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# The effects of land-use abandonment on bryophyte and vascular plant vegetation of mountain grasslands
# A case study from the Stubai Valley, Tyrol, Austria

# Die Auswirkungen der Auflassung der agrarischen Nutzung auf Moos- und Gefäßpflanzenvegetation von Almwiesen
# Eine Fallstudie aus dem Stubaital, Tirol, Österreich

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**Schlagwörter:** Auflassung der agrarischen Nutzung, Diversität, Sukzessionsgradient, Zeigerwerte nach LANDOLT, Taxonomische Gruppen, Funktionale Gruppen, Lebensformen, Moose, Gefäßpflanzen.

Key words: land-use abandonment, diversity, successional gradient, LANDOLT indicator values, taxonomic groups, functional groups, life forms, bryophytes, vascular plants.

**Zusammenfassung:** Seit einigen Jahrzehnten unterliegen die Almen im Alpenraum massiven Landnutzungsänderungen, zahlreiche Flächen werden nicht mehr bewirtschaftet. Die Auflassung der agrarischen Nutzung führt zu bedeutenden ökologische Veränderungen, so z.B. einem Biodiversitätsverlust oder, als Folge eines geänderten Wasserhaushalts, auch zu Umweltkatastrophen wie Muren und Überschwemmungen. Die Auswirkungen der Auflassung der agrarischen Nutzung auf Gefäßpflanzen-Gesellschaften wurden intensiv untersucht, wohingegen der Moosvegetation bisher kaum Beachtung geschenkt wurde. Entlang eines Sukzessionsgradienten in der subalpinen Stufe der Zentralalpen wurde auf einer extensiv genutzten Fläche (aktuell beweidet, vor wenigen Jahren jährlich gemäht) und auf drei Brachflächen, ehemals Mähwiesen (Auflassung der agrarischen Nutzung vor 15, 20-30 und 30-40 Jahren) sowohl die Moos- als auch die Gefäßpflanzenvegetation untersucht. Die beobachteten Vegetationsveränderungen wurden hinsichtlich taxonomischer und funktionaler

Gruppen, Lebensformen und Landolt-Zeigerwerten analysiert. Die Moosvegetation wurde durch die Auflassungen stark beeinträchtigt. Sowohl Deckung als auch Diversität waren auf den Brachflächen deutlich geringer, nahmen aber in den älteren Sukzessionsstadien wieder zu. Auf der Weide betrug der Anteil der Moose an der Gesamtdiversität 26%, auf den Brachflächen dagegen nur 9-18%. Es wurde ein starker Artenwechsel beobachtet. Nur vier Arten kamen sowohl auf der Weide als auch auf den Brachflächen vor. Der Anteil der akrokarpen Laubmoose wurde durch die Auflassungen negativ beeinflusst. Bezüglich Gefäßpflanzen wurden die bekannten Effekte beobachtet: in Folge der Auflassung nahm die Diversität ab und Zwergsträucher kamen auf. Die Landolt-Zeigerwerte der Gefäßpflanzen unterschieden sich zum Teil deutlich. Die Wechselfeuchte-Zahl war auf den Brachflächen höher wohingegen die Stickstoff-Zahl auf der Weide höher war. Bezüglich Feuchtezahl konnten keine signifikanten Unterschiede festgestellt werden.

