

Nitrogen Relations of Ruderal Communities (*Rumicion alpini*) in the Northern Calcareous Alps

H. Rehder

Institut für Botanik und Mikrobiologie der Technischen Universität München, Arcisstr. 21, D-8000 München 2,
Federal Republic of Germany

Summary. The total nitrogen and nitrate turnovers of three plots of plant communities typical of cattle resting sites in the Bavarian Alps were investigated. Annual net N mineralisation of the soil and N content of the above-ground phytomass at maximum development are low in the *Senecio cordatus* dominated community “W” at 1,450 m altitude (80 and 57 kg N/ha respectively) and highest in the nearly pure *Rumex alpinus* stand “K” (1,240 m) (156 and 148 kg N/ha). The subalpine mixed *Rumex alpinus* community “S” (1,790 m) is intermediate with low mineralisation but high N content in the aboveground parts (69 and 128 kg N/ha). In general the mineralisation values are below those from other comparable plant communities. The main component of N mineralisation is nitrification in all three plots.

The nitrate content in the phytomass at full development increases from 0.1 g/m² in W to 0.3 g/m² in S and to 1.0 g/m² in K. With one exception (*Adenostyles alliariae*) no species showed a real nitrate accumulation in the leaf laminae towards the end of the growing season.

Introduction

In mountain pasture areas there are generally centers where cattle habitually rest, for instance near the stables but also at other suitable places, where the excrement of the animals enriches the soils in nutrients, especially nitrogen. In consequence at such sites special plant communities of nitrophilous herbs are established. They belong to the perennial ruderal communities and are called in German “Lägerflur”. Above the tree line, that is in the alpine zone, usually under the influence of prevailing sheep grazing, they appear as low turf or mat communities which, in contrast to the surrounding mats, are rich in soft-leaved dicotyledonous herbs accompanying the dominant soft grass *Poa alpina*, whereas in the subalpine and montane zones we find communities of tall broad-leaved herbs at the corresponding places. They are often dominated by the Alpine Dock (Monk’s Rhubarb, *Rumex alpinus*) which is conspicuous by its large shiny leaves. Though this widespread and distinct “*Rumicetum alpini*” and other related communities of the alliance “*Rumicion alpini*” are mentioned or described in nearly all monographs or other comprehensive publications on the vegetation of the Alps (e.g. Schröter 1908; Lüdi 1921; Braun-Blanquet 1964; Oberdorfer 1957; Ellenberg 1978), we still lack detailed ecological investiga-

tions of these vegetation units, especially with regard to nitrogen turnover. In a previous publication (Rehder 1970) the expected high net mineralisation rate of nitrogen (ca. 20 g N/m² × a⁻¹, mainly in the form of nitrate accumulation) was demonstrated in the soil of a subalpine “*Rumicetum*”. It remained, however, uncertain how far this result was representative for that type of vegetation, and whether the amount of mineralisation would correspond with the fluctuation of nitrogen within the phytomass. Moreover it seemed desirable to check such an obviously nitrophilous plant community with regard to the storage of unused nitrate in at least some of its members. So far as nitrate is not reduced within the plants we have to consider the possibility of a separate nitrate cycle within the comprehensive cycle of total nitrogen between plant and soil. Such accumulation of nitrate is known from members of several families, especially of *Amaranthaceae*, *Chenopodiaceae*, *Urticaceae* and *Umbelliferae* (Hegnauer 1962–1973; Marthaler 1937; Bauer 1938; Jaeniesch 1973), but it has not been investigated for ruderal herbs of the Alps.

In order to obtain this missing information on the extent of nitrogen circulation and on the mode of utilisation of the nitrate ion by subalpine plants, we made quantitative studies on three stands of “Lägerflur” in the Northern Calcareous Alps (Bavaria) in the second part of the growing season in 1979 and during the growing season in 1980.

Subjects of investigation

The sample areas for turnover studies should be accessible by car and a short walk. This condition was fulfilled for the limited period of 1979 only by two sample areas at lower altitudes:

1. “*Krautkaseralm*” = K, situated 1 km north-west of Mount Jenner, Calcareous Alps of Berchtesgaden, altitude 1,240 m. Planation within the north-western slope (exposure 1° WNW). Clay soil upon moraine.

Rumex alpinus is dominant in isolated patches of different extent within the area of rich pastures. At maximum development the height of the plants here is about 40 cm and they cover 100% of the soil surface. The following species were listed (species quantity figures according to Braun-Blanquet (1928), nomenclature from Tutin et al. (1964–1980), except the collective species *Alchemilla vulgaris*, cf. Oberdorfer 1979):

5 *Rumex alpinus* + *Potentilla erecta*
 1 *Poa alpina* + *Ranunculus repens*
 1 *Alchemilla vulgaris* + *Pimpinella major*
 + *Trifolium repens* + *Veronica chamaedrys*
 + *Leontodon hispidus*

2. "*Wettersteinalm*" = *W*, part of the Wetterstein Mountains, altitude 1,450 m. Plateau 1 km north of the main ridge of Wetterstein (exposure 1° N). Clay facies of the triassic "Raibler Strata".

In this area we find tall herb communities of higher diversity, about 40 cm in height and also covering 100% of the surface, for which the following list is considered representative:

3 *Senecio cordatus* + *Trollius europaeus*
 2 *Deschampsia cespitosa* + *Cardamine pratensis*
 2 *Poa alpina* + *Chrysosplenium alternifolium*
 2 *Festuca pratensis* + *Trifolium pratense*
 2 *Ranunculus repens* + *Chaerophyllum hirsutum*
 2 *Alchemilla vulgaris* + *Veronica chamaedrys*
 1 *Rumex arifolius* + *Veronica serpyllifolia*
 1 *Adenostyles alliariae* + *Phyteuma spicatum*
 + *Poa trivialis* + *Achillea millefolium*
 + *Agrostis capillaris* + *Bellis perennis*
 + *Rumex alpinus* + *Taraxacum officinale*
 + *Ranunculus acris*

In the growing season of 1980 we were able to concentrate our investigations on a typical stand of the "Rumicetum alpini":

3. "*Schachengrund*" = *S*, Wetterstein Mountains, altitude 1,790 m. Plain hill surface (0°) east of Schachen hut, within a depression north of „Frauenalpe“. Same clay facies as in *W*.

