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0014-4754/87/020115-13$1.50 + 0.20/0
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Criteria for permissible browse impact on sycamore maple *(Acer pseudoplatanus)* in mountain forests

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Summary. A naturally regenerated young-growth in the 'Buchser Hochwald' area in the Canton of St. Gallen, Switzerland, was used to determine the silviculturally permissible browsing limit for sycamore maple *(Acer pseudoplatanus)*. The investigated area is situated at an altitude ranging from 1280 to 1310 m a.s.l. on an *Abieti-Fagetum typicum* site. Browsing was done by red deer *(Cervus elaphus)* and roe deer *(Capreolus capreolus)*. A total of 57 sycamore maples, 1.30 m high, were examined. The actual browse impact on these plants was assessed by determining the frequency of browsing marks on the stem axis. To this end, the plants were cut into sections of 5 cm each and then split radially. On this basis it was possible to calculate permissible shares of browsed plants for four different size categories between 0.10 and 1.30 m. The permissible share of plants with two or more visible browsing marks on the stem axis amounted to 37.8% as an average value for the total risk period. This corresponds to a quota of 26.9% browsed terminal shoots per annum.
Key words. Sycamore maple *(Acer pseudoplatanus)*; game browsing; red deer and roe deer *(Cervus elaphus* and *Capreolus capreolus)*; browse impact limits.

1. Introduction

A considerable amount of literature is available on deer browsing, but previous research has dealt almost exclusively with game distribution, the varied causes and effects, suitable preventive measures, or the need for game population control. None of these investigations can yet supply satisfactory information for the purposes of ecology and game policy on what criteria would be suitable to show excessive browse impact on the young forest generation.

Some ten years ago Mayer[8] showed that browsing had become a serious problem for forest regeneration in large parts of the Alps. Mountain forests are particularly liable to game browsing. The reasons for this are the frequent lack of sufficient young growth and the slow growth of young forest trees. In addition to suffering from game browsing, these trees are also exposed to extreme climatic conditions, to the influence of snow and fungi, and to competition from the herbaceous layer. Moreover, technical protection measures are possible in exceptional cases only.

Continuous natural forest regeneration is not only important for timber production but is also essential for the stability of forest stands, and this stability is absolutely necessary to ensure the various protective functions expected of mountain forests. Browsing of young forest trees will become of even greater importance, in the mountains in particular, wherever forest decline makes it imperative that extensive areas are quickly regenerated with plantations which will be susceptible to browsing. Objective information on the critical extent of browsing damage is therefore urgently required and is absolutely essential for any game damage inventory to be used as basic information for game management.

2. Problem

The following questions need to be clarified in order to establish the 'silviculturally tolerable' browsing threshold upon an undisputable basis:

- How can the actual browse impact be measured precisely and be converted into practicable assessment criteria?
- How does browse impact affect growth and mortality of the young forest trees?
- What kind of disturbances of development due to browsing are of decisive influence for the calculation of the permissible browsing threshold?
- What is the range of tolerance of game browsing for various tree species on different sites?

Our first intensive studies in this field also concerned sycamore maple *(Acer pseudoplatanus)*. This species, similarly to ash or silver fir, is particularly threatened by game browsing since it is a great favorite with game and is being browsed all the year round. Sycamore maple is mainly found in colline and submontane areas, but according to Ellenberg and Klötzli[7] it also occurs naturally in montane mountain forests, and in certain forest communities it may even be found at the subalpine level. Since sycamore maple is considered a valuable species for protection forests due to its soil fixing ability and its good healing capacity when suffering from rockfall injuries, and because of its usefulness as a natural pioneer species in beech/silver fir forests with tall forbs, its conservation is also highly desirable in higher forest regions. To this end, knowledge of the critical browse impact under the specific growth conditions of mountain sites is absolutely essential.

In view of the methodological difficulties involved in assessing game browsing, our survey has been made with comparatively small investigating units. This should make it possible to apply the subsequent studies to other tree species and sites and thus take into consideration all three types of hoofed game which may be involved in browsing young forest trees.