Summary: In the last decades mountain grasslands were subjected to extensive land use changes, many areas are abandoned. Land-use abandonment of mountain grasslands causes considerable ecological consequences, e.g., the loss of high biodiversity or, as a consequence, changed hydrological conditions provoke natural disasters such as landslides or flooding. The effects of land-use abandonment on vascular plants have broadly been studied whereas bryophytes have only been marginally considered until now. At the subalpine zone in the Central Alps bryophyte- as well as vascular plant communities were examined on a extensively managed site (actually grazed, mown annually few years ago) and three abandoned, formerly mown sites representing a successional gradient (abandonment of land-use since 15, 20-30, 30-40 years). The changes observed were analyzed considering functional and taxonomic groups as well as life forms and Landolt indicator values of vascular plants. Abandonment strongly affected the bryophyte communities. Cover as well as diversity was reduced at abandoned sites but tended to increase in the older successional stages. At the pasture bryophytes contributed 26% to total plant diversity, at abandoned sites only 9-18%. High species dynamics were observed. Only four bryophyte species occurred both at the pasture and at the abandoned sites. The fraction of acrocarpous mosses were negatively affected by abandonment. Regarding vascular plants the well-known patterns were observed: as a consequence of abandonment diversity decreased and dwarf shrubs increased. Landolt indicator values differed markedly between the sites. Seasonal moisture values were higher at abandoned sites whereas nutrient values were higher at the pasture. Moisture values did not differ between the sites.

## 1. Introduction

In Tyrol mountain grasslands occupy 6300 km², i.e. nearly 50% of the total area. About 10% of these grasslands are abandoned (PALDELE 1994). The abandonment leads to considerable ecological changes which were the crucial factors for many natural disasters occurring during the last decades (e.g. CONTI & FAGARAZZI 2004).

The ecological consequences of land use changes on mountain grasslands have therefore been broadly studied within many research projects. Altered infiltration and runoff were detected to be main consequences of abandonment (DIETL 1998) leading to soil instability (STEHRER 1987, MÖSSMER 1985), landslides (TASSER et al. 2003, ERTL 1987) and flooding (PALDELE 1994, TASSER et al. 2001). Changes in the hydrology of soils have been attributed to decreased cover and diversity of vascular plants as well as altered macrostructure of vegetation (TASSER et al. 2001).

Bryophytes have only been marginally considered until now, although they are known to have high water storage capacities and fast water uptake. These are important ecological properties especially in mountain climates which are characterized by strong precipitation events with high amounts of water accumulating within a short time. Cover and diversity of bryophytes in mountain grasslands may be considerable.

Studies carried out in Switzerland revealed that traditionally managed subalpine-alpine grasslands belong to the most bryophyte-rich habitats (KOORDINATIONSSTELLE BIODIVERSITÄTS-MONITORING SCHWEIZ 2009). In the Swiss bryophyte inventory, even more than 60 bryophyte species were found on a 10x10 m plot on a subalpine meadow (unpublished data). Abandoned areas, however, are usually poor in bryophyte species (for abandoned fens, e.g., PEINTINGER & BERGAMINI 2006). So far, data concerning Tyrol are scarce.

The contribution of bryophytes to total plant diversity is high (DENGLER 2009), thus plant diversity studies should definitely include them. In Austria, the actual number of confirmed bryophyte taxa is 1102 (KÖCKINGER et al. 2010) and the proportion of endangered bryophyte species is even slightly higher (41.9%) than the proportion of endangered vascular plants (40.2%, NIKLFELD 1999). Furthermore, bryophytes have high ecological significance as they behave differently from vascular plants (SHAW & GOFFINET 2000). Especially species-environment and species-area relationships deviate strongly between vascular plants and bryophytes (HERBEN 1987, LÖBEL et al. 2006). Bryophytes respond more quickly to changed conditions (AUSTRHEIM et al. 2007) and therefore have high indicative value.

The abandonment of mountain grasslands causes changes in the structure, the chemistry and the hydrological properties of the soils (BITTERLICH et al. 1999, SALCHNER 1997), which result in altered ecological conditions. Indicator values are an appropriate instrument for assessing ecological conditions indirectly (LANDOLT 1977, ELLENBERG 1996). KLEIN (2010) as well as TASSER et al. (1999) showed that on abandoned mountain grasslands, Ellenberg indicator values coincide well with the altered ecological conditions. Landolt indicator values are mainly based on the first two editions of Ellenberg's indicator values (LANDOLT 1977).

