out in the region of the Ofenpass in the eastern Central Alps. It is characterized by a relatively low precipitation of about 1140 mm per year (Committee for scientific research in the National Park 1966). As study sites, the grassland Il Fuorn (Coord. 811 860/171750; 3.7 ha, 1790 m a.s.l) and the grassland of Stabelchod (Coord. 814 500/171400; 2.6 ha, 1910 m a.s.l.) were chosen. Both subalpine grasslands are bounded mainly by the pass and by Erico-Pinetum mugo (nomenclature of plant communities follows Zoller (1995)).

Il Fuorn was in agricultural use until 1970. Since then the grasslands have been cut only a few times. Well weathering bed rock (Verrucano), location at the base of a slope, good water supply, as well as nutrients of the former agriculture favour plant growth. Campell & Trepp (1968) described the grasslands of Il Fuorn as varieties of a Trisetetum flavescentis.

Stabelchod is a dryer grassland which was used as a pasture until the foundation of the SNP; former irrigation ditches are still visible. The grassland lies on an alluvial fan of dolomite and shows a mosaic of three plant communities that indicate less nutrient-rich conditions (Crepido-Festucetum nigrescentis, Seslerio-Caricetum sempervirentis, Medicagini-Mesobrometum raeticum).

5.3.2 Red deer
The red deer population of the SNP uses different summer and winter home ranges (Voser 1987). Between the end of April and the beginning of June they migrate periodically on traditional routes from the winter habitats in the Engadine and Münstertal to the summer habitats within the SNP. The migration from summer to winter habitats usually begins in October after the rut, but can start in August or late in November, depending on weather conditions and food resources.

Fig. 5.1 shows the densities of red deer during 1995 on both study sites.
About one week after the snow had melted, the first red deer were sighted on the grassland II Fuorn. During the whole period investigated, only hinds and calves grazed on both study sites, whereas chamois and roe deer were rarely observed. Stags used the study sites mainly at the end of summer and during the rut. The average densities of red deer were always higher on II Fuorn than on Stabelchod.

Fig. 5.1. Densities of red deer on the study sites II Fuorn (○) and Stabelchod (△) (Parkdirektion 1995).

5.3.3 Consumed phytomass
The phytomass consumed by red deer was calculated by means of the difference method (Cox & Waithaka 1989; Klapp 1971). A paired-sample design was used on both study sites, where a grazed and an ungrazed plot (each 50 cm x 50 cm; distance 2.5–4 m) formed pairs for observation. Grazed control and ungrazed experimental plots were located randomly. The experimental plots were protected from grazing by wired off exclosures (70 cm x 70 cm x 60 cm; mesh size 20 mm) with a strip of 10 cm as a buffer zone around the plots.

5.3.3.1 Experimental design
At the beginning of the study, the grassland of II Fuorn was subdivided in a facies A (without litter; N = 14) and a facies B (with feltlike litter; N = 6). The amount of litter of a given plot depends on the grazing pressure of the previous year which in turn is a product of species composition (Achermann 1995).

The difference method overestimates the consumed phytomass, if it is applied for long grazing periods, because of the undisturbed growth on the ungrazed plots (Klapp 1971; Linehan, Lowe & Stewart 1952). Hence the consumed phytomass was determined after three to four weeks. From May to August 1995, both grasslands II Fuorn and Stabelchod (N = 15) were studied during
three subsequent periods. Due to a long period of unfavourable weather in June, the first period was prolonged on Il Fuorn (36 days, only facies A) and on Stabelchod (43 days) in comparison to the second and third period (each about 24 days).

After each period the paired samples were set up on previously grazed areas.

5.3.3.2 Clipping
At the end of each period, the grazed control and ungrazed experimental plots were clipped at 1.5 cm above ground. This corresponds to the lowest cropping height of red deer on facies A.

The dry weight (\(DW\)) of the plant material was determined separately for graminoids (Cyperaceae, Juncaceae and Poaceae), forbs, and dead plant material. Afterwards, the nutritional value of the dried plant material was determined.

5.3.4 Nutritional value
The crude protein (RAP-ME11403O.710) and crude fibre content (RAP-ME10901O.710) of three samples of both graminoids and forbs were analysed at the Swiss Federal Research Station for Animal Production (RAP) in Posieux for the control and the experimental plots of each study site and period. For technical reasons, only three samples could be analysed for each category; hence no statistical analyses were performed.

5.3.5 Calculations
(1) New growth (g \(DW\) m\(^{-2}\)) = (Sampled phytomass at the end of each period; for both experimental and control plots) - (Average phytomass of the previous period on the control plot).
(2) Rate of consumption (g \(DW\) m\(^{-2}\) d\(^{-1}\)) = \{(Average phytomass on experimental plot) - (Average phytomass on control plot)\} (Number of days per period\(^{-1}\)).
(3) Rate of production (g \(DW\) m\(^{-2}\) d\(^{-1}\)) = \{(Average phytomass on experimental plot) - (Average phytomass on previous control plot)\} (Number of days per period\(^{-1}\)).
(4) Density of red deer (N ha\(^{-1}\)): The number of red deer per area was calculated separately for hinds and calves based on data of Parkdirektion (1995).
(5) Energy requirement of red deer (MJ ha\(^{-1}\)): The requirement depending on body weight (\(BW\) in kg) was calculated as follows: Requirement = \(x BW^{0.75}\) (Bubenik 1984). For hinds, \(x\) was estimated as 1.26 MJ per kg \(BW\) because of
lactation (Bubenik 1984), which amounts to 33.6 MJ per hind per day for a body weight of 80 kg (Blankenhorn et al. 1979). For calves, x was assumed as 0.67 MJ per kg BW. Because the BW of calves increased during summer, the energy requirement per calf increased from 7.5 MJ d\(^{-1}\) during the first period to 9.6 MJ d\(^{-1}\) during the second period and to 10.7 MJ d\(^{-1}\) during the third period.

(6) Digestible energy content (MJ kg\(^{-1}\)): The digestibility of the organic matter in per cent was calculated for both graminoids and forbs using crude fibre content. The digestible crude protein was calculated on the basis of crude protein content. The digestible energy (MJ kg\(^{-1}\)) was calculated using digestible crude protein and digestible organic matter. (Forschungsanstalt für viehwirtschaftliche Produktion 1994: pp. 311–312).

(7) Available and consumed energy (MJ d\(^{-1}\)): The available and consumed energy per day were calculated for both graminoids and forbs by multiplication of the rate of production and consumption by the digestible energy content. Numbers in Table 5.1 are the sum of energy of graminoids and forbs. On the grassland Il Fuorn, the amount of facies A and B in relation to the total area were estimated 2/5 and 3/5, respectively.

## 5.4 Results

### 5.4.1 Food supply and consumption

#### 5.4.1.1 Il Fuorn (A)

The dry weight (DW) of the aboveground phytomass increased from the first to the third period on the steadily grazed plots from 12 to 47 g m\(^{-2}\). The highest new growth occurred during the third period with 24 g m\(^{-2}\), and was mainly caused by the new growth of graminoids (Fig. 5.2).

At the end of all periods, the DW of the phytomass was significantly higher on the ungrazed experimental plots than on the grazed control plots (P < 0.002, Wilcoxon test). The rate of consumption increased by 0.3 g m\(^{-2}\) d\(^{-1}\) from the first to the second period and then remained stable at 2.2 g m\(^{-2}\) d\(^{-1}\). During the first and second periods 85% of the new growth was consumed, during the third period 67%.

#### 5.4.1.2 Il Fuorn (B)

During the three periods, the phytomass (DW) increased on the steadily grazed plots from 127 g m\(^{-2}\) to 286 g m\(^{-2}\) (Fig. 5.2). The phytomass after the first and
third period was significantly higher on the ungrazed plots than on the grazed ones ($P < 0.05$, Wilcoxon test). During the first period the rates of production and consumption (10 g m$^{-2}$ d$^{-1}$ and 5 g m$^{-2}$ d$^{-1}$) were higher on facies B than on facies A. During the first period 41%, during the second 16%, and during the third 54% of the new growth was consumed.

![Graph showing phytomass and consumption rates](image)

**Fig. 5.2.** Phytomass (g m$^{-2}$) of ungrazed experimental (■) and grazed control (□) plots (mean ± 1 SE) of II Fuorn (A) (facies A, without litter), II Fuorn (B) (facies B, with feltlike litter) and Stabelchod; additionally, the calculated rate of production (●) and consumption (○) (g m$^{-2}$ d$^{-1}$) are given. F1a, 5.5.–10.6. (36 d); F1b, 15.5.–10.6. (25 d); F2, 10.6.–4.7. (24 d); F3, 5.7.–28.7. (23 d); S1, 10.5.–22.6. (43 d); S2, 22.6.–19.7. (27 d); S3, 20.7.–11.8. (22 d).