Table 1. Definitions of plant characteristics investigated

Characteristic	Abbreviation	Class, definitions
Total number of browsing marks	V_t	Browsing marks completely ingrown and also those visible externally
Number of visible browsing marks	V_s	Browsing marks still visible externally
Age of plants Years	$A_{1.30}$	Number of years at which the plants reached a height of 1.30 m
Length of live crown	L	1) 1/1 length of stem 2) > 2/3 length of stem 3) < 2/3 length of stem 4) dwarfed
Form of stem axis	F	1) straight 2) forked, one shoot being clearly better developed 3) forked, two shoots ± equally developed 4) multi-forked or bushy
Curvature of stem axis	K	1) completely straight 2) bent to one side. 3) tortuous growth

3. Method

3.1 Terms and definitions

In addition to browse impact and age, length of live crown as well as form and curvature of the stem axis of sycamore maples were also assessed. All plant characteristics investigated are listed in table 1 together with definitions and abbreviations used.

Some of the concepts used frequently in this paper require uniform definition.

This applies to the following terms:

- Risk period: Average age of plants at the time when they reach browse line.
- Browse line: Average plant height at which the number of browsing marks in the uppermost 10 cm of the stem axis amount to less than 1% of total browse impact.
- Total browse impact: Average number of browsing marks per plant occurring on stem axis during total risk period.
- Browsing intensity: Share of browsed terminal shoots per annum in percent of total number of plants.
- Critical browse impact: Frequency of browsing marks on the stem not to be exceeded in consideration of the permissible loss of increment.
- Degree of damage: Number of browsing marks per plant still visible externally on stem.

3.2 Selection of sampling material

The plants investigated were taken from the 'Buchser Hochwald', a region in the Canton of St. Gallen, Switzerland, situated within the upper Cretaceous of the Säntis and Churfirsten intermediate layer. The investigated area is situated on lime deposits at an altitude ranging from 1280 m to 1310 m a.s.l. and belongs to the typical silver fir/beech forest *(Abieti-Fagetum typicum)* according to the Ellenberg/Klötzli nomenclature[7]. It is a naturally regenerated rich mixture of tree species with the coordinates 751450/224125, comprising 4 ha (fig. 1). It is part of a permanent habitat of red deer *(Cervus elaphus)* and roe deer *(Capreolus capreolus)*.

A total of 57 plants, 1.30 m high, were selected in this natural regeneration in summer 1984 in order to assess browse impact on the young sycamore maples. Cutting points – regularly distributed over the young-growth –

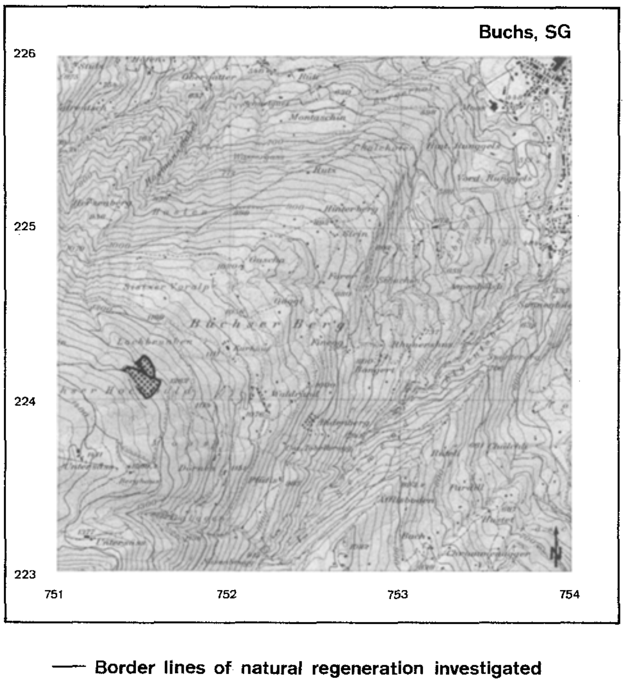

Figure 1. Situation of investigated area. Map of Switzerland, 1:25000, Map sheet No. 1135 'Buchs'. Reprinted with permission of the Federal Office of Topography of May 6th, 1986.

were first plotted in the field. Starting from those points the nearest plants of the size indicated were then cut. By strictly observing this rule biased sampling of plant material with respect to browsing and vitality could be avoided.