The sample area is not far from the area "R 1" investigated by Rehder (1970), and the species composition of the two stands is similar. Since we intended to have this place under repeated observation we protected it from cattle grazing with an electric fence.

Here again *Rumex alpinus* is dominant, but accompanied by many other species in different proportions from one spot to another. Fertile stems of *Rumex alpinus* were rarely present in *S* or in *K*. The mean height is about 30 cm and the plant cover again 100%. The typical species composition is shown by the following list:

3 *Rumex alpinus* + *Caltha palustris*
 2 *Deschampsia cespitosa* + *Potentilla aurea*
 2 *Rumex arifolius* + *Alchemilla fissa*
 2 *Alchemilla vulgaris* + *Trifolium repens*
 1 *Poa alpina* + *Trifolium pratense*
 1 *Phleum alpinum* + *Ligusticum mutellina*
 1 *Stellaria nemorum* + *Chaerophyllum hirsutum*
 1 *Cardamine amara* + *Primula elatior*
 + *Festuca rubra* + *Veronica serpyllifolia*
 + *Veratrum album* + *Campanula scheuchzeri*
 + *Cerastium fontanum* + *Cirsium spinosissimum*
 + *Ranunculus nemorosus* + *Leontodon hispidus*
 + *Trollius europaeus* + *Taraxacum officinale*

The type of soil in the three areas is nearly the same. As described for "R 1" (Rehder 1970) it is designated as "Mullgley" (nomenclature of Kubiena 1953). It is profoundly free of debris, clayish-loamy with a dark humous

Table 1. Average dry weight (DW) of soil per volume, content of carbon and nitrogen (% of DW) and nitrogen relative to carbon of the upper soil layers of three "Lägerflur" stands

	Soil-depth cm	<i>K</i> 1,240 m	<i>W</i> 1,450 m	<i>S</i> 1,790 m
DW g/100 ml	0- 5	59.4	62.7	48.4
	5-10	76.4	71.6	87.1
	10-15	92.6	84.0	83.2
C%	0- 5	9.1	8.5	21.9
	5-10	7.5	7.4	9.0
	10-15	5.2	5.2	7.0
N%	0- 5	0.8	0.8	2.2
	5-10	0.7	0.8	0.8
	10-15	0.5	0.5	0.5
N C × 100	0- 5	8.8	9.5	10.0
	5-10	9.3	10.8	8.9
	10-15	9.6	9.6	7.1

("Mull") horizon of 6-12 cm depth interspersed with the main portion of roots. The humus content of this horizon is distinctly higher in the subalpine stand *S* than in the lower situated stands *K* and *W*. The soil is more or less acid. In *S* we found pH 3.1-3.3 (soil suspended in H₂O) from 0 to 15 cm soil depth. In *K* and *W* the values were between 4 and 5. Some important soil parameters are listed in Table 1.

Corresponding to the different altitudes and based on the data of nearby meteorological stations (cf. Rehder 1970) the average annual air temperature can be estimated for the three plots as 4° C (*K*), 3° C (*W*) and 1° C (*S*), the duration of the period with mean temperatures above 5° C (= presumed growing season) being about 22, 21 and 18 weeks respectively. Mean annual precipitation is about 2,000 mm in each of the plots with the maximum during summer.

Methods

Sampling was done by harvesting the total above-ground phytomass of each plot from defined areas of typical floristic composition and structure. This was possible only once (14 and 20 August 1979) from undisturbed parts of *W* and *K* with 1 m² surface each. At *S* the plant cover was cut six times from different 0.1225 m² areas between 20 June and 1 October 1980 at 3-week intervals. In addition volumetric soil cuts were taken from 15 cm depth and 0.1450 m² (*W*) or 0.1225 m² (*K* and *S*) surface, including the main part of the root mass. The above-ground and below-ground phytomass were cleaned and, as far as possible, separated into species, living or dead parts and in some cases also into different organs. After drying at 105° C the different parts were weighed, homogenised and, if available in sufficient amounts, used for determination of total nitrogen and nitrate content. The total nitrogen (without nitrate) was determined by the Kjeldahl method (Steubing 1965; cf. Rehder 1976; Rehder and Schäfer 1978) in plant material and dried soil samples, whereas for nitrate the high-pressure liquid chromatography method (Thayer and Huffaker 1980) was employed, using hot water extracts of the dried plant material.

From the sides of each volume cut soil samples were taken from 0-5, 5-10 and 10-15 cm depth. They were

evenly mixed by hand and cleared of roots as far as possible. About half of each mixture was used for subsequent determination of the initial mineral nitrogen (Nm) content. The rest was stored in a polyethylene bag (30 µm), enveloped by another bag, buried at the site in the appropriate depth and used for Nm determination after 6 weeks incubation (cf. Rehder 1970, 1976).

Soil Nm content was determined with the distillation apparatus according to Bremner and Keeney (1965) (cf. Gerlach 1973), in which the NH₄- and the NO₃-bound nitrogen are successively titrated in one procedure. Since 40 g of the fresh soil sample are used for extraction with 100 ml of a 1% KAl(SO₄)₂ solution it is necessary to determine the water content of a parallel sample by drying at 105° C. The average weight per volume of dry soil is recorded by several volumetric cuts (Table 1) so that we can convert the results into terms per area.

We use the following formula for calculation of the Nm content per area in each layer of 5 cm depth:

$$m \times v \times \left(\frac{245}{t} - 1.75 \right) = \text{mg Nm/m}^2 \quad (1)$$

where m = amount (ml) of titrated $\frac{n}{200}$ H₂SO₄ (1 ml equivalent to 0.07 mg Nm). v = average dry weight of soil per volume (g/100 ml, cf. Table 1). t = dry soil proportion (g) of 40 g fresh soil corresponding to the sample used for determination.

Formula (1) is derived thus: the total amount of extracting solution is the sum of water content of the fresh soil sample (40 - t) and the applied solution (100 g) = 140 - t , from which after shaking and filtering 20 g are used for the distillation.

Therefore we get:

$$m \times 0.07 \times \frac{140 - t}{20} \times \frac{v}{t} = \text{mg Nm/100 ml dry soil} \quad (2)$$

and, the volume of the 5 cm layer under 1 m² surface being 50,000 ml:

$$m \times 0.07 \times \frac{140 - t}{20} \times \frac{v}{t} \times 500 = \text{mg Nm/m}^2 \quad (3)$$

After transformation we get Formula (1).