### 5.4.1.3 Stabelchod

From the first to the third period, the phytomass ($DW$) on the steadily grazed plots increased from 30 g m$^{-2}$ to 85 g m$^{-2}$ (Fig. 5.2). During the second period, the rate of production reached its peak with 2 g m$^{-2}$ d$^{-1}$. However, during all periods the rates of production were always lower on Stabelchod than on II Fuorn.

During the first period, the rate of consumption on Stabelchod (0.6 g d$^{-1}$ m$^{-2}$) was about three times lower than on facies A of II Fuorn. Only after the first period was the $DW$ of the phytomass significantly higher on the experimental plots.
than on the control plots ($P < 0.002$, Wilcoxon test). During the second period, the rate of consumption was 0.3 g m$^{-2}$ d$^{-1}$ and decreased to 0.2 g m$^{-2}$ d$^{-1}$ during the third period.

During the first period 46% of the new growth was consumed, during the second 14%, and during the third 33%.

### 5.4.2 Crude protein and crude fibre content

#### 5.4.2.1 Il Fuorn

Crude fibre content of graminoids on ungrazed plots increased from the first to the second period from 190 g kg$^{-1}$ (facies A) and 250 g kg$^{-1}$ (facies B) for both facies by about 60 g kg$^{-1}$ (Fig. 5.3a). The heavily grazed control plots of facies A showed the same high value at the end of the third period as the ones of facies B at the end of the first period.

![Fig. 5.3. Changes in crude fibre (▲△) and crude protein (●○) content of (a) graminoids and (b) forbs (mean of three samples) on Il Fuorn (A), Il Fuorn (B) and Stabelchod. Filled symbols, ungrazed experimental plots; open symbols, grazed control plot.](image)
Crude protein content of graminoids decreased from the first to the third period by about 30 g kg\(^{-1}\) on the grazed control plots of facies A and amounted to 200 g kg\(^{-1}\) by the third period. On facies B, the decrease from 250 g kg\(^{-1}\) to 150 g kg\(^{-1}\) in crude protein content of graminoids was three times higher than on facies A. At the beginning of the growing season, crude fibre and crude protein content were similar on both facies A and B. However, in the course of the growing season, steady grazing on facies A caused for both graminoids and forbs to a smaller increase in crude fibre and a smaller decrease in crude protein content than on facies B.

Facies A differed from facies B also with respect to the nutritional value of forbs (Fig. 5.3b). Crude protein content of forbs decreased from the first to the second period on the control plots of facies A from 258 g kg\(^{-1}\) to 238 g kg\(^{-1}\) and then increased to 246 g kg\(^{-1}\). Crude protein content of forbs on facies B decreased from the second to the third period from 215 g kg\(^{-1}\) to 160 g kg\(^{-1}\); no data are available for the first period. Crude fibre content of forbs on facies B was 200 g kg\(^{-1}\) during the third period, whereas on facies A it amounted to only 155 g kg\(^{-1}\).

### 5.4.2.2 Stabelchod

Only at the end of the second period did the crude fibre and crude protein content of graminoids on the experimental plots differ appreciably from the grazed control plots. During all periods, the crude fibre content of forbs from the grazed plots was smaller by 10 g kg\(^{-1}\) than that of the ungrazed experimental plots (Fig. 5.3b).

### 5.4.3 Energy budget of red deer

During the first and third period, red deer nearly covered their daily energy requirements with their energy intake on Il Fuorn (Table 5.1). Thus, they consumed about 56% of the energy available in vegetation. During the second period red deer covered only 59% of their daily energy requirements on this grassland. During the first and third periods phytomass energy was not limiting, however, the red deer consumed only 34% of the available energy.

During the first observation period on Stabelchod, red deer covered only 72% of their energy requirements from this grassland, although with 54% a similar amount of the available energy was consumed as on Il Fuorn (Table 5.1). To meet their requirements, 76% of the available energy should have been con-
sumed. During the second and most productive period on Stabelchod there was about the same density of red deer on this grassland as during the first period. However, they consumed only 14% of the available energy and thus covered their energy requirements only to 40%. During the third period they covered 75% of their daily requirements by consuming 32% of the available energy, but the average density of red deer was about three times smaller than during the first and second periods.

Table 5.1. Energy budget of red deer on two subalpine grasslands (II Fuorn, Stabelchod). Comparison of energy requirement of red deer (R), energy available in phytomass (A) and energy consumed by red deer (C). Three energy ratios enable comparison of the three periods of observation and the two study sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Period</th>
<th>Red deer ha⁻¹</th>
<th>Energy (MJ ha⁻¹ d⁻¹)</th>
<th>Energy ratios</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Hinds</td>
<td>Calves</td>
<td>R</td>
</tr>
<tr>
<td>II Fuorn</td>
<td>F1 (5.5.-10.6.)</td>
<td>11.9</td>
<td>1.3</td>
<td>410</td>
</tr>
<tr>
<td></td>
<td>F2 (11.6.-4.7.)</td>
<td>7.4</td>
<td>0.8</td>
<td>253</td>
</tr>
<tr>
<td></td>
<td>F3 (5.7.-28.7.)</td>
<td>8.8</td>
<td>1</td>
<td>311</td>
</tr>
<tr>
<td>Stabelchod</td>
<td>S1 (10.5.-22.6.)</td>
<td>2.8</td>
<td>1.1</td>
<td>99</td>
</tr>
<tr>
<td></td>
<td>S2 (23.6.-19.7.)</td>
<td>2.3</td>
<td>0.9</td>
<td>85</td>
</tr>
<tr>
<td></td>
<td>S3 (20.7.-11.8.)</td>
<td>0.8</td>
<td>0.3</td>
<td>30</td>
</tr>
</tbody>
</table>

On II Fuorn, red deer consumed a larger proportion of the energy available in phytomass in comparison to Stabelchod (34–57%). Only during the first period was a similar amount (54%) consumed on Stabelchod. However, the average density of red deer was about four times higher and available energy about nine times higher on II Fuorn than on Stabelchod. During the second and third periods on II Fuorn, the three to nine times higher density of red deer consumed about twice the amount of the energy available as compared to Stabelchod.

Interestingly, during the second period, red deer covered only 59% and 40% of their energy requirements on the two grasslands. On both sites, the deer covered about 55% of their energy requirements during the first and third periods. During all periods, consumption of energy required was lower by 20–30% on Stabelchod compared to II Fuorn.
5.5 Discussion

Phytomass and new growth were smaller on Stabelchod than on II Fuorn. This is probably caused by the well weathering bed rock (Verrucano) and the better water supply on II Fuorn. Nutrients of the former agriculture may also play a role on II Fuorn, whereas the geological substrate of Stabelchod is clearly less nutrient-rich (alluvial fan of dolomite).

In May, soon after the snow had melted, the first hinds were observed on II Fuorn and Stabelchod. Atzler (1984) suggested that seasonal migrations of red deer adapt to spatial and temporal changes in quality of food. In May, crude fibre content increases at lower elevations, whereas at higher altitudes, fibre content of graminoids and forbs remains low because of delayed growth (Georgii 1980). In May or June hinds give birth to their calves. The observed concentration of hinds on II Fuorn may be caused by the fact that hinds, compared to stags, prefer more nutrient-rich grasslands for grazing (Charles, McCowan & East 1977; Osborne 1984) in order to meet their higher energy requirements due to pregnancy and lactation (Staines, Crisp & Parish 1982). In addition, the subalpine grasslands of the SNP are surrounded by large forests, which provide shelter for hinds and calves.

Atzler (1984) stressed the importance of protein and fibre content for the quality of food. Bonengel (1969) showed with feeding trials that red deer are able to select fodder with a high protein content. Moss, Welch & Rothery (1981) also observed highest grazing pressure of red deer on the most nutrient-rich places. During the growing season, crude protein and crude fibre content developed inversely in undisturbed vegetation: Protein content of plants decreased whereas fibre content increased, both on facies B of II Fuorn and on Stabelchod. However, steady grazing during the growing season on facies A of II Fuorn led both graminoids and forbs to smaller increases of fibre content and smaller decreases of protein content than on facies B, although both facies showed a similar fibre and protein content at the beginning of the season. Therefore, the grassland of II Fuorn and especially facies A are of a high quality and important for red deer. Clutton-Brock & Albon (1989) observed that red deer prefer lawn-like turfs similar to facies A of II Fuorn.