3.3 Assessment of browse impact and loss of increment

The number of browsing marks on the stem axis was used to determine browse impact. This method was first applied successfully by Mlinšek[9] for producing a browsing chronology, and careful preliminary studies[2,3] showed a close correlation between the number of browsing marks and increment losses. In order to determine the number of browsing marks on the stem, the plants were cut in sections of 5 cm each and then split radially. Even completely ingrown browsing marks, not visible externally, could be identified and counted accurately (fig. 2).

Mean height and average age of the plants were used to assess increment losses caused by game. Age was determined separately for each section, in intervals of 5 cm, by counting the annual rings with a magnifying glass. Reconstruction of height growth under the impact of browsing was thus easily possible.

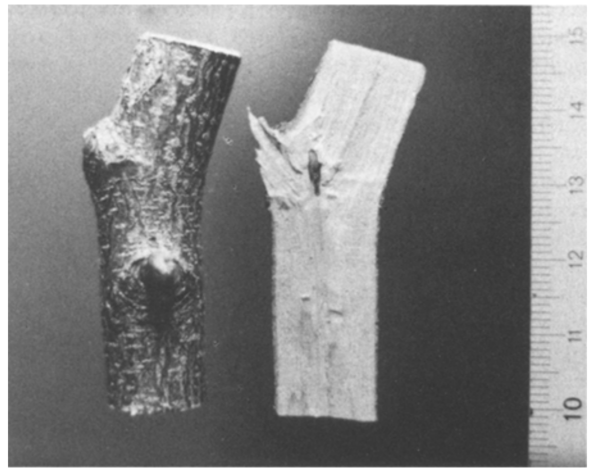

Figure 2. Section of the stem axis of a young sycamore maple. The radial cut shows clearly the completely ingrown browsing mark.

3.4 Assessment criterium

Widely-spread natural regeneration, extending over a large period of time, is essential for the future stability of forest stands in the mountains. It is therefore highly important that the possibilities provided by natural regeneration should not be given up lightly. Perko[10] showed that silver fir succumbs to fatal browsing to a measurable degree when the average increment loss of the existing plants reaches 35%. Research by Burschel[1] on silver fir, spruce, beech, and sycamore maple showed comparable results. His figures were based on a close comparison of fenced and non-fenced areas and allowed calculation of plant losses in relation to increment losses. Considering that in this case increments of fatally browsed plants were not taken into account, critical increment loss for the setting-in of mortality was reduced to 30% (fig. 3).

In view of the fact that some plants suffering from high losses in vitality may still die at a time when they have already outgrown the browse line, permissible increment loss was fixed at 25% for the purposes of the present investigation. With this figure the risk of fatal browsing affecting large areas can practically be eliminated for all tree species.

4. Results

4.1 Plant characteristics and browse impact

First substantial results are gained from the relationships between plant characteristics and browse impact (table 2).

Table 2. Relationships between plant characteristics and browse impact

Regression equations No.	y	=	$a + bx_1 + cx_2$	R-square, B Partial x_1	x_2	Multiple x_1, x_2
1	L	=	$3.40620 - 0.10339\ A_{1.30} + 0.03066\ V_t$	0.049	0.006	0.076
2	$A_{1.30}$	=	$7.20850 - 0.47096\ L + 0.67050\ V_t$	0.049	0.645***	0.670***
3	F	=	$-0.21787 + 0.49858\ L + 0.33133\ V_t$	0.058	0.322***	0.330***
4	F	=	$2.28747 - 0.18854\ A_{1.30} + 0.44110\ V_t$	0.038	0.227***	0.315***
5	K	=	$2.41952 - 0.00847\ L + 0.06216\ V_t$	0.000	0.053	0.055
6	K	=	$2,82951 - 0.07361\ A_{1.30} + 0.11327\ V_t$	0.020	0.064	0.074

Significance: $*P_{0.05}$, $**P_{0.01}$, $***P_{0.001}$.

According to the partial regressions mentioned, there is no substantial connection between length of live crown and browse impact. It is therefore not possible to assess browsing extent on the basis of crown measures as was done in some previous research on game damage. However, browse impact has a decisive effect on the age at which plants reach 1.30 m in height, as well as for the stem form which may suffer considerably from a silvicultural point of view.