In addition to the total nitrogen content (Kjeldahl method, see above) the carbon content of the dried soil samples was determined by the gas analyser "Carmograph" (Wösthoff o.H.G.) (Table 1).

Results

1. Sample area "Krautkaseralm" = K

At the time of sampling this lowest situated *Rumex alpinus* community seemed to be in the state of optimum development. In analysing the above-ground phytomass, however, we found about 25% already dead (Table 2). Assuming some loss of substance in this part, the above-ground phytomass is estimated to be only about 25% of the total, but containing 40% of the nitrogen. The below-ground phytomass is concentrated with 77% in the upper soil layer (0-5 cm); that is 61% of the total phytomass, and more than 50% of the total N content of the community is located here. This is also the main region of storage roots of the predominant *Rumex alpinus*.

Table 2. Analysis of phytomass in K, 20 August 1979

	Dry substance g/m ²	N g/m ²	NO ₃ -N mg/m ²
Above-ground phytomass			
Living parts			
<i>Rumex alpinus</i>			
Young leaves	14	0.93	1.6
Developed leaf lamina	162	9.17	56.7
Leaf stalks	131	3.76	177.9
Yellowed leaves	26	0.72	10.1
Other species	6	0.19	0.4?
	339	14.77	247
Dead parts (of same growing season)			
<i>Rumex alpinus</i>			
Other species	3	0.05	0.2?
	114	2.33	40?
Below-ground phytomass (mostly <i>Rumex alpinus</i> , alive)			
0-5 cm soil depth	1,303	22.15	620
5-10 cm soil depth	232	2.34	146
10-15 cm soil depth	146	1.16	106
	1,681	25.63	872
Total phytomass	2,134	42.73	1,159

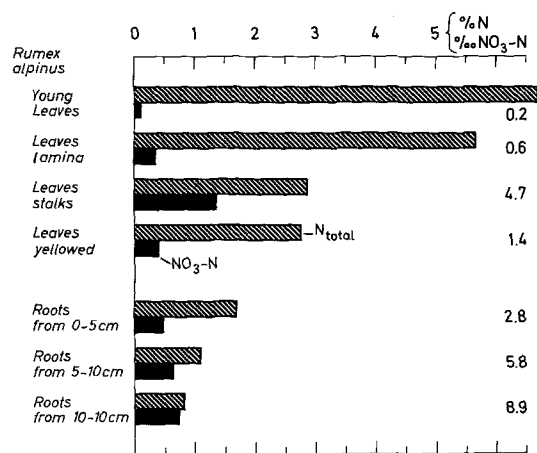


Fig. 1. Content of total nitrogen (% N of dry weight) and nitrate (% NO₃-N of dry weight) in different parts of *Rumex alpinus* from the area K (20.8.1979). Right side: Percentages of NO₃⁻ N referred to total N

In contrast to total nitrogen (Fig. 1) the nitrate content in the root mass rises slightly with soil depth. Aboveground an increase of nitrate together with a decrease of total nitrogen is indicated from young to full-developed and to yellowed leaves. The highest concentration of nitrate is found in the leaf stalks.

In total the phytomass contains about 1 g NO₃-N (Table 2). This is 2.7% of the total N. Of this nitrate 15% is located in the leaf stalks and 75% in the roots. So we

Table 3. Analysis of phytomass in *W*, 14 August 1979

	Dry substance g/m ²	N g/m ²	NO ₃ -N mg/m ²
Above-ground phytomass			
Living parts			
<i>Senecio cordatus</i>	154	2.51	5.7
<i>Deschampsia cespitosa</i>	59	0.93	3.0
<i>Ranunculus repens</i>	32	0.59	5.0
<i>Poa alpina</i>	31	0.50	1.4
<i>Alchemilla vulgaris</i>	26	0.52	1.4
<i>Festuca pratensis</i>	11	0.15	0.4
<i>Adenostyles alliariae</i>	7	0.15	16.5
<i>Rumex arifolius</i>	7	0.13	1.7
<i>Agrostis capillaris</i>	3	0.05	0.1
<i>Trifolium pratense</i>	2	0.05	0.1
Other species	5	0.08	0.5
	337	5.66	36
Dead parts (of same growing season)	6	0.08	1?
Below-ground phytomass (mostly alive, 0-15 cm soil depth)			
<i>Senecio cordatus</i>	351	3.05	13.7
Other species	709	7.87	56.7
	1,060	10.92	70
Total phytomass	1,403	16.66	107

may state that 90% of it is found still in the transition space between soil and the assimilatory organs.

From the field incubation tests which were performed only twice towards the end of the growing season we obtained accumulation rates of 4.85 and 3.66 or on average 4.26 g Nm/m² in 6 weeks (Fig. 3). This is an increase to more than 400% of the mean initial amount (1.34 g) and includes an increase to 668% of the initial NO₃-N, which is in part at the expense of the NH₄-N present at the start, which is nearly consumed after incubation. If the mean value of net N mineralisation given above were regarded as normal for the growing season (22 weeks) we arrive at 15.6 g Nm/m² for this period. This is near the amount of total nitrogen present in the above-ground phytomass produced in the same time.

2. Sample area "Wettersteinalm" = *W*

When analysing the phytomass of this community our main interest was in the differences in nitrogen relations between the diverse component species. The root mass was not separated by soil layers, but based on random tests we found 86% in 0-5 cm, 11% in 5-10 cm and 3% in 10-15 cm soil depth (77%; 14%; 9%; in *K*).

The above-ground phytomass is less than that in *K* but again it is about 25% of the total, containing only 34% of the nitrogen (Table 3). Compared with *Rumex alpinus* in *K* the percentages of total nitrogen are lower here (Fig. 2). The grasses particularly show values below that of *Senecio cordatus*, whereas the dicotyledonous herbs accompanying this dominant species exceed it. But even *Rumex arifolius* is far behind its relative in *K*.