A three to nine times higher density of red deer was observed on II Fuorn as compared to Stabelchod. Despite this higher density, red deer could satiate their energy requirements by consuming 51–60% of the energy available on II
Fuorn, which they actually did during the first and third observation periods. Red deer never covered their daily energy requirements exclusively on Stabelchod, although it would have been possible with the observed average density of 1–4 red deer per hectare. The differing composition of species on Stabelchod and II Fuorn (Achermann 1995) may have led to a more pronounced food selection on Stabelchod, and consequently to a smaller intake. By analysing long-term studies, Krüsi et al. (1995) concluded that the impact of red deer and chamois is rather too low to preserve the percentage of subalpine grasslands in the SNP. If consequently the open areas become scarce in the subalpine belt, a local decrease in botanical diversity will result.

If red deer are undisturbed during the day, they keep a regular pattern of grazing periods. In regions with frequent disturbance, however, the grazing periods are prolonged during the night, which can lead to an increase in browsing or removal of the bark in the resting quarters during the day (Bützler 1991). On II Fuorn and Stabelchod, red deer grazed only during the night because of disturbances by tourists. Since red deer covered their energy requirements only during the first and third periods on II Fuorn, they must have had additional food during all other periods (including the ones of Stabelchod) from the surrounding forests or in nearby shrub (*Pinus mugo*) or alpine grasslands. Bützler (1991) stressed in this context the physiological significance of additional food from trees or shrubs for digestion of red deer. Based on faeces analysis in the SNP Hegg (1961) showed that summer food of red deer consists to 35% of graminoids, to 40% of forbs and to 25% of evergreen plants. Unfortunately, this study provided no information about the places where faeces were collected. To answer the question of how much food is grazed in alpine grasslands or browsed in the surrounding forests, new analyses of faeces are necessary.
6 Determination of production and herbivore-carrying capacity of an alpine region with GIS

6.1 Summary
(1) In the view of the high density of ungulates, especially of red deer (*Cervus elaphus* L.), in the Swiss National Park, data on available phytomass were needed to understand these animals' effect on the vegetation. In this study the aboveground green phytomass of grasslands was determined with a non-destructive radiometric method. The grasslands (20 km²) of the study area (106 km²) were classified into 41 vegetation categories by means of a Geographic Information System (GIS; ARC/INFO), using a vegetation map, as well as slope and exposure data which have been derived from a digital elevation model. In 31 categories, which covered 99% of the grasslands, 76 sample points were selected and at every sample point the phytomass of 20 plots was measured by the radiometer technique. Subsequently a multiple regression was calculated with the phytomass as the independent variable and with the three following dependent variables: vegetation category, elevation and the number of plots with low grazing pressure. On the basis of the resulting parameters the phytomass was modelled for the study area by means of GIS for three scenarios: (a) PRESENT grazing level, (b) MAXIMUM POSSIBLE grazing, and (c) NO GRAZING. The differences (c) – (a) and (c) – (b) were assumed to be an estimate of the amount of phytomass removed (i.e. calculated offtake) under present and maximum possible grazing levels, respectively. Then the calculated offtake was compared with the requirements of different consumer groups to evaluate the plausibility of the model and to calculate the carrying capacity of the grasslands.

(2) Under the present grazing pressure the net community productivity of herbage varied between 1.5 – 2.2 t ha⁻¹ yr⁻¹ for subalpine and 0.8 – 1.2 t ha⁻¹ yr⁻¹ for alpine grasslands. The production of phytomass for the grasslands of the whole study area amounted to 1750 t yr⁻¹, 642 t yr⁻¹ and 2723 t yr⁻¹ for the models of PRESENT, MAXIMUM POSSIBLE and NO GRAZING pressure, respectively. Thus, the calculated offtake was 973 t yr⁻¹ under PRESENT and 2081 t yr⁻¹ under MAXIMUM POSSIBLE grazing pressure.
The requirements of the main consumer groups (ungulates, rodents and grasshoppers) accounted for 85% and 40% of the calculated offtake under present and maximum possible grazing pressure, respectively. Thus, for the year of the investigation, the assumption that the offtake can be calculated by subtracting (a) from (c) holds true, since the 85% accounted for are within the 95% confidence interval of the radiometric measurements for determining phytomass (±28%).

The number of herbivores present in 1996 required only 40% of the maximum available phytomass. Therefore, it could be concluded that the herbivore-carrying capacity of the Swiss National Park is about 2.5 times the present number. This conclusion must be treated with caution, because heavy grazing pressure is known to reduce productivity. Also, productivity varies between seasons. For example, a dry summer can lead to a very reduced production resulting in a bottleneck situation for herbivores. It is probably more appropriate to say that the maximum sustainable number of herbivores during the summer is about 1.5 times the present number.

### 6.2 Introduction

The Swiss National Park was founded in 1914 to preserve nature from man, to let nature develop according to its own rules and to enable long-term scientific research. To minimize the influence of man on the ecosystem, visitors are restricted to the trails and no access is permitted to some valleys. At the time of foundation, of the larger herbivores only roe deer (*Capreolus capreolus* L.) and chamois (*Rupicapra rupicapra* L.) were present in the Swiss National Park and its surrounding areas. Alpine ibex (*Capra ibex* L.) were introduced in 1920 (Filli 1995b). From Austria immigrated red deer (*Cervus elaphus* L.) were observed shortly after the foundation of the Park (Luchsinger 1962). Since that time the population of ungulates in the Swiss National Park has increased, reaching a maximum in the late seventies (Voser 1987).

To study the effects of ungulates on vegetation and the spatio-temporal behaviour of the ungulates themselves, many studies have been carried out in the Swiss National Park. Hofmann & Nievergelt (1972) investigated the seasonal distribution pattern of ruminants in the valley of Trupchen. Voser (1987) determined the impact of red deer on cultivated meadows in the Lower Engadine and Münstertal. Stüssi (1970) described the succession of different types of grasslands with increasing grazing pressure on Alp la Schera. Hemmi (1991) studied
the grazing pressure of ibex, red deer and chamois on alpine grasslands in the valley of Trupchun. Zimmermann (1990) investigated in co-operation with Hemmi the small-scale pattern of vegetation use. Bonfils (1989) and Brandt (1993) studied the effects of ungulate trampling on the vegetation cover and the erosion of alpine grasslands. Newest results from long-term studies on permanent plots established 80 years ago indicate that the present impact of ungulates is if anything too low, if the goal were to maintain the present extent of grassland in the Swiss National Park (Krusi et al. 1995 and 1996).

In this context the question arose, how much phytomass is available for ungulates to graze and how many animals can be sustained by the Swiss National Park, i.e. what is the herbivore-carrying capacity of the Swiss National Park?

![Fig. 6.1. Location and extent of study area. Data source: Geographic Information System of the Swiss National Park (GIS-SNP).](image)

In this study a non-destructive and fast radiometric method for measuring above-ground green phytomass was applied. A stratified sampling design was worked out within the Geographic Information System of the Swiss National Park (GIS-SNP) as a basis for sampling about two thirds of the area of the Swiss National Park. Subsequently the phytomass present was measured. These data
were related to vegetation type, exposure and slope using a multiple regression analysis. Using the resulting parameters, the distribution of phytomass was estimated within the study area under different grazing pressure with the help of GIS. The requirements of different consumer groups, i.e., ungulates, rodents and grasshoppers, were compared with the obtained calculated offtake to test whether the method gives plausible results, and to calculate the carrying capacity of the grasslands regarding grazing.

6.3 Site description and methods
The flow chart in Fig. 6.2 gives an overview of how the offtake and the carrying capacity were calculated. It shows in a concise form information from the chapters 6.3.2 – 6.3.6.

6.3.1 Site description
The study was performed in grasslands of the Ofenpass area in the Swiss National Park (Fig. 6.1). The Swiss National Park is located in the Engadine which belongs to the eastern Central Alps. The climate is characterised by a relatively low annual average of precipitation of about 1140 mm per year for the total Park area (Committee for scientific research in the National Park 1966).