4.2 Distribution of browsing marks according to size categories

Attribution of the visible and ingrown browsing marks to the different height levels (table 3) shows that browsing is highly concentrated within the range of 0.00 to 0.70 m – namely 83% – and that its accumulation ends at 1.15 m. According to Zai[11] this distribution is typical for roe deer browsing and shows that young forest trees are threatened particularly in their early development by fatal browsing. Distribution of the browsing marks according to individual size categories is essential for conversion of the critical browse impact, calculated for plants of 1.30 m in height, for application to smaller plants. Since the height range from 0.00 to 0.10 m does not lend itself easily to browsing checks, this range was excluded.

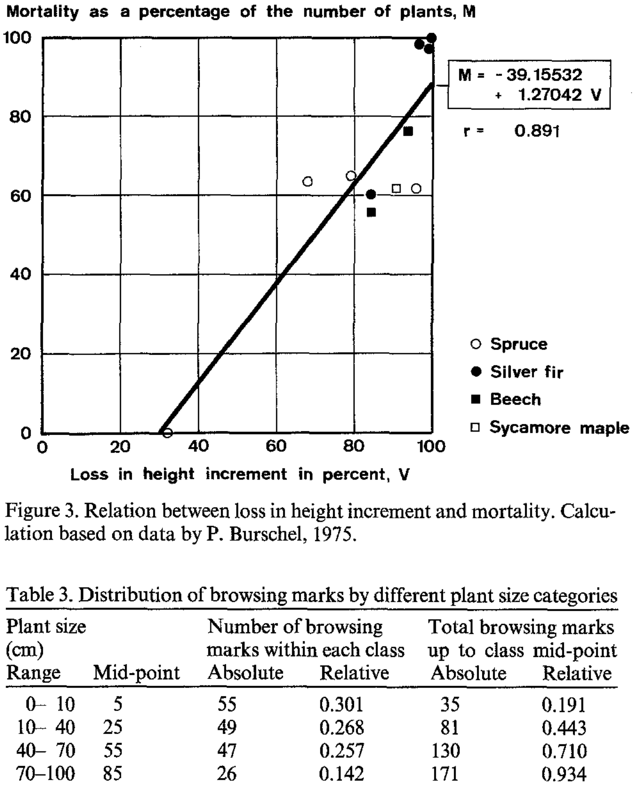

Figure 3. Relation between loss in height increment and mortality. Calculation based on data by P. Burschel, 1975.

Table 3. Distribution of browsing marks by different plant size categories

Plant size (cm) Range	Mid-point	Number of browsing marks within each class Absolute	Relative	Total browsing marks up to class mid-point Absolute	Relative
0– 10	5	55	0.301	35	0.191
10– 40	25	49	0.268	81	0.443
40– 70	55	47	0.257	130	0.710
70–100	85	26	0.142	171	0.934
100–130	115	6	0.033	181	0.989
10–130	70	128	0.699	151	0.825
—	130	183	1.000	183	1.000

Table 4. Plant growth

Plant size (cm) Range	Mid-point	Age increase within classes Absolute (years)	Relative	Average age up to class mid-point Absolute (years)	Relative
0– 10	5	1.807	0.223	1.123	0.139
10– 40	25	2.333	0.288	3.123	0.385
40– 70	55	1.754	0.216	5.123	0.632
70–100	85	1.175	0.145	6.684	0.825
100–130	115	1.035	0.128	7.701	0.950
10–130	70	6.298	0.777	5.895	0.727
—	130	8.105	1.000	8.105	1.000

Table 5. Comparison of observed frequencies with theoretical ones

Number of browsing marks per plant	Frequency observed	Frequency calculated by means of Binomial distribution	Poisson distribution	Neg. binomial distribution
0	8.77	1.88	4.03	5.43
1	10.53	9.41	12.95	14.40
2	14.03	20.88	20.79	20.34
3	26.32	27.02	22.25	20.34
4	21.05	22.47	17.86	16.14
5	10.53	12.47	11.46	10.81
6–15	8.77	5.87	10.66	12.54
S	100.00	100.00	100.00	100.00
χ^2		29.47	9.94	9.44
P	(FG)	< 0.001(5)	> 0.05(5)	> 0.025(4)
Parameter		$\bar{x}$=3.21053 p=0.35673 q=0.64327	$\bar{x}$=3.21053	$\bar{x}$= 3.21053 p=– 0.21045 q= 1.21045 k= 15.25523