It is the purpose of this study to examine the effects of abandonment of land-use of mountain grasslands along a successional gradient considering 1) bryophyte vegetation regarding cover, diversity and taxonomic groups, 2) vascular plant vegetation regarding cover, diversity, major functional groups and life forms and 3) Landolt indicator values (moisture, seasonal moisture, nutrients, and soil reaction) of vascular plants.

## 2. Methods

### 2.1. Study area

The study area is located at the Kaserstattalm (E 11°18'07.18''; N 47°07' 40.22''), Stubai Valley, Tyrol, Austria. The climate of the region is described as temperate-continental inner-alpine (FLIRI 1983). Mean annual precipitation amounts to around 1100 mm, mean annual temperatures are around 3° C (Hydrographical Service, Tyrolean Regional Government). The parent rock material consists of siliceous rocks (gneiss, paragneiss) intermingled with limestone material deriving from alkaline strata higher up

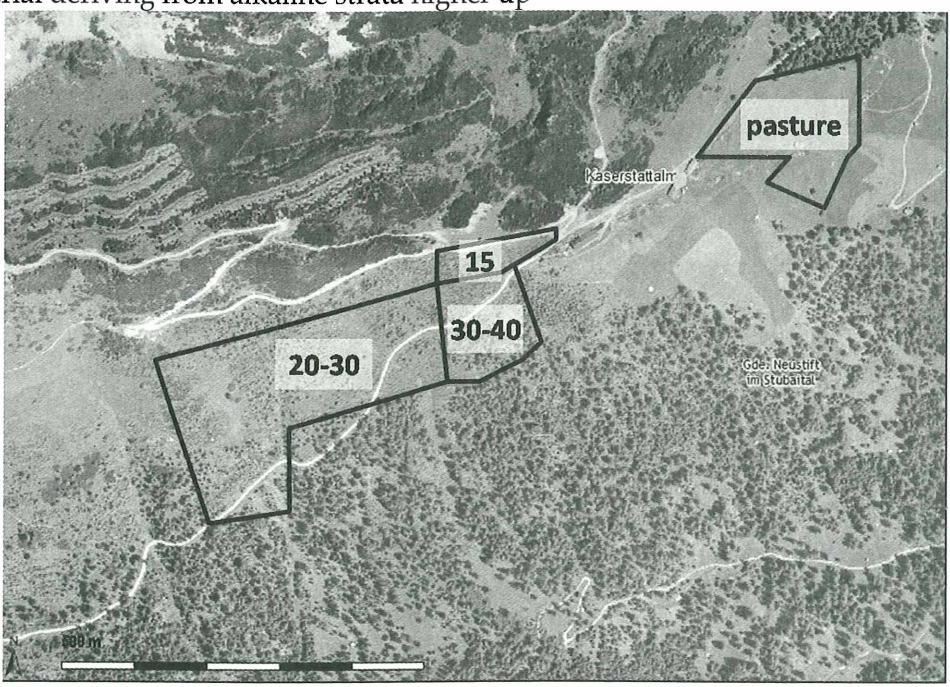


Fig. 1: The study area: Kaserstattalm, Stubai Valley, Tyrol, Austria. Numbers indicate the years since abandonment of land-use of the three abandoned sites. Orthofoto: ©2010 Amt der Tiroler Landesregierung, Abteilung Geoinformation.

Four sites, a pasture and three abandoned sites representing different stages of abandonment (abandoned for 15 years, abandoned for 20-30 years,

abandoned for 30-40 years) were selected (Fig. 1). The sites are situated between 1870 and 1920 m a.s.l.. The predominant soil types are brown earths, which are partly podzolized at the abandoned sites. The pasture is grazed by cattle and sheep. A few years ago it still had been mown annually. In addition to the excrements of the grazing animals, this site is fertilized with dung. Given the spotty application, it is hard to quantify the amount applied per unit of area every year. Most probably, the site had also been fertilized at times when it still had been mown annually. The abandoned sites were extensively managed formerly; in 1954, they were mown every two years (MUNK 2003). It is fair to assume that temporarily they were also grazed. *Trisetetum flavescentis* Rübel 1911 (MUCINA et al. 1993) is the vegetation type developed at the pasture. The vegetation of the abandoned sites is difficult to classify. Elements from the former grassland as well as from dwarf shrubs communities and in the older stages elements associated with the expected climax vegetation, the *Vaccinio-Pinetum cembrae* (Pallmann & Haffter 1933) Oberd. 1962. (WILLNER & GRABHERR 2007) occur. Table 1 provides further information on the sites.