The grasslands investigated are situated mostly on calcareous soils or on a mixture of calcareous and siliceous soils and range from 1660 m to 2660 m a.s.l.. Grasslands on pure siliceous soils are rare. Nutrient-rich subalpine grasslands such as Trisetetum flavescentis (nomenclature of plant associations follows Zoller (1995)) and Crepido-Festucetum nigrescentis are heavily grazed by red deer. The other vegetation types investigated are subalpine or alpine grasslands (Medicagini-Mesobrometum raticum, Nardetum alpigenum typicum, Seslerio-Caricetum sempervirentis, Trifolio-Festucetum violaceae) or dwarf shrub associations (Junipero-Arctostaphyletum, Rhododendretum ferruginei, Rhododendretum hirsuti).

6.3.2 Stratified sampling design with GIS-SNP
The study area covers about 108 km² in which grasslands amount to 19.5 km². Only 10% of the grasslands are located in the subalpine zone.

The grasslands were classified with the help of GIS (ARC/INFO) by intersecting the following site parameters: (1) five vegetation categories of the vegetation map by Zoller (1992), (2) three slope categories (0–5°, 5–30°, >30°) and
Fig. 6.2. Flow chart for determining the impact of herbivores and the carrying capacity of the Swiss National Park for ungulates and other consumer groups. Special emphasis is put on the use of a Geographic Information System (GIS) for point and area related analyses.
(3) four exposure categories (N, E, S, W). To (1): Zoller (1992) used the following five categories: nutrient-poor subalpine grasslands (178 ha); nutrient-rich subalpine grasslands (9 ha); alpine grasslands on calcareous soils (1600 ha); alpine grasslands on a mixture of calcareous and siliceous soils (148 ha) and alpine grasslands on siliceous soils (20 ha). The parameters (2) and (3) have been derived from a digital elevation model with a resolution of 20 m x 20 m, resampled to 10 m x 10 m. This procedure resulted in the creation of 41 vegetation classes (Appendix 6.1).

The number of sample points per vegetation class was calculated in proportion to the area of the vegetation class as follows:

\[ N \text{ samples} = 1.5 \sqrt{\text{Frequency in \%}} \quad \text{eqn 1} \]

This equation was chosen, because it provided for the whole study area about 95 sample points. If more than one sample point per vegetation class were to be taken, the sample points were distributed from low to high elevation.

Due to the strict access ban of some of the park’s areas and for logistic reasons (6–7 sample points per day) the sample points were distributed manually, based on a grid of 100 m x 100 m (Fig. 6.3).

The measurements were carried out at peak phytomass. Because vegetation growth is delayed with increasing elevation, the day of measuring was determined as follows: for every 100 m increase in elevation, the beginning of the growth period is considered to be delayed by three days for south and by five days for north exposed areas (Forschungsanstalt für viehwirtschaftliche Produktion 1994). For east and west exposed areas four days were assumed. As a phenological indicator for the starting point of the growth period larch needle sprouting (17 May 1996) at Il Fuorn in the centre of the Park at 1790 m a.s.l. was used. The first sample point was measured 46 days (2 July), the last sample point 95 days (20 August) after sprouting.

**6.3.3 Measured parameters at sample points**

At every sample point, vegetation structure characteristics, as e.g. vegetation height, percent cover of green vegetation, percent cover of forbs, or the ten most abundant plant species were recorded. The biomass of the green and total plant material was measured using a radiometric technique (for further details cf. chapter 4).
Legend

- Sample points
- Trails

Vegetation types

- Alpine grassland on calcareous soils
- Alpine grassland on mixed soil
- Alpine grassland on siliceous soils
- Nutrient-rich subalpine grassland
- Nutrient-poor subalpine grassland

Fig. 6.3. Vegetation types and distribution of sample points (●) in the study area. Data source: Geographic Information System of the Swiss National Park (GIS-SNP).
6.3.3.1 Radiometric measurement of green phytomass

The main instrument used was a Tektronix J17 Photometer with a J1812 Irradiance sensor, giving readings in watts per squaremetre (Tektronix Inc., Oregon). The sensor was mounted on a 90 cm long hand-held boom. During reading, the sensor was held perpendicular to the surface measured. The distance from surface to sensor was 101 cm and the angle of view was narrowed down with a tube to 20°. The measurements were carried out under conditions ranging from cloudless to overcast sky. The only restriction was that the irradiance should not change between the successive measurements of near-infrared and red.

Measurements were carried out at 807.5 ± 3.5 nm (filter for near-infrared) and 676.8 ± 10 nm (filter for red) and were taken between 10 a.m. and 5 p.m. CET. The filters, produced by Balzers AG (FL), were mounted on a rotatable disc and could be switched within one second.

To calibrate the radiometric measurements against aboveground green phytomass the simple ratio (SR) was used:

\[
SR = \frac{\text{near-infrared}}{\text{red}} \quad \text{eqn 2}
\]

At every sample point 20 plots were measured with the radiometer and every plot was categorized as UNGRAZED, GRAZED OR DWARF SHRUB. UNGRAZED stands for ungrazed or slightly grazed grassland vegetation where only the tips of grasses or forbs have been eaten. GRAZED means heavily grazed grassland vegetation in which grazing pressure has caused a shift from taller grasslands to a short turf.

6.3.3.2 Calibration of radiometric measurements against green phytomass

For calibrating the SR value against green aboveground phytomass, vegetation samples of 26 squares (0.125 m²) were clipped at ground-level (0 cm) after the radiometric measurements (four replicates) had been made. The samples were separated into dead and green plant material, and its dry weight (80 °C) was determined. Every measured square was categorized as UNGRAZED, GRAZED OR DWARF SHRUB. Stems of dwarf shrubs were included in total aboveground phytomass but not in green plant material. Mosses and lichens were not taken into consideration.

A general linear regression was calculated, in which the log of SR and the category were explanatory variables and the log of dry weight was the target variable. Using the resulting parameters, the dry weight of green phytomass was
calculated as follows:

- **GRAZED**
  
  \[ \text{dry weight} = 32.07 \times SR^{1.81} \]
  
  \text{eqn 3}

- **UNGRAZED**
  
  \[ \text{dry weight} = 85.98 \times SR^{1.81} \]
  
  \text{eqn 4}

- **DWARF SHRUB**
  
  \[ \text{dry weight} = 38.99 \times SR^{1.81} \]
  
  \text{eqn 5}

### 6.3.4 Models applied for calculating green phytomass in study area

For every sample point the mean of the dry weight of green phytomass was calculated using equations 3 to 5. The 95% confidence interval of prediction amounts to ±28%. Then, the following multiple regression was applied:

\[
\log(\text{dry weight})_i = a + b \times \text{elevation}_i + c \times \text{v_class}_i + d \times \text{not grazed plots}_i 
\]

\text{eqn 6}

where \(i\) represents the \(i\)-th sample point (with 20 measured plots), \(\text{elevation}\) is the measured elevation a.s.l. in m, \(\text{v_class}\) is one of the 41 derived vegetation classes and \(\text{not grazed plots}\) is the percentage of not grazed plots in relation to the total of measured plots (\(N=20\)) at the \(i\)-th sample point. Afterwards, for every grassland cell of the 10m x 10m grid, the dry weight of green phytomass was calculated using the parameter values of equation 6 (Appendix 6.1).

In ten vegetation classes no data could be taken because of the very small area present or because access proved very difficult. These classes only cover about 1% of the total 20 km\(^2\) of grasslands investigated. For these vegetation classes the following multiple regression was used:

\[
\log(\text{dry weight})_i = a + b \times \text{elevation}_i + c \times \text{vegetation}_i + d \times \text{exposure}_i \\
+ e \times \text{slope}_i + f \times \text{not grazed plots}_i
\]

\text{eqn 7}

where \(\text{vegetation}\) is one of the five categories used by Zoller (1992), \(\text{exposure}\) one of the four categories N, E, S or W and \(\text{slope}\) one of the three categories 0–5\(^\circ\), 5–30\(^\circ\) and >30\(^\circ\). The dry weight of green phytomass was subsequently calculated using the parameter values of equation 7 (Appendix 6.1).

Using equation 6 or 7, the following three cases were modelled: (1) **NO GRAZING**, the percentage of \(\text{not grazed plots}\) was set 100 for all vegetation classes, (2) **PRESENT GRAZING**, the present measured percentage of \(\text{not grazed plots}\) was used, and (3) **MAXIMUM POSSIBLE GRAZING**, the percentage of \(\text{not grazed plots}\) was set 0.
6.3.5 Digestible energy content of phytomass in study area

First, the digestibility of the organic matter in per cent was assessed on the basis of the mean crude fibre content of 12 analyses samples for alpine, 12 for nutrient-poor subalpine and 22 for nutrient-rich subalpine grasslands (samples taken in June and July 1995). The digestible crude protein was calculated on the basis of crude protein content. The digestible energy (GJ t⁻¹) was calculated using digestible crude protein and digestible organic matter. All the calculations were carried out according to the guidelines of the Forschungsanstalt für viehwirtschaftliche Produktion (1994: pp. 311–312).