4.3 Growth development of the plants

The rapid juvenile growth of sycamore maples (table 4), requiring only 8.1 years to outgrow the browse line of 1.30 m, is confirmed by counting the annual rings. Juvenile growth of the sycamore maples investigated was quite comparable in its rapidity to that of Scots pine on good-quality sites[5], and was considerably faster than that of spruce or even silver fir[4,6]. Sycamore maples therefore tolerate a comparatively high browsing intensity because there is no risk that browsing will accumulate over very long periods of time. Information on the age structure of the plant material available is essential for the calculation of the critical browsing intensity. This can be done correctly for the different size categories only on the basis of table 4.

4.4 Frequency distribution of browse impact

Browsing does not affect the individual plants regularly but follows a specific frequency distribution. To determine the type of frequency distribution, the frequencies observed were compared with three theoretical frequencies (table 5).

This comparison showed that the Poisson distribution reflects the observed frequencies better than the binomial distribution. It also fits better than the negative binomial distribution, because in our case variance of the browsing marks was smaller than their mean value.

Not all investigated units showed the same browse impact frequency distribution. The pattern of frequency distribution is, however, of great importance for the calculation of the critical total impact and should therefore be assessed carefully in each individual case.

4.5 Share of visible browsing marks

The share of visible browsing marks in the total number of existing browsing marks is an indispensable element for the calculation of the permissible proportion of browsed plants (table 6). As our research showed, the

Table 6. Shares of visible browsing marks

Plant size (cm) Range	Mid-point	Age Years	V_s: V_t	Regression equations Plant size 1.30 m $y = a + bx$
0– 10	5	1.123	0.946	
				$V_t = -4.46119 + 0.94651\ A_{1.30}$
10– 40	25	3.123	0.851	
40– 70	55	5.123	0.755	B = 0.653*** $\bar{V}_t = 3.21052$
70–100	85	6.684	0.680	
100–130	115	7.702	0.631	
				$V_s = -0.95890 + 0.36073\ A_{1.30}$
10–130	70	5.895	0.718	
				B = 0.195*** $\bar{V}_s = 1.96491$
—	130	8.105	0.612	

Significance: $^*P_{0.05}$, $^{**}P_{0.01}$, $^{***}P_{0.001}$.

share of visible browsing marks is closely connected with the occlusion time needed, i.e. with the average age of the plants. The ratio V_s:V_t was calculated only for plants of 1.30 m in height so that adaptation to the lower height classes was necessary. This was done by assuming that the quotient V_s:V_t, with decreasing plant age, would approach the limit 1.00 in a linear way.

The occlusion time of sycamore maple is remarkably short because of its rapid juvenile growth. This means that the share of visible browsing marks in the total browse impact on plants of 1.30 m in height is extremely high, namely 61.2%.

4.6 Plant age and browse impact

In order to calculate losses in increment a fitting curve is required reflecting the average plant age in relation to the browse impact (table 7). To this end, various variants were examined, all showing that, despite the small sample size, there was a highly significant connection between age and browse impact on the plants. The best R-square was provided by regression equation 2 with the independent variables L and V_t, and this fitting curve was subsequently used for the deduction of the critical total browse impact (fig. 4).

4.7 Critical total browse impact

Before anything can be said about the permissible browsing limit in the various size categories, the critical total browse impact for the time when the plants outgrow the browse line has to be defined (table 8). Approximating calculations and interpolations easily lead to the Poisson distribution corresponding to the permissible increment loss of 25%. With an average of 3.21 browsing marks per plant, browse impact on sycamore maple was considerably higher in the investigated area in the past 8 years than the 2.22 browsing marks which must be considered to be the critical figure with respect to the setting-in of mortality.