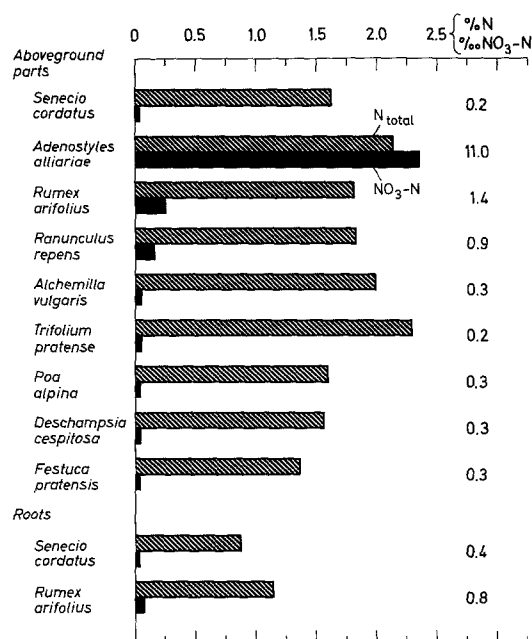


Fig. 2. Content of total nitrogen and nitrate (as in Fig. 1) in different species from area *W* (14.8.1979)

The nitrate content is very low in *Senecio cordatus* in both above-ground and below-ground parts. From the other member of the Compositae, *Adenostyles alliariae*, on the contrary, we obtained an extremely high percentage. It was not possible to analyse the roots of most species separately, but in *Rumex arifolius* it was interesting to find the nitrate content higher on average in its above-ground parts than in its roots, and than in the other species investigated (except *Adenostyles*).

Within the total phytomass the nitrate content (Table 3) is only about 0.1 g/m² (=0.64% of total N) as against 1 g/m² (2.7%) in the *Rumex alpinus* stand *K*. Here 65% of the nitrate (cf. 75% in *K*) is located in the roots.

Due to an interference in the first incubation attempt we were able to record the net N mineralisation only for one period in late autumn. The result may be compared with that of the second period for *K* (Fig. 3). The increase (1.97 g Nm/m²) is only to about 320% of the initial amount (including an increase to 560% for nitrate) and about 54% of that in *K*. Taking this relation and the shorter growing season (21 weeks) as a basis for calculation we get about 8 g Nm/m² accumulated in the soil (0-15 cm) during this time. This would, however, still be higher than the nitrogen content (5.74 g/m²) of the above-ground phytomass. Altogether the lower net N mineralisation clearly corresponds to the lower incorporation of N in the phytomass of *W* compared with *K*.

3. Sample area "Schachengrund" *S*

The maximum phytomass development of this community is attained about the same time (21 August) as harvesting and sampling was done for *K* and *W* in the previous year (Fig. 4). The dominating *Rumex alpinus* contributes about 50% of dry substance from June to August and then disappears rapidly. Of course there are changes in the relative proportions of species present in each cut, but at least we see a clear fluctuation of above-ground phytomass during

Area	K	W	S
Altitude	1240m	1450m	1790m
Year	1979	1979	1980
Date	OW. 20.8. 1.10. 6W. -1.10. -12.11.	26.9. -7.11.	20.6. 10.7. 31.7. 21.8. 16.7. -31.7. -21.8. -11.9. -1.10. -26.8.

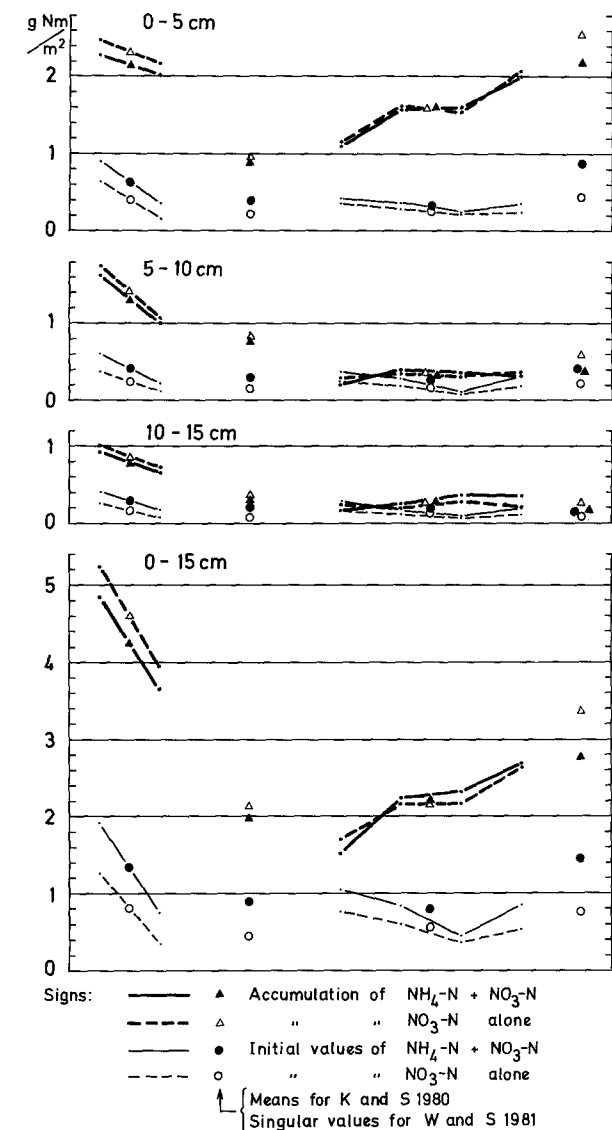


Fig. 3. Net nitrogen mineralisation (=accumulation=difference between values after 6 weeks field incubation and initial values) and initial values of mineral nitrogen of the three areas for different incubation periods 1979–1981. Values are shown above for the three soil layers (0–5, 5–10, 10–15 cm depth) and summarised (0–15 cm) below

the growing season. This is not possible for the below-ground phytomass. Since we wished to correlate the roots with the above-ground parts of the different species we did not separate the root mass according to the 5 cm layers of soil in this series. We can only state that the above-ground phytomass (including the dead parts and some loss of dry substance herewith) is about 35% of the total at maximum development and about 30% on average.