6.3.6 Energy requirements of consumers

The energy required was calculated for different consumer groups such as ungulates, marmots, voles and grasshoppers. Detailed countings of ungulates were provided by the Park authorities of the Swiss National Park, whereas density estimations, body weight (BW) and consumption for the other consumer groups were obtained from the literature and represent only rough assumptions (Table 6.2).

Energy required per capita per day (MJ capita⁻¹ d⁻¹) was calculated for ungulates and rodents as follows: Energy required = x • BW⁰.⁷⁵ where x is the maintenance in MJ d⁻¹ kg⁻¹ and BW the body weight in kg capita⁻¹ (Bubenik 1984). The energy required by grasshoppers was calculated based on data giving the amount of fodder consumed during summer (Schäller & Köhler 1981).

Subsequently, energy required per consumer group per year (GJ yr⁻¹) was calculated as follows: Energy required = ER • N • A, where ER is the energy required per capita per day in GJ capita⁻¹ d⁻¹, N the number of animals and A the period of activity in days.

6.4 Results

The above-ground production (in t yr⁻¹) and the productivity (in t ha⁻¹ yr⁻¹) of the five vegetation types are given in Table 6.1 for the present grazing pressure (PRESENT GRAZING), and for the models where either no grazing (NO GRAZING) or a maximum possible grazing pressure (MAXIMUM POSSIBLE GRAZING) were supposed. For present grazing the alpine grasslands produced 800-1160 kg ha⁻¹ yr⁻¹, the subalpine grasslands 1460-2150 kg ha⁻¹ yr⁻¹ (Table 6.1). If no grazing occurred, alpine grasslands were supposed to produce 1170-1850 kg ha⁻¹ yr⁻¹ and subalpine grasslands 2870-3960 kg ha⁻¹ yr⁻¹. For maximum possible grazing the values were
Table 6.1. Aboveground production (t yr⁻¹) and productivity (t ha⁻¹ yr⁻¹) of the five vegetation types for the three models NO GRAZING, PRESENT GRAZING and MAXIMUM POSSIBLE GRAZING. The data are presented separately for the sampled vegetation classes, i.e. where equation 6 was applied to calculate production and productivity, and for not sampled vegetation classes where equation 7 was applied. %, amount of grazed phytomass in comparison to the model NO GRAZING; N, number of vegetation classes.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Area</th>
<th>NO GRAZING (yr⁻¹)</th>
<th>PRESENT GRAZING (yr⁻¹)</th>
<th>MAXIMUM GRAZING (yr⁻¹)</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ha</td>
<td>t</td>
<td>t ha⁻¹</td>
<td>t</td>
<td>t ha⁻¹</td>
</tr>
<tr>
<td>Sampled vegetation classes (calculation of dry weight: eqn 6)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alpine grasslands on calcareous soils</td>
<td>1600.0</td>
<td>1876.1</td>
<td>1.17</td>
<td>1277.9</td>
<td>0.80</td>
</tr>
<tr>
<td>Alpine grasslands on mixed soils</td>
<td>133.7</td>
<td>247.1</td>
<td>1.85</td>
<td>130.3</td>
<td>0.97</td>
</tr>
<tr>
<td>Alpine grasslands on siliceous soils</td>
<td>19.3</td>
<td>33.2</td>
<td>1.72</td>
<td>22.4</td>
<td>1.16</td>
</tr>
<tr>
<td>Nutrient-rich subalpine grasslands</td>
<td>5.6</td>
<td>22.3</td>
<td>3.96</td>
<td>12.1</td>
<td>2.15</td>
</tr>
<tr>
<td>Nutrient-poor subalpine grasslands</td>
<td>168.3</td>
<td>483.1</td>
<td>2.87</td>
<td>246.0</td>
<td>1.46</td>
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<tr>
<td>Not sampled vegetation classes (calculation of dry weight: eqn 7)</td>
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<td></td>
<td></td>
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<tr>
<td>Alpine grasslands on mixed soils</td>
<td>14.3</td>
<td>20.2</td>
<td>1.41</td>
<td>20.2</td>
<td>—</td>
</tr>
<tr>
<td>Alpine grasslands on siliceous soils</td>
<td>0.7</td>
<td>0.4</td>
<td>0.60</td>
<td>0.4</td>
<td>—</td>
</tr>
<tr>
<td>Nutrient-rich subalpine grasslands</td>
<td>3.4</td>
<td>8.6</td>
<td>2.53</td>
<td>8.6</td>
<td>—</td>
</tr>
<tr>
<td>Nutrient-poor subalpine grasslands</td>
<td>9.7</td>
<td>32.1</td>
<td>3.30</td>
<td>32.1</td>
<td>—</td>
</tr>
<tr>
<td>Sum</td>
<td>1955</td>
<td>2722.9</td>
<td>1749.9</td>
<td>642.2</td>
<td></td>
</tr>
</tbody>
</table>
Table 6.2. Body weight (BW in kg), number of animals (N) in study area and total required energy per consumer group per year. Maintenance in MJ d⁻¹ kg⁻¹; *, data provided by Park authorities; **, Bubenik (1984); †, Niethammer & Krapp (1982); ††, Sänger (1973); †††, Schäller & Köhler (1981); ‡, Hauser (1995); †, Illich & Winding (1989).

<table>
<thead>
<tr>
<th>Consumers</th>
<th>BW (kg)</th>
<th>Energy required (MJ)</th>
<th>Density</th>
<th>Total N</th>
<th>Activity (d)</th>
<th>Energy required (GJ yr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Maintenance cap⁻¹ day⁻¹</td>
<td>N ha⁻¹</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Red deer</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>110</td>
<td>1.05 **</td>
<td>35.5</td>
<td>—</td>
<td>263 *</td>
<td>184</td>
</tr>
<tr>
<td>Female</td>
<td>80</td>
<td>1.26 **</td>
<td>33.6</td>
<td>—</td>
<td>311 *</td>
<td>184</td>
</tr>
<tr>
<td>Immature</td>
<td>40</td>
<td>0.84 **</td>
<td>13.3</td>
<td>—</td>
<td>142 *</td>
<td>184</td>
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<tr>
<td>Chamois</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>30</td>
<td>0.63 **</td>
<td>8.0</td>
<td>—</td>
<td>195 *</td>
<td>365</td>
</tr>
<tr>
<td>Female</td>
<td>30</td>
<td>0.63 **</td>
<td>8.0</td>
<td>—</td>
<td>381 *</td>
<td>365</td>
</tr>
<tr>
<td>Immature</td>
<td>15</td>
<td>0.63 **</td>
<td>4.8</td>
<td>—</td>
<td>245 *</td>
<td>365</td>
</tr>
<tr>
<td>Ibex</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>75</td>
<td>1.05 **</td>
<td>26.7</td>
<td>—</td>
<td>41 *</td>
<td>365</td>
</tr>
<tr>
<td>Female</td>
<td>35</td>
<td>1.05 **</td>
<td>15.1</td>
<td>—</td>
<td>2 *</td>
<td>365</td>
</tr>
<tr>
<td>Immature</td>
<td>15</td>
<td>1.05 **</td>
<td>8.0</td>
<td>—</td>
<td>1 *</td>
<td>365</td>
</tr>
<tr>
<td>Marmots (Marmota marmota)</td>
<td>4</td>
<td>0.628 ‡</td>
<td>1.78</td>
<td>1.2</td>
<td>2345</td>
<td>180</td>
</tr>
<tr>
<td>Voles (Microtus arvalis)</td>
<td>0.032 †</td>
<td>0.569 †</td>
<td>0.043</td>
<td>20</td>
<td>39083</td>
<td>365</td>
</tr>
<tr>
<td>Grasshoppers (Orthoptera)</td>
<td>0.0003 † †</td>
<td>0.121 † ††</td>
<td>0.00028</td>
<td>5000</td>
<td>9.8E+6</td>
<td>120</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
238-410 kg ha⁻¹ yr⁻¹ and 680-930 kg ha⁻¹ yr⁻¹ for subalpine and alpine grasslands, respectively. Compared with NO GRAZING, 32–47% of the alpine and 46–49% of the subalpine grassland's phytomass was on average grazed at present grazing pressure. Compared to NO GRAZING, about 71–77% of the produced green phytomass could be grazed at maximum possible grazing pressure.