Table 7. Age of plants as related to browse impact

Regression equations No.	$y = a + bx_1 + cx_2$	B
1	$A_{1.30} = 5.70451 + 0.82590\ V_t - 0.01767\ V_t^2$	0.657***
2	$A_{1.30} = 7.20850 - 0.47096\ L + 0.67050\ V_t$	0.670***
3	$A_{1.30} = 7.03383 + 0.07549\ V_t^2$	0.535***
4	$A_{1.30} = 5.89116 + 0.68964\ V_t$	0.653***

Significance: $^*P_{0.05}$, $^{**}P_{0.01}$, $^{***}P_{0.001}$.

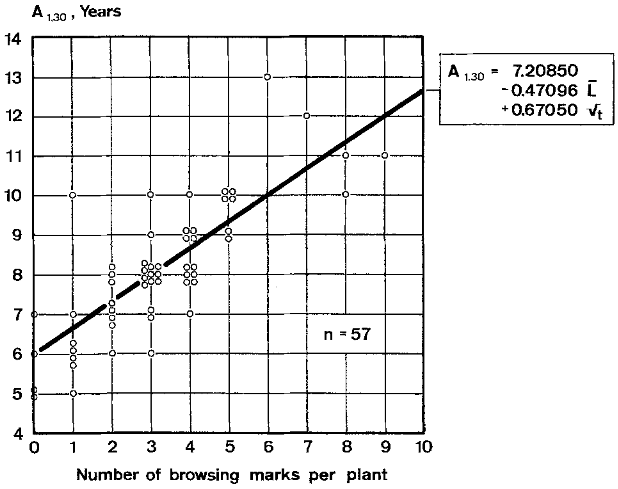

Figure 4. Plant age and browse impact. Investigated area: 'Buchser Hochwald SG', sycamore maple.

4.8 Critical browse impact within the size categories

Conversion of the critical total impact for the lower size categories was done by reducing the mean number of browsing marks per plant (table 9). Adaptation of the critical parameter $\bar{x} = 2.21959$ was first made for the total number of browsing marks by reducing total browse impact proportionally to the share of the browsing marks

Table 8. Frequency distribution of critical total browse impact

Number of browsing marks per plant	Share of plants (%) Observed	Critical	$A_{1.30}$ (years)	Total number of years Observed	Critical
0	4.034	10.865	5.953	24.010	64.677
1	12.950	24.117	6.623	85.768	159.727
2	20.788	26.765	7.294	151.618	195.210
3	22.247	19.802	7.964	177.166	157.699
4	17.856	10.988	8.635	154.178	94.878
5	11.465	4.878	9.305	106.686	45.389
6	6.135	1.804	9.976	61.200	18.001
7	2.814	0.572	10.646	29.956	6.091
8	1.129	0.159	11.317	12.779	1.797
9	0.403	0.039	11.987	4.829	0.469
10	0.129	0.009	12.658	1.637	0.110
11	0.038	0.002	13.328	0.503	0.023
12	0.010		13.999	0.141	
13	0.002		14.669	0.037	
S	100.00	100.00	—	810.507	744.072
Parameter	$\bar{x}$=3.21053	$\bar{x}$=2.21959	Increase in % of 595.261	36.16	25.00

Table 9. Critical number of browsing marks per plant

Plant size (cm) Range	Mid-point	Total number of browsing marks: Shares up to class mid-point	Number per plant	Visible browsing marks: Share of visible browsing marks	Number per plant
0– 10	5	0.191	0.424	0.946	0.401
10– 40	25	0.443	0.982	0.851	0.836
40– 70	55	0.710	1.577	0.755	1.190
70–100	85	0.934	2.074	0.680	1.410
100–130	115	0.989	2.195	0.631	1.386
10–130	70	0.825	1.831	0.718	1.315
—	130	1.000	2.220	0.612	1.358

Table 10. Permissible shares of browsed plants

Plant size (cm) Range	Mid-point	Permissible shares of browsed plants (%) Number of visible browsing marks per plant > 0	> 1	> 2	> 3	> 4	> 5
0– 10	5	33.08	6.20	0.80	0.08	0.01	0.00
10– 40	25	56.64	20.40	5.27	1.05	0.17	0.02
40– 70	55	69.58	33.38	11.84	3.29	0.75	0.14
70–100	85	75.60	41.18	16.90	5.49	1.47	0.33
100–130	115	74.99	40.33	16.31	5.22	1.37	0.30
10–130	70	73.14	37.84	14.63	4.46	1.11	0.24
—	130	74.29	39.37	15.65	4.91	1.27	0.28

up to class mid-point. The values thus obtained were then reduced to the next stage by a factor corresponding to the share of visible browsing marks.