The total nitrogen percentages (Figs. 6 and 7) again are markedly higher in the above-ground parts than in the roots of nearly all species investigated here. For *Rumex alpinus* we find similar relations as in *K*, though it is surprising that the main roots (storage roots) and other roots of more than 2 mm diameter, generally confined to the uppermost

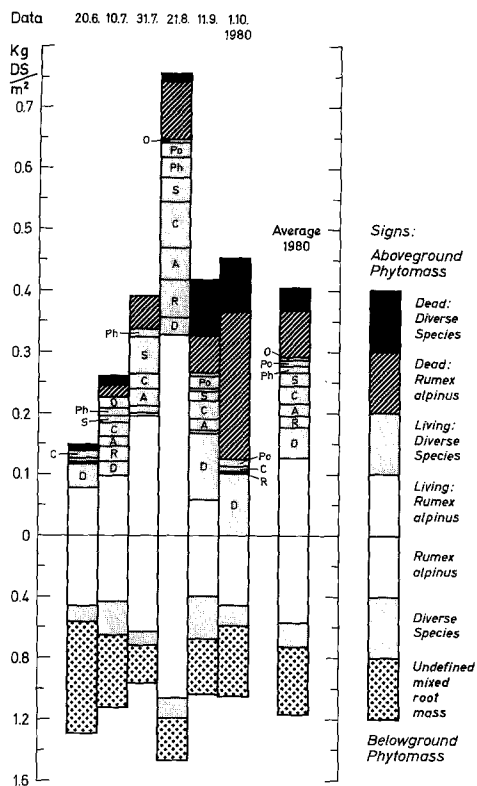


Fig. 4. Amounts of dry substance (DS) of the phytomass components of "Schachengrund" (S). Each column represents the DS of one cut of 0.1225 m² surface area. Below abscissa: Below-ground phytomass scaled down 1:4. Species: *D*, *Deschampsia cespitosa*; *R*, *Rumex arifolius*; *A*, *Alchemilla vulgaris*; *C*, *Cardamine amara*; *S*, *Stellaria nemorum*; *Ph*, *Phleum alpinum*; *Po*, *Poa alpina*; *O*, Other species

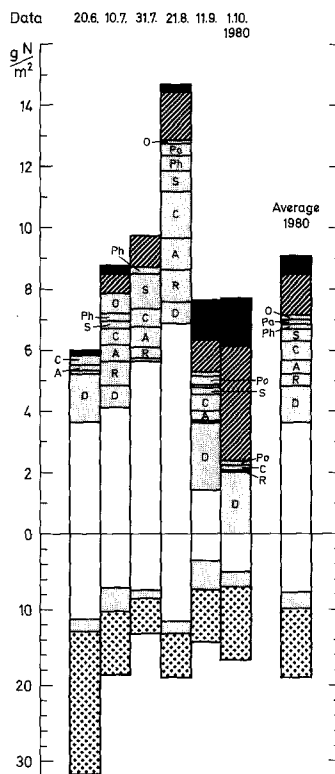


Fig. 5. Amounts of nitrogen (N) in the phytomass components of *S*. Symbols as in Fig. 4. The values are derived from those in Figs. 4, 6 and 7. In cases of insufficient amounts for N determination a rough estimation of N percentages was applied

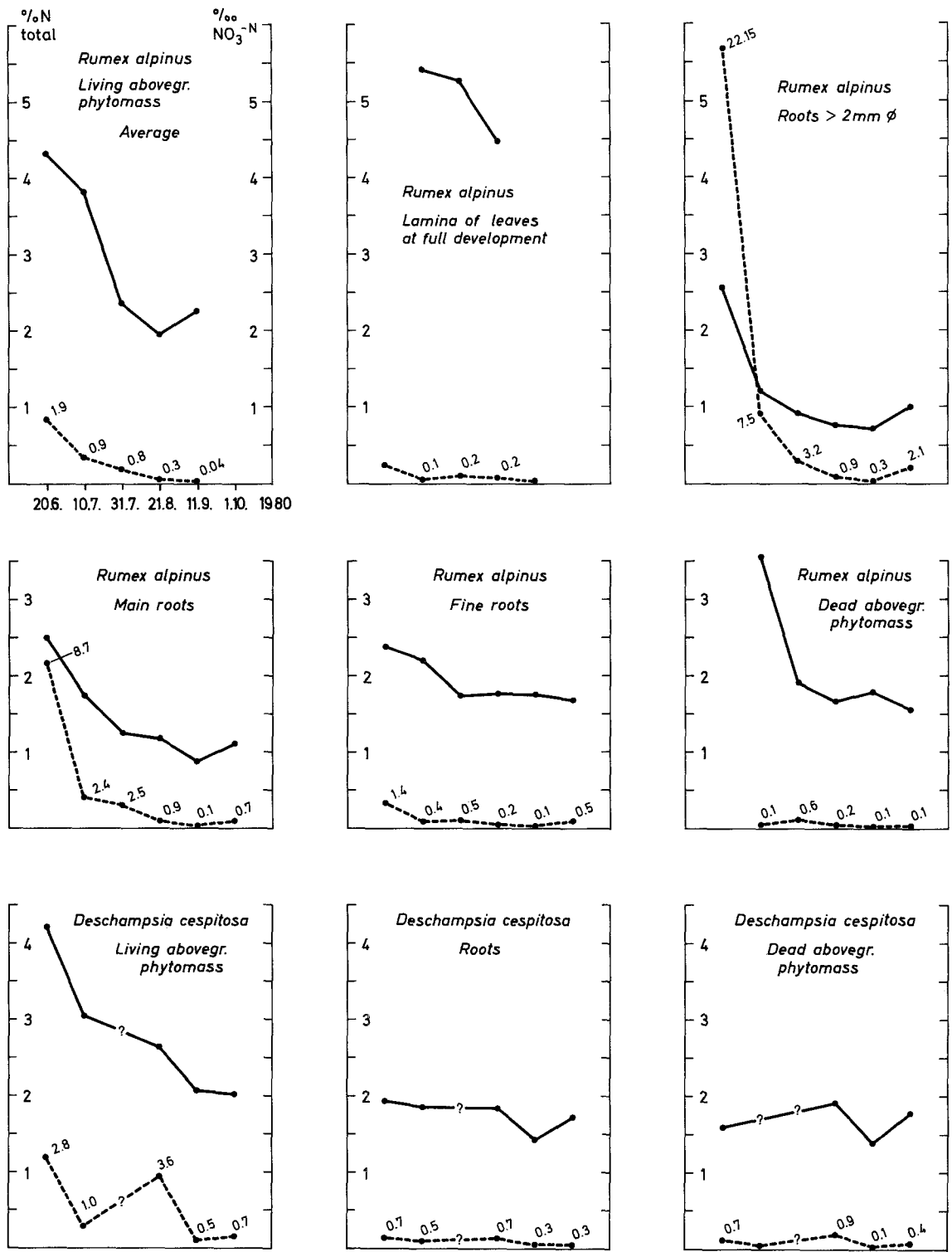


Fig. 6. Content of total nitrogen (% N of dry weight) and nitrate (% NO₃-N of dry weight) in different species from area S on six dates in 1980 (diagram above left) Signs see Fig. 7

soil layers, are lower in nitrogen here compared with the fine roots. The lower average N percentage in the living above-ground phytomass in *Rumex alpinus* compared with the separated laminac is explained by the presence of stalks (cf. Fig. 1). As far as investigated we find a distinct decrease of nitrogen percentage in all living above-ground parts during the growing season. This is not so for all roots or for dead above-ground material which is about in the range

of the roots. In parts of the root components we observe a slight tendency to increase towards the end of the growing season.