The calculated phytomass (t) and energy (GJ) offtake are given in Table 6.3 for alpine, as well as nutrient-rich and nutrient-poor subalpine grasslands. The total energy offtake amounted to 10804 GJ yr⁻¹ and 23059 GJ yr⁻¹ for the models PRESENT and MAXIMUM POSSIBLE GRAZING, respectively.

In order to analyse whether the difference between the models NO GRAZING and PRESENT GRAZING represent the present offtake and whether it would be possible to estimate the amounts consumed by different consumer groups, their required energy was calculated (Table 6.2).

Table 6.3. Mean digestible energy content (DE), and the amount of calculated offtake (green phytomass or energy). For alpine, nutrient-rich subalpine and nutrient-poor subalpine grasslands in the study area, Present was calculated as the difference between the models NO GRAZING and PRESENT GRAZING and Maximum as the difference between the models NO GRAZING and MAXIMUM POSSIBLE GRAZING.

<table>
<thead>
<tr>
<th>Vegetation</th>
<th>DE (GJ t⁻¹)</th>
<th>Phytomass offtake (t yr⁻¹)</th>
<th>Energy offtake (GJ yr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total consumed phytomass (t yr⁻¹)</td>
<td>973.0</td>
<td>2080.8</td>
<td>10804.3</td>
</tr>
<tr>
<td>Total consumed energy (GJ yr⁻¹)</td>
<td>—</td>
<td>—</td>
<td>23059.0</td>
</tr>
</tbody>
</table>

For ungulates exact countings, including estimated number of unreported cases, were provided by the Park authorities. For marmots, voles and grasshoppers data about body weight, density and required energy were obtained from the literature, allowing a rough estimate of their contribution to grazing. The total amount of energy required in the study area by all the consumer groups mentioned is 9185 GJ yr⁻¹ (829 t dry weight of green phytomass) for 1996 (Fig. 6.4).
Fig. 6.4. Comparison of the in 1996 by herbivores required phytomass with the calculated offtake at the present grazing pressure (in t dry weight y⁻¹). Ideally the required phytomass and the offtake are identical. In 1996, the considered herbivores required 85% of the calculated phytomass offtake, which lies within the 95% confidence interval (vertical bar) of the applied technique for measuring phytomass.

Fig. 6.5. The in 1996 required phytomass was compared with the maximum possible offtake to determine the herbivore-carrying capacity of grasslands in the Swiss National Park. In 1996, the herbivores required 40% of the maximum possible offtake; this indicates that a maximum of 2.5 times the current number of herbivores could live in the Swiss National Park.
Fig. 6.4 shows that ungulates required about 70% of the consumed phytomass (675 t), rodents 13% (123 t) and grasshoppers 3% (30 t). Thus, 85% of the consumed phytomass (or energy) could be explained with the requirements at present grazing pressure. This lies within the 95% confidence interval for the prediction of phytomass measured with the radiometer technique (±28%).

For the model maximum possible grazing (Fig. 6.5) about 40% were used by the number of herbivores present in 1996 which implies that the study area could support 2.5 times the current number of herbivores.

6.5 Discussion

6.5.1 Use of GIS for assessing above-ground phytomass

The main goals of the study were to measure the phytomass of grasslands in the Swiss National Park and to estimate its carrying capacity for herbivores. GIS was used for three purposes: (a) for the sampling design, where categories were built up by the means of a vegetation map, exposure and slope, (b) for calculating the day of measuring depending on elevation and exposure (it was intended that measurements should be made at peak phytomass), and (c) for extrapolating the point related phytomass data to area related ones by means of modeling. The accuracy of the categories depends on the scale of the vegetation map and errors can be due to the generalizations made when drawing a map, which include the portrayal of fuzzy boundaries, small inclusions within larger areas, or the smoothing of area boundaries to create a cleaner appearance (Goodchild 1994). The scale of the map used (1:50000) was appropriate for the limited number of five grassland vegetation types; in spite of the extended study area of 20 km² of grasslands, only 41 vegetation categories were necessary. Some errors may have been introduced by converting the polygon data of the map to raster data (Goodchild 1994), which were used for GIS analysis in this study. However, 97% of the planned sample points were more or less easily accessible, and only at about 3% of the planned sample points could the measurements not be carried out because no access was possible or the map was outdated (succession of vegetation) or incorrect. The selection of the sample points was not fully automated because: (a) in alpine regions there is often no access without mountain climbing gear, (b) in various valleys no access is allowed by the park authorities, and (c) the feasibility (measuring four to seven sample points per day) had to be guaranteed.
6.5.2 Herbivore-carrying capacity of the Swiss National Park

Three methodological issues must be considered when the estimates of available phytomass are considered: firstly, the radiometric measurements have an accuracy of ±28%, which means that the measured phytomass lies to 95% between the given value ±28%. Secondly, it was assumed that measurements took place at peak phytomass, which was calculated using elevation and exposure. Possible shading by nearby trees, rocks or distant mountains was not taken into account. Thirdly, only the present phytomass at present grazing pressure was measured. But because at every sample point the number of heavily grazed plots, i.e. where the grazing pressure caused a shift from taller grasslands to a short turf, was determined, scenarios for absent grazing pressure and for maximum possible grazing pressure were modelled.

The difference in phytomass between the model assuming no grazing and that for present grazing pressure was subsequently used to calculate the amount of phytomass removed (offtake). The offtakes amounted to 32–49%. Krüsi et al. (1996), based on Dietl (1994), calculated the total yield of the grasslands of the Swiss National Park and gave in addition a yield that was corrected for the Central Alps: if the values are adapted for the 1950 ha of this study area, the yields are 990 t yr\(^{-1}\) (based on Dietl 1994) or 2270 t yr\(^{-1}\) (corrected for the Central Alps). These values are quite close to our determined grazed amounts of 973 t yr\(^{-1}\) under present and 2080 t yr\(^{-1}\) under maximum possible grazing pressure.

The total requirements of the consumer groups accounted for 85% of the calculated offtake. This value lies within the confidence interval of the used method for determining phytomass. This estimate does neither include roe deer, which are rare in the Swiss National Park, nor herbivorous invertebrates other than grasshoppers. This may slightly increase the grazed amount and thus the percentage accounted for. On the other hand, it was assumed that ungulates only feed on grasslands, although Bützler (1991) stresses for red deer the physiological significance of additional food from trees or shrubs for digestion. Voser (1987) analysed rumen contents of red deer in the Swiss National Park - their summer range - in 1981 and found no signs of woody species in rumen that were collected during summer. Hegg (1961) analysed faeces collected in the Swiss National Park and found that summer food of red deer consists to 25% of evergreen plants, including dwarf shrubs. However, these studies neither prove
nor disprove herbage intake by ungulates in forests; to do this it would be necessary to distinguish between grass, forb and shrub species of forests and grasslands.

In the present study another assumption was that grazing has no effect upon productivity or food quality. Whether herbivory increases or decreases productivity is subjected to heated discussion. Painter & Belsky (1993), e.g., point out that the evidence for increased productivity due to grazing is scanty. Patten (1993) concludes that the theory of overcompensation cannot be supported for western rangelands of the USA. A more balanced view, namely that over- or undercompensation depend on pre- and postharvest conditions of the plants and their environment, including abiotic and biotic factors, (Trlica & Rittenhouse 1993) and on the intensity of herbivory (Dyer, Turner & Seastedt 1993), seems more appropriate. There is evidence that productivity can be both increased (e.g. Hodgson & Grant 1981; McNaughton 1993; McNaughton 1976) or decreased by herbivores (even in the presence of wolf populations not subject to human control (Manseau 1996)). In other studies no grazing-related reduction in productivity could be measured (Hoefs 1984). At the site Il Fuorn heavy grazing caused a shift from taller grasslands to a short turf with broad-leaved plants and thus decreased the production (Frank & McNaughton 1992; Holzgang, Achermann & Gigon 1996). On the other hand the quality of the fodder may have increased and thus less fodder is needed (Frank & McNaughton 1992; Holzgang et al. 1996).

In addition, reliable countings were only available for ungulates, whereas density and intake data for rodents and grasshoppers are lacking for the Swiss National Park. For the present investigation the assumptions were based on data from other studies (Niethammer & Krapp 1982; Sänger 1973; Schäller & Köhler 1981; Illich & Winding 1989).