4.9 Permissible shares of browsed plants

The permissible percentage of browsed plants is a result of the frequency distributions calculated by the reduced parameters $\bar{x}$ for visible browsing (table 9). The Poisson distribution was once again used as a basis to find the permissible shares of browsed plants (table 10).

The permissible browsing percentages reveal, retrospectively, whether critical browse impact was exceeded before a specific size category was reached by the young forest trees. Field investigation can only assess this on the basis of visible browsing marks, and this assessment has moreover to be based on clearly defined degrees of damage (fig. 5). The silviculturally acceptable and permissible browsing percentage for the sycamore maples investigated amounts to 37.8. This figure is an average value for the size categories 0.10–1.30 m and concerns specifically those plants with two or more browsing marks visible on the stem axis.

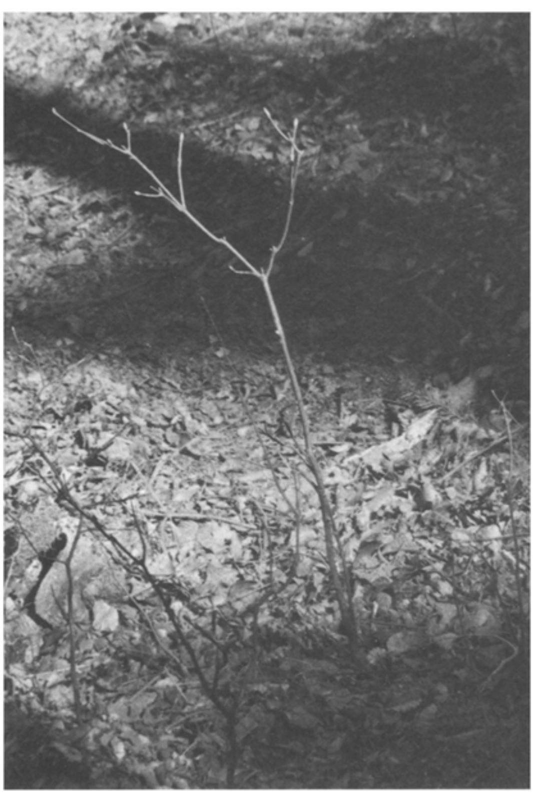

Figure 5. The browsing marks visible on the stem axis form only part of the total browse impact. To determine permissible game browsing, precise knowledge of this relationship is essential.

4.10 Permissible browsing intensity

Data on permissible browsing intensity is required in order to find out whether present browsing activity is compatible with silvicultural requirements (table 11). Calculation of permissible browsing intensity is based on the maximum number of browsing marks tolerated within individual size categories as well as on the period of time the plants require to outgrow specific size categories. Permissible browsing intensity is expressed as a percentage of browsed plants per annum and may thus be determined by assessing terminal shoot browsing. An average value of 26.9% per annum was calculated for the height range of 0.10–1.30 m for the sycamore maples in question. This value may not be exceeded on the average in the risk period since otherwise total impact would exceed the critical value.

5. Discussion

The following conclusions can be drawn from the results of the present study: Objective assessment of game browsing is only possible when figures on permissible browsing are no longer based on estimation but are the result of exact surveys. A suitable method to this end is the counting of browsing marks on the stem axis together with growth analyses. Whereas the effects of game browsing are the result of all the browsing marks in their totality, whether ingrown or visible, field investigation only reveals visible browsing. The limits applicable to visible browsing should consequently be derived from the actual total browse impact.

In the interests of the best possible use of natural regeneration the silviculturally tolerable browsing threshold should be fixed in mountain forests in a way that would prevent fatal browsing over a significantly large area. An average increment loss of 25% – from seeding to outgrowing the browse line – would fulfil this condition.