On average the above-ground phytomass contains about 9 g N/m² during the growing season reaching nearly 15 g N/m² at maximum whereas the root mass fluctuates around 19 g N/m² (Fig. 5).

The net N mineralisation (Fig. 3) increased during the

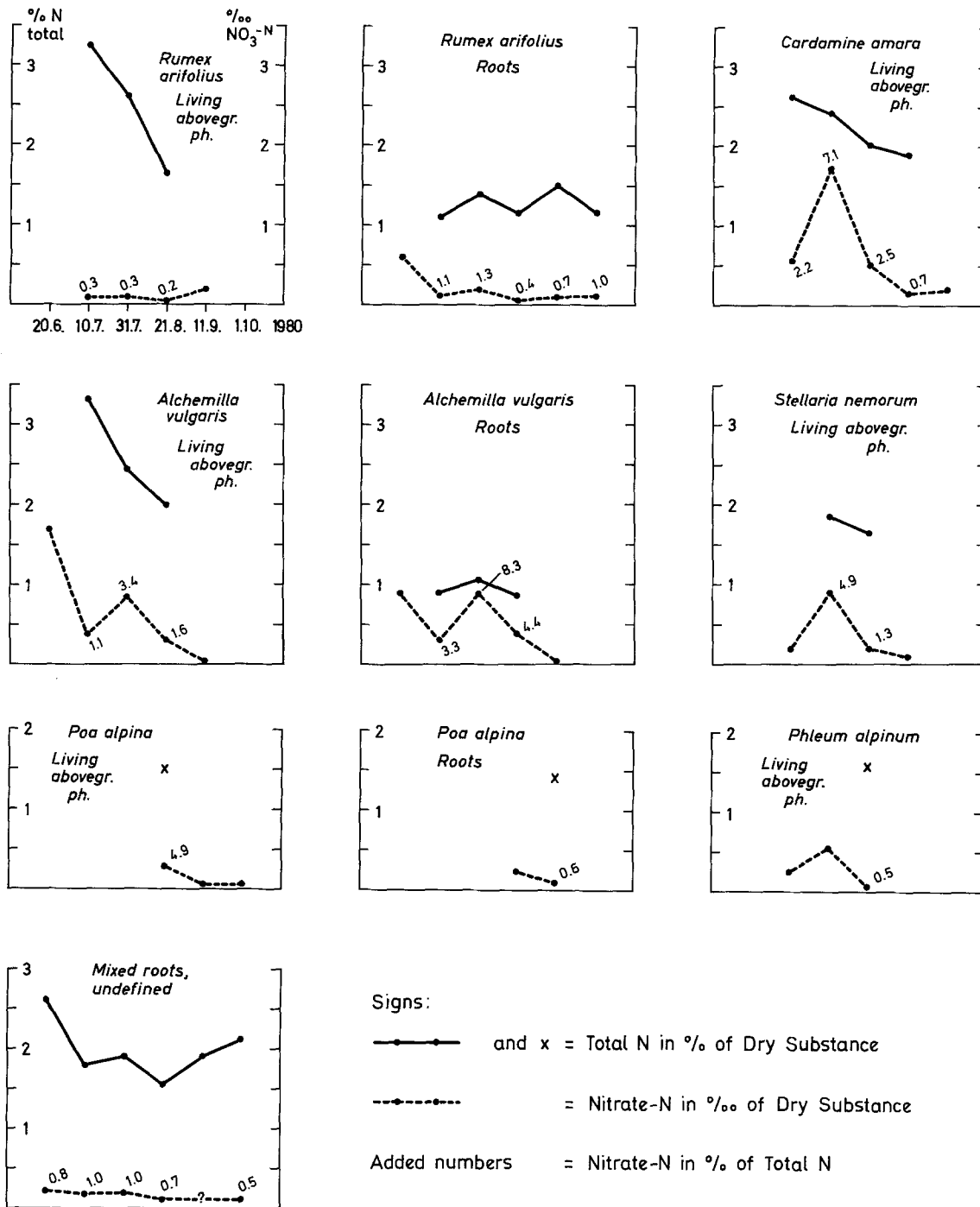


Fig. 7. Content of total nitrogen and nitrate (as in Fig. 6) in different species from the area *S* in 1980 (for abscissa see Fig. 6)

growing season of 1980 and was on average 2.19 g Nm/m^2 per 6 weeks or about 6.6 g Nm/m^2 for the growing season (18 weeks). Incubation was repeated in one single test in summer 1981 from which 2.77 g Nm/m^2 were obtained. With this the average per 18 weeks is elevated to 6.9 g Nm/m^2 . In every case these mineralisation values are surprisingly low compared with those of *K* and even *W*, with the high values of "R 1" (Rehder 1970), and also with the N content values we found in the maximum above-ground phytomass alone. We are unable to explain this deviation by the N/C ratios or the density values of the soil which are in the same range in *K*, *W*, and *S* (Table 1).