All these factors must be considered when extrapolating from present grazing to maximum possible grazing. The latter is assumed to reflect the carrying capacity. In addition, this study presents only data of one year and sward growth is greatly affected by temperature and radiation (Menzi, Blum & Nösberger 1991) and precipitation (Hoefs 1984; Silvertown et al. 1994). Therefore, one must be cautious to say that about 2.5 times as many herbivores as at present grazing pressure could live in the study area.

Despite all the uncertainties, it seems probable that during summer the Swiss National Park could support a higher density of herbivores. Krüsi et al. (1995
and 1996) even indicate that the present impact of red deer and chamois is too low, rather than too high, to preserve the percentage of grassland in the Swiss National Park. But conservation of the status quo is no management goal of the Swiss National Park: in contrast, a natural development should be possible (Eidgenössische Nationalparkkommission & Wissenschaftliche Nationalparkkommission 1989). Krtcsi et al. (1996) calculated that the possibly available amount of fodder could theoretically feed 11000 – 25000 red deer. However, it hardly makes sense to calculate the available amount of fodder for only one herbivore species and take no account of other herbivores or year to year changes in amount of fodder. Intra- and interspecific competition may play a more important role with increasing density and thus become a limiting factor in spite of abundant fodder.

In conclusion, it is more appropriate to say that the present number of herbivores during summer is two thirds of the maximum possible. In that case, the latter corresponds, for red deer, to the highest density counted in the Swiss National Park (2400 red deer) in the seventies (Voser 1987), when hundreds of animals died during winter.

To improve the reliability of the calculations, data on densities and intake are needed for rodents and herbivorous invertebrates and measurements should be repeated for successive years to obtain data on the variation in growth from year to year. Variation in growth in response to variable weather conditions could also be modelled. Furthermore, the relationship between grazing pressure and productivity has to be investigated.
Appendix 6.1. List of the 41 classes, their site descriptors and applied parameters in equation six or seven. *: a, 2.75; b, -0.00053; d, 0.0063. **: a, 2.98; b, -0.00059; f, 0.0053. Nomenclature of plant communities follows Zoller (1995).

<table>
<thead>
<tr>
<th>Class</th>
<th>Slope</th>
<th>Exposure</th>
<th>Not grazed</th>
<th>Parameter eqn 6*</th>
<th>Parameters eqn 7**</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>plots (%)</td>
<td>Class c</td>
<td>Vegetation c</td>
<td>Slope e</td>
<td>Exposure d</td>
</tr>
</tbody>
</table>

### Alpine grasslands on calcareous soils
(Cricetum firmae, Seslerio-Caricetum sempervirentis, Arabidetum coeruleae)

| 1 | 5–30° | W | 69 | -0.0570 | — | — | — |
| 2 | 5–30° | N | 35 | -0.0299 | — | — | — |
| 3 | 0–5° | S | 98 | -0.1257 | — | — | — |
| 4 | >30° | S | 76 | -0.3175 | — | — | — |
| 5 | 5–30° | S | 99 | -0.1130 | — | — | — |
| 6 | 5–30° | E | 83 | -0.0969 | — | — | — |
| 7 | >30° | W | 61 | -0.1205 | — | — | — |
| 8 | >30° | E | 55 | 0.0237 | — | — | — |
| 9 | >30° | N | 76 | 0 | — | — | — |

### Alpine grasslands on mixed soils
(Seslerio-Caricetum sempervirentis, Elynetum myosuroidis, Trifolietum-Festucetum violaceae, Caricetum ferrugineae, Caricetum curvulæ, Festucetum halleri, Caricetum sempervirentis, Geo montani-Nardetum, Arabidetum coeruleae, Salicetum herbaceae)

| 20 | 5–30° | S | — | — | 0.1381 | 0.0114 | -0.0869 |
| 21 | 5–30° | E | 23 | 0.2782 | — | — | — |
| 24 | >30° | S | 55 | 0.0825 | — | — | — |
| 26 | 5–30° | W | 65 | 0.1024 | — | — | — |
| 27 | 0–5° | S | 80 | 0.1030 | — | — | — |
| 28 | >30° | W | 80 | 0.0575 | — | — | — |
| 29 | >30° | E | 10 | 0.3583 | — | — | — |
| 31 | 5–30° | N | 40 | 0.1787 | — | — | — |
| 32 | >30° | N | 0 | -0.0209 | — | — | — |

### Alpine grasslands on siliceous soils
(Cetrario-Loiseleurietum, Caricetum curvulæ, Festucetum halleri, Caricetum sempervirentis, Geo montani-Nardetum, Salicetum herbaceae)

| 34 | 5–30° | N | 70 | 0.0807 | — | — | — |
| 35 | >30° | W | — | — | -0.0763 | 0 | 0 |
| 36 | >30° | N | 85 | -0.3558 | — | — | — |
| 37 | 5–30° | W | 90 | -0.0092 | — | — | — |
| 38 | 5–30° | E | 80 | 0.0418 | — | — | — |
| 39 | 0–5° | W | — | — | -0.0763 | 0.0858 | 0 |
Continuation of Appendix 6.1

<table>
<thead>
<tr>
<th>Class</th>
<th>Slope</th>
<th>Exposure</th>
<th>Not grazed</th>
<th>Parameter eqn 6*</th>
<th>Parameters eqn 7**</th>
<th>Class c</th>
<th>Vegetation c</th>
<th>Slope e</th>
<th>Exposure d</th>
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<tbody>
<tr>
<td></td>
<td></td>
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<td>plots (%)</td>
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<td>Exposure d</td>
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<tr>
<td>40</td>
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<td></td>
</tr>
</tbody>
</table>

**Nutrient-rich subalpine grasslands**

(Trisetetum flavescentis, Crepido-Festucetum nigrescentis, Rumicetum alpini, Chenopodie-tum boni-henrici)

<table>
<thead>
<tr>
<th>Class</th>
<th>Slope</th>
<th>Exposure</th>
<th>Not grazed</th>
<th>Parameter eqn 6*</th>
<th>Parameters eqn 7**</th>
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<td>-</td>
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</tr>
<tr>
<td>19</td>
<td>5-30°</td>
<td>S</td>
<td>-</td>
<td>-0.0115 0.0114</td>
<td>-0.0869</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>0-5°</td>
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<tr>
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<td>5-30°</td>
<td>E</td>
<td>-</td>
<td>0.0115 0.0114</td>
<td>0.0880</td>
<td></td>
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</tbody>
</table>

**Nutrient-poor subalpine grasslands**

(Seslerio-Caricetum sempervirentis, Centaureo-Gentianetum cruciatae, Trifolio-Festucetum violaceae, Caricetum ferrugineae, Caricetum sempervirentis, Geo montani-Nardetum, Dra-cocephalo-Potentilletum, Laserpitio-Avenuletum pratensis, Diantho deltoidis-Agrostietum tenuis, Agrostietum agrostiflorae)

<table>
<thead>
<tr>
<th>Class</th>
<th>Slope</th>
<th>Exposure</th>
<th>Not grazed</th>
<th>Parameter eqn 6*</th>
<th>Parameters eqn 7**</th>
<th>Class c</th>
<th>Vegetation c</th>
<th>Slope e</th>
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7 General Discussion

The goal of this study was to determine the carrying capacity of the Swiss National Park for herbivores. Carrying capacity means the maximum population of a given organism or group of organisms that a particular environment can sustain (Allaby 1994). According to McNaughton et al. (1989), herbivore biomass and consumption are closely correlated with plant productivity, suggesting that the latter is a principal integrator and indicator of functional processes in food webs. Therefore, above-ground plant production was used in this study for assessing carrying capacity.

In this concluding chapter the following topics will be discussed: the assessment of plant production (chapter 7.1), the impact of small-scale foraging behaviour onto grasslands of differing plant production (chapter 7.2), and the carrying capacity and its application for this case study (chapter 7.3). Chapter 7.4 gives an outlook on how to improve the assessment of herbivore-carrying capacity of the Swiss National Park.

7.1 Assessment of above-ground phytomass production

As chapters 4 and 6 show, the non-destructive assessment of green phytomass and production with radiometric measurements is possible on a regional scale. To determine green phytomass, the radiometric measurements must be calibrated by clipping selected plots. For the calibration of the radiometric measurements against phytomass, vegetation structure (e.g. leaf angle or leaf transmittance) rather than the plant association must be taken into account (Kimes et al. 1984; Kuusk 1991; Scurlock 1992; Scurlock & Prince 1993).