An equalization function bringing plant age into relation with browse impact, is required for the calculation of increment losses. With only 60 plants per investigated unit the lower impact levels may be insufficiently represented. Calculation of increment losses is thus hindered. The shares of browsed plants considered as permissible have the necessary informative value only when they refer to plants with exactly defined degrees of damage. This

Table 11. Permissible browsing intensity

Plant size (cm) Range	Mid-point	Number of browsing marks within classes Relative	Per 100 units	Age increase within classes Relative	Years	Share of browsed plants per year (%)
0– 10	5	0.301	66.710	0.223	1.659	40.21
10– 40	25	0.268	59.432	0.288	2.142	27.75
40– 70	55	0.257	57.006	0.216	1.611	35.40
70–100	85	0.142	31.536	0.145	1.079	29.23
100–130	115	0.033	7.276	0.128	0.950	7.66
10–130	70	0.699	155.249	0.777	5.782	26.85
—	130	1.000	221.959	1.000	7.441	29.83

basic requirement should already be taken into account in instructions for game damage inventories.

The present study tries to put assessment criteria for game browsing on an objective basis and to adapt them to the specific growth conditions of high altitude forests. Its prime purpose was to find a suitable method of investigation, and it only gives a first indication of the silviculturally permissible browsing limit for sycamore maple. Further repetitions and different site conditions are needed to complement the above analyses.

Acknowledgment: The present paper is part of a comprehensive research project on the silviculturally acceptable browse impact in mountain forests. We are indebted to the Committee of the Swiss Fund for the Promotion of Forest and Wood Research for financial assistance.

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0014-4754/87/020127-07$1.50 + 0.20/0
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Cardiac cellular electrophysiology: past and present

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Summary. The time-course of the cardiac action potential can be accounted for in terms of ionic currents crossing the cell membranes. Depolarizing current is carried by Na^+ or Ca^{2+} entering the cells, repolarizing current by K^+ leaving the cells. Membrane permeability for the passive movement of these ions is thought to be voltage-dependent as well as time-dependent. Net transfer of charge may also result from active transport, 2 Na^+ out against 1 K^+ in; or coupled exchange, 3 or 4 Na^+ in against 1 Ca^{2+} out. This review follows the path by which present-day knowledge has been reached. It also gives a few examples to illustrate that electrophysiology has provided concepts useful to clinical cardiology.

Key words. Cardiac potentials; membrane currents, heart; cell coupling, heart; electrophysiology, heart; ion flux, heart; active transport; pacemaker.

The present review is addressed to the non-specialist biologist. Accordingly, an effort has been made to simplify, rather than to point out difficulties and uncertainties. It is hoped that the historical approach used will enable the reader to distinguish between experimental facts and interpretations. Facts should remain reproducible, whereas interpretations have changed in the past and will change in the future.

Early monophasic recordings

The construction of the Lippmann capillary electrometer[86] as a means of recording voltage fluctuations with a reasonably high degree of fidelity opened the way for studying the so-called 'injury action potential' (Burdon-Sanderson and Page, 1883, fig. 1). Two electrodes were placed on the exposed surface of a frog's heart. By injuring the tissue underneath one of these electrodes a record was obtained showing a rapid upstroke (a negative swing at the undamaged site), a long-lasting plateau, and a relatively well-defined downstroke, the whole deflection lasting for 2 s.

Cardiac muscle when damaged has a remarkable tendency to 'heal over' i.e. to set up an electrical barrier between undamaged and damaged tissue[34]. It is the general experience in student practicals that a monophasic record obtained by injury near one of the electrodes returns to a biphasic record within a few minutes. A major step towards stable monophasic recording was made in the 1930s by Schütz and his colleagues[123] who

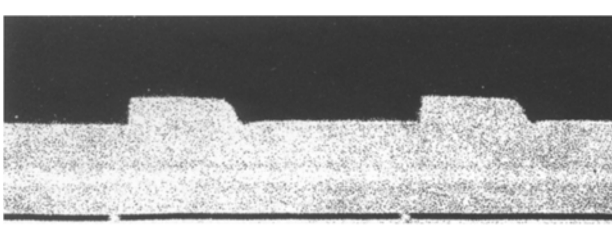

Figure 1. Voltage fluctuations of a frog's heart as recorded by a capillary electrometer. One electrode is placed at the base of the ventricle. The other electrode is placed near the apex, where the tissue is injured by a hot wire. Breaks in the black line are 5 s apart and mark direct ventricular stimulation[13].