This reduced Nm supply coincides with the reduced nitrate accumulation in the above-ground parts of *Rumex alpinus* at this site compared with *K* (Fig. 6). In the roots, however, a very high storage of nitrate is found at the beginning of the growing season, followed by a strong decrease with a slight increase towards the end again. A similar tendency is observed in the roots of *Rumex arifolius* (Fig. 7). Some accompanying species which contained minimal nitrate amounts in *W* on the contrary show markedly elevated above-ground values in *S*, especially in the earlier part of the growing season, namely *Deschampsia cespitosa* (Fig. 6) and *Alchemilla vulgaris* (Fig. 7). The same is obvious in

Table 4. Amounts of nitrate in the phytomass components of *S* on area basis (mg NO₃-N/m²) and in %. Estimated values in ()

Date (1980)	20.6.	10.7.	31.7.	21.8.	11.9.	1.10.
Above-ground phytomass						
Living parts						
Rumex alpinus	49.1	21.6	33.5	16.7	0.7	–
Deschampsia cespitosa	44.3	7.1	(1.5)	25.3	10.6	15.1
Rumex arifolius	(0.3)	1.9	1.3	2.5	1.0	(0.3)
Alchemilla vulgaris	9.6	6.3	22.3	15.9	0.6	(0.1)
Cardamine amara	16.4	11.9	42.1	38.7	4.1	1.6
Stellaria nemorum	–	2.2	55.3	8.4	1.2	–
Phleum alpinum	–	3.0	6.6	2.3	(0.3)	(0.1)
Poa alpina	–	–	–	17.6	1.0	0.7
Other species	–	2.4	(0.7)	(1.1)	(0.7)	–
	119.7	56.4	143.3	128.5	20.2	17.9
Dead parts						
Rumex alpinus	–	0.7	6.3	2.9	0.6	4.8
Other species	1.1	0.8	(0.1)	2.2	2.1	6.1
	1.1	1.5	6.4	5.1	2.7	10.9
Below-ground phytomass						
Rumex alpinus	1,054.4	212.1	179.9	91.6	5.2	50.5
Other species	54.6	30.7	35.1	19.4	16.5	9.2
Mixed roots (undefined)	74.7	105.3	29.6	55.7	28.9	49.9
	1,183.7	348.1	244.6	166.7	50.6	109.6
Total phytomass	1,304.5	406.0	394.3	300.3	73.5	138.4
Percentages of total						
Above-ground living	9.2	13.9	36.3	42.8	27.5	12.9
Above-ground dead	0.1	0.4	1.6	1.7	3.7	7.9
Below-ground	90.7	85.7	62.0	55.5	68.8	79.2

Cardamine amara and Stellaria nemorum whereas Rumex arifolius remains far from its above-ground values in *W*.

Regarding the absolute amounts of nitrate and their changes in the phytomass during the growing season (Table 4), we record their steady decrease in the total phytomass from more than 1 g/m² to about 0.1 g/m², chiefly based on the same tendency in the root mass which contains 91% of the total at the start, but only 56% at the state of maximal above-ground development. At this time, however, nitrate is already decreasing in the above-ground parts too. A steady increase of nitrate is only obvious in the dead above-ground parts. But even here the amount attained at the end of growing season is less than 10% of the total nitrate in the phytomass.

Discussion

The most striking result of this survey is the marked difference between the three sites compared here, even taking into consideration that the methods, the extent, and the time of sampling could not be equal. Only plot *K* approaches the high net N mineralisation values of the previously investigated subalpine Rumicetum "R 1", and only here do we find adequate total nitrogen bound in the above-ground organic substance. The mineralisation values of *K*, *W* and *S* are estimated as 156, 80 and 69 kg Nm/ha (0–15 cm) for the growing season, assumed to be near the annual values. Plot *S*, neighbouring to "R 1" and appear-

ing similar in species composition and site conditions, ranges at the end of this sequence. The N content of the living above-ground phytomass near the state of maximum development in the three communities (in the same sequence) are 148, 57 and 128 kg N/ha. In this respect the two Rumex alpinus communities, *K* and *S*, are not far from each other, but the divergence between N mineralisation and N content of the phytomass in *S* is all the more surprising, whereas for the Senecio cordatus community *W* it is reverse and less significant. Of course we should not expect always to find a correspondence between these two parameters, as was more or less evident in some cases already (Rehder 1971; Rehder and Schäfer 1978). The existence of "plant internal" nitrogen cycles beside the "external" cycles (cf. Ellenberg 1977), the possibility of stimulation of mineralisation by exudates in the rhizosphere, and many other factors may interfere with this relation. So we only have to state the N cycling to be rather high in the montanic Rumicetum *K*, low in the Senecio cordatus community *W*, whereas the subalpine Rumicetum *S* seems to fall somewhere in-between.

As to the comparison of the two neighbouring plots *S* and "R 1", it should be mentioned here that Rumex alpinus appeared with the Braun-Blanquet abundance number 4 (covering above 50%) in "R 1" as against 3 (below 50%) for the average of the area *S* only. At the stage of optimal development, however, the above-ground living phytomass was only 5.41 tonne/ha in "R 1" as against 6.45

tonne/ha in *S*, though this single value (and also the N content value derived from it) may be somewhat elevated compared with normal. Net N mineralisation (195 kg Nm/ha) was calculated for 0–22 cm soil depth in “R 1”. Since the layer from 15 to 22 cm contributed 5.6% only, we may assume 184 kg Nm/ha for 0–15 cm soil depth in “R 1”.

It may further be mentioned that the net mineralisation values of these three plots rank with the lower values for ruderal vegetation types investigated by Kronisch (1975) (cf. Ellenberg 1977) in the lowlands near Göttingen, where communities with *Urtica dioica* attained values between 155 and 307 kg Nm/ha $\times a^{-1}$. The plots *S* and *W* were even surpassed by some individuals of subalpine-alpine mat communities (Seslerio-Semperviretum, Caricetum ferrugineae), though the average of the mats was about 50 kg Nm/ha (Rehder 1970, 1971) or, including those under more extreme alpine conditions, much lower (Rehder and Schäfer 1978). Further investigation in other examples of Rumicetum alpini and related communities should extend our knowledge of the range of total nitrogen turnover in these special ecosystems.

Another question referred to the role of nitrate within this turnover. Here it would be useful to define exactly the concept of “nitrate storage” or “nitrate accumulation” in plants. At least three conditions should be fulfilled in order to range a species as a real “nitrate accumulator”:

1. The quantity of nitrate should surpass a fixed value, for instance 0.5‰ of dry weight or 1% of total nitrogen.
2. This amount should not be found only in roots, stems or leaf stalks but chiefly in the leaf lamina.
3. Nitrate should occur at this level not only in early stages of development but still remain present towards the end of the growing season and the decay of leaves.

Several ruderal plants examined by Bauer (1938) fulfilled the first condition, but the nitrate accumulation was found either in stems or in early stages only. Real “nitrate accumulators” according to our definition were only *Amaranthus retroflexus*, *Chenopodium album*, *Atriplex nitens*, *Sisymbrium altissimum* and perhaps *Hyoscyamus niger*. Jaeniesch (1973) found higher nitrate concentrations in *Anthriscus sylvestris* and *Aegopodium podagraria*, but in the young plants only. Austenfeld (1972) reported decrease of nitrate with age in *Chenopodium album*.

Among the species investigated in our studies *Rumex alpinus* in *K* indicated a slight tendency to nitrate increase in leaf lamina with age, but the amounts were small and the result was not repeated in *S*. Since we found higher nitrate content in the leaf stalks than in the laminae of *Rumex* in *K*, we conclude that the ions delivered are rapidly reduced at the main places of photosynthesis. This was confirmed by subsequent investigations (Gebauer, unpublished) on *Rumex obtusifolius*. In *W* only *Adenostyles alliariae*, a characteristic large-leaved perennial of natural subalpine tall herb communities on moist and fertile soils, showed extremely high nitrate concentrations in the leaves. The somewhat elevated values for *Rumex arifolius* found in *W* were not repeated in *S*. Other species mentioned for *S* tend to decrease nitrate levels towards the end of the growing season and in part they also behave contradictorily to the results of *W*.

Taking the results together, especially those presented in Table 4, we come to the conclusion that it was not possible to observe a real nitrate accumulation anywhere in the typical Rumicetum alpini community. Even less was this

the case in the *Senecio cordatus* community, if we put aside the phenomenon of *Adenostyles alliariae*. So there is no particular nitrate cycle beside the total nitrogen cycle between plant cover and soil to be taken into consideration. This means that there are no significant amounts of nitrate passing the phytomass without reduction and so returning to the soil directly after decay of above-ground plant organs. If such a short circuit did exist an accelerated loss of nitrogen from the ecosystem could be imagined due to less soil absorption of the NO_3 ion compared with that of the NH_4 ion. Since, however, this is not observed, we find an explanation for the result, mentioned already in 1928 by Braun-Blanquet, that *Rumex alpinus* communities remain the same at former cattle resting-places even if the animals have been absent for many decades.

Acknowledgements. These investigations were supported by the Deutsche Forschungsgemeinschaft. The author is also obliged to the cooperators H. Bach, G. Gebauer, A. Holzmayr, F. Kerler, G. Krause, K. Kühner, A. Melzer, V. Möller, M. Müller and M. Olbrich for their various services and to the administrations of the National Reserve of Berchtesgaden and the Conservation Area Schachen (Wetterstein Mts.) for the permission to use the areas and roads.

References

- Austenfeld FA (1972) Untersuchungen zur Physiologie der Nitratspeicherung und Nitrataassimilation von *Chenopodium album*. *Z Pflanzenphysiol* 67:271–281
- Bauer J (1938) Beiträge zur Physiologie der Ruderalpflanzen. *Planta* 28:381–428
- Braun-Blanquet J (1928, 1951, 1964) *Pflanzensoziologie*. Springer, Berlin-Wien-New York
- Bremer JM, Keeney DR (1965) Steam distillation methods for determination of ammonium, nitrate and nitrite. *Anal Chim Acta* 32:485–495
- Ellenberg H (1977) Stickstoff als Standortsfaktor, insbesondere für mitteleuropäische Pflanzengesellschaften. *Oecol Plant* 12:1–22
- Ellenberg H (1978) *Vegetation Mitteleuropas mit den Alpen*. Ulmer Stuttgart
- Gerlach A (1973) Methodische Untersuchungen zur Bestimmung der Stickstoffnettomineralisation. *Scripta Geobotanica*, Bd. 5. Goltze, Göttingen
- Hegnauer R (1962–1973) *Chemotaxonomie der Pflanzen*, Bd. 1–6. Birkhäuser, Basel-Stuttgart
- Jaeniesch P (1973) Ökophysiologische Untersuchungen an Umbelliferen nitrophiler Säume. *Oecol Plant* 8:335–352
- Kronisch R (1975) Zur Stickstoff-Versorgung von Ruderalpflanzen-Gesellschaften in Göttingen. Examination paper, Univ. Göttingen
- Kubiena WL (1953) *Bestimmungsbuch und Systematik der Böden Europas*. Enke, Stuttgart
- Lüdi W (1921) Die Pflanzengesellschaften des Lauterbrunnentales und ihre Sukzession. *Beitr Geobot Landesaufn d Schweiz* 9. Rascher, Zürich
- Marthaler H (1937) Die Stickstoffernährung der Ruderalpflanzen. *Jb wiss Bot* 87:76–106
- Oberdorfer E (1957) *Süddeutsche Pflanzengesellschaften*. Fischer, Jena
- Oberdorfer E (1979) *Pflanzensoziologische Exkursionsflora*. Ulmer, Stuttgart
- Rehder H (1970) Zur Ökologie, insbesondere Stickstoffversorgung subalpiner und alpiner Pflanzengesellschaften im Naturschutzgebiet Schachen (Wettersteingebirge). *Diss Bot*, Bd 6. Cramer, Lehre
- Rehder H (1971) Zum Stickstoffhaushalt alpiner Rasengesellschaften. *Ber dtsh Bot Ges* 84:759–767

- Rehder H (1976) Nutrient turnover studies in alpine ecosystems. I. Phytomass and nutrient relations in four mat communities of the Northern Calcareous Alps. *Oecologia (Berl)* 22:411–423
- Rehder H, Schäfer A (1978) Nutrient turnover studies in alpine ecosystems. IV. Communities of the Central Alps and comparative survey. *Oecologia (Berl)* 34:309–327
- Schröter C (1908) *Das Pflanzenleben der Alpen*. Raustein, Zürich
- Steubing L (1965) *Pflanzenökologisches Praktikum*. Parey, Berlin-Hamburg
- Thayer JR, Huffaker RC (1980) Determination of nitrate and nitrite by high pressure liquid chromatography. – Comparison with other methods for nitrate determination. *Analyt Biochem* 102:110–119
- Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA (1964–1980) *Flora Europaea*, Vol. 1–5. Cambridge University Press, Cambridge

Received March 18, 1982