Tab. 1: Location, altitude, exposition and description of the study sites.

| Years since land-use abandonment | Location | | Altitude (m a.s.l.) | Exposition | Description |
|---|---|---|---|---|---|
| | E | N | | | |
| 0 (pasture) | 47.12909° | 11.30405° | 1882 | SW | pasture; grazed by cattle and sheep, fertilized with dung |
| 15 | 47.12693° | 11.29832° | 1920 | SSW | open grassland with scattered *Larix decidua* and *Pinus cembra* (height about 1.5 m) |
| 20-30 | 47.12604° | 11.29547° | 1890 | SSW | open grassland with scattered *Larix decidua* and *Pinus cembra* (height about 3-4 m) |
| 30-40 | 47.12602° | 11.29822° | 1870 | SSW | open forest with *Larix decidua* and *Pinus cembra* (height about 10-15 m) |

## 2.2. Data collection

The field work was carried out between August and October 2010. The abundance of bryophyte species as well as of higher plant species were analysed by performing vegetation relevés according to BRAUN-BLANQUET (1964) with the extended scale after REICHELT & WILMANNS (1973) in 1x1 m plots. Total plant cover, cover of the herb layer and cover of the bryophyte layer were estimated. Altitude and exposition were recorded. Five plots per site were examined. The first plot was placed in the centre of the site and the other four in a distance of 10 m in the four directions following the slope. Special habitats like stones, wet

hollows or tree trunks were excluded. In case a plot was situated on such a habitat it was shifted for further 5 m in the same direction. Species undeterminable in the field were collected and determined in the laboratory.

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### 2.3. Data analyses

Altitude and exposition vary marginally between sites and plots, thus they were not included in the analyses. The vegetational changes along the successional gradient were analysed following a functional-taxonomic approach. Species were classified in bryophytes, graminoids, herbs and dwarf shrubs. Bryophytes were subclassified in liverworts, acrocarpous mosses and pleurocarpous mosses. Additionally, for vascular plants a second classification regarding life forms was used by grouping species in annuals, biennials, cryptophytes, hemicryptophytes, herbaceous chamaephytes and woody chamaephytes (dwarf shrubs).

For all statistical analyses Braun-Blanquet abundance values were transformed using Van der Maarel-Transformation (VAN DER MAAREL 1979). Cover values of graminoids, herbs and dwarf shrubs were calculated from the abundance data of the single species. In order to detect differences between the four sites regarding cover and diversity of taxonomic groups, functional groups and life forms Permutation Tests (10.000*) for independent samples were applied. The same test was applied for the Landolt indicator values (LANDOLT 1977) of vascular plants moisture, seasonal moisture, nutrients and soil reaction. In addition, canonical correspondence analysis (CCA) and detrended correspondence analysis (DCA) were applied. To test whether the four sites can be separated by changes in bryophyte vegetation, a first CCA was performed based on abundance data of bryophyte species and using Landolt indicator values (seasonal moisture, nutrients and soil reaction) of vascular plants as environmental variables. The moisture value was detected to be insignificant by Monte Carlo permutation test (1999 unrestricted permutations) and thus excluded. To test how the taxonomic groups (acrocarpous mosses, pleurocarpous mosses and liverworts) are arranged along the successional gradient, a second CCA based on abundance data of bryophyte species was performed, including time since abandonment as an environmental variable. To test whether the four sites can be separated by changes in vascular plant vegetation, DCA was performed based on abundance data of