The radiometric measurements were found to depend on the time of day and generally showed lowest values at noon (chapter 4). This dependence was also reported by Kimes et al. (1984), Duggin (1977) and Middleton (1991). However, Kimes et al. (1980) measured the highest value at noon. Thus, Middleton (1991) concludes that a general "correction" to remove sun angle effects on spectral ratios is inappropriate. Nevertheless, applying the technique described in chapter 4, it is recommended to measure around solar noon, i.e. between 9:30 and 14:30.

The 95% confidence interval for the prediction of the actual dry weight, based on 20 radiometric measurements, was ±28% and ±45% for the green and total above ground phytomass, respectively. A comparison of the accuracy of
prediction with regressions described in the literature is difficult, because information on accuracy is often lacking.

A geographic Information System (ARC/GIS) was used for classifying vegetation into classes according to exposure, slope and vegetation type. Despite the restrictions (which are discussed in chapter 6), this procedure resulted in reasonable estimates of (a) produced green phytomass and (b) calculated offtake under the grazing pressure present in 1996.

In conclusion, the method described in chapter 6 is appropriate for assessing the green biomass of subalpine and alpine grasslands as well as dwarf shrub communities on a regional scale.

7.2 Small-scale impact of herbivores on productivity and fodder quality

The grazing of the free ranging red deer resulted in a patchy grassland at Il Fuorn in 1995 (chapter 5). Intensive grazing caused a shift from taller grasslands to short and rosette-dominated turfs (Achermann 1995; Stüssi 1970). Clutton-Brock & Albon (1989) observed that red deer prefer lawn-like turfs similar to the heavily grazed areas at Il Fuorn. The pattern of the patches seemed to be quite stable, but the relevant data have not yet been analysed. The strong influence of grazing on species composition is not discussed in more detail.

During the growing season protein content of plants decreases whereas fibre content increases. This was observed on the moderately grazed vegetation areas at Il Fuorn and at Stabelchod in 1995. Steady grazing during the growing season, however, resulted for both graminoids and forbs in a smaller increase of fibre content and a smaller decrease of protein content than under moderate grazing (chapter 5).

From May to August 1995 between 67% and 85% of the above-ground phytomass produced was consumed by the herbivores in the heavily grazed areas at Il Fuorn. In the moderately grazed areas at Il Fuorn and on the nutrient-poor site of Stabelchod a comparatively small amount of above-ground phytomass was used (33–54%) in May, July and August; in June only 14–16% were consumed. The latter coincides with the start of the growing season of alpine grasslands. Since at the beginning of the growing season the fibre content is low and the protein content is high, it was concluded that red deer grazed in the nearby alpine grasslands.

The productivity of the heavily grazed areas was about half compared with
that of the moderately grazed one. Thus, heavy grazing reduced the productivity but led to a high fodder quality, a fact also observed e.g. by McNaughton (1976) for migratory ungulates in Africa.

Because the ungulates are free ranging, the use of the studied grasslands is less efficient than that of managed agricultural areas. Oesterheld, Sala & McNaughton (1992) compared natural and agricultural ecosystems of South America. They calculated that agriculture leads to a tenfold higher use of the ecosystems than under natural conditions. The management implies providing water holes, veterinary care, the control of predators and parasites, and the subdivision of ranches into paddocks. Therefore, agricultural considerations cannot be applied if the herbivore-carrying capacity of a naturally ruled ecosystem is to be determined.

7.3 Herbivore-carrying capacity of the Swiss National Park

Under the weather conditions of 1996, phytomass was no limiting factor for the number of herbivores present. It was calculated that during summer the herbivore-carrying capacity of the study area amounts to about 2.5 times the present amount of herbivores (chapter 6).

Sward growth varies greatly in relation to temperature and radiation (Menzi et al. 1991) as well as precipitation (Hoefs 1984; Silvertown et al. 1994). Hoefs (1984) and Langvatn et al. (1996) state that precipitation, temperature and insolation influence plant phenology, forage quality and biomass production, which in turn affect the habitat carrying capacity. Thus, under unfavourable weather conditions a bottleneck situation can occur. Hobbs et al. (1982) calculated the winter-range carrying capacity for elks from forage energy supply during two subsequent years. The carrying capacity of the second year amounted to only 67% of the first year’s carrying capacity due to decreased precipitation. The authors therefore concluded that carrying capacity should be viewed as a labile rather than a static characteristic of the habitat.

Kriisi et al. (1995) and (1996) indicate that the present impact of red deer and chamois is too low, rather than too high, to preserve the percentage of grassland in the Swiss National Park. They calculated that the amount of fodder could nourish 11000 – 25000 red deer, i.e. a six- to fourteenfold amount of the number of the 1995 census which according to Filli & Robin (1996) was 1800 animals. However, it makes hardly sense to make these calculations and consid-
erations for only one herbivore species when others are known to roam the area. Intra- and interspecific competition may play a more important role with increasing density and thus become a limiting factor in spite of abundant fodder. Furthermore, their calculations were based on agricultural yield, thus assuming an optimal and efficient foraging by red deer. But, as discussed in chapter 7.2, the use of an ecosystem by wild ungulates can be ten times lower than under simple agricultural management (Oesterheld et al. 1992).

One purpose of the Swiss National Park is to let nature develop according to its own rules. Natural development was defined as follows: the ecosystems and biocoenoses existing in the Park as well as the structures of the landscape should be able to develop according to the conditions given by nature, together with their pheno- and genotypic potential. Concerning the herbivores, it is stated that the area of the Park should not be dominated by the ungulates (Eidgenössische Nationalparkkommission & Wissenschaftliche Nationalparkkommission 1989). Thus, it can be concluded that it is no goal for the Swiss National Park to attain the full herbivore-carrying capacity. Since the large carnivores are (still) missing in the Park, man may interfere from time to time. The data of this investigation can contribute to decide if, when, where, and how this interference may be necessary.

In conclusion, it is assumed that the number of herbivores present in 1996 attained the summertime herbivore-carrying capacity of the Swiss National Park to two thirds. This number corresponds for red deer to the highest density counted in the Swiss National Park (2400 red deer) in the seventies (Voser 1987). Then a high winter mortality occurred, which is, since top predators as wolves, lynx and bear are lacking, perhaps a natural regulation of the population. Reduced fertility was not found to be responsible for the observed red deer population decline (Buchli 1979).

7.4 Outlook

The search for the crucial factor(s) determining herbivore-carrying capacity of the Swiss National Park must be intensified. The study area should in future cover the whole Park. To determine the influence of the weather conditions on plant production in the course of the years, the amount of fodder must be assessed during successive growing seasons. Such successive measurements could be used for modelling the herbivore-carrying capacity of the Park and thus help to search for the most sensitive factors determining the carrying ca-
pacity and/or the present number of herbivores.

In order to increase the accuracy of data on herbivores' consumption, densities and intake must be known for rodents and herbivorous invertebrates. As far as ungulates are concerned, the amount of fodder intake in forests should be quantified by analysing faeces or rumen contents on the plant species level. The impact of grazing on grasslands' species composition and thus chemical composition of the fodder should be studied in more detail.

And, in order to determine the role of winter, the amount of available fodder in winter ranges of the herbivores must be studied.
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Special thanks go to Guolf and Daniela Denoth-Grass and Anastasia Grass of the Hotel Il Fuorn for making me feel welcome and for treating me like a member of the family.
Last but not least I want to thank my parents for making my studies possible in first place and Ida Dober for supporting me in many ways during most of the last four years.

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10 Curriculum vitae

I was born in Lucerne (Switzerland), on February 18, 1966. After attending the primary school in Küsnacht am Rigi, I went to the college in Immensee where I obtained my Matura type B diploma in 1985. From 1985 until 1986 I studied architecture at the Swiss Federal Institute of Technology (ETH) in Zurich. After working on various jobs, I started studying Environmental Sciences at the ETH in Zurich in 1987. In 1990, I worked during one semester as a probationer for the OEKO-B AG in Stans (NW). In 1992 I obtained my diploma. The subject of the diploma thesis was «The influence of management on vegetation in vineyards in Fläsch (Grisons) with regard to biological control» and was carried out under the direction of Prof. A. Gigon (Geobotanical Institute ETH, Zurich) and Dr. D. Gut (Swiss Federal Research Station for Fruit-Growing, Viticulture and Horticulture). Between 1993 and 1996 I was assistant for plant ecology at the ETH, Zurich. I have been working as a Ph.D. student under the guidance of Prof. A. Gigon at the Geobotanical Institute, Stiftung Rübel, ETH Zurich since May 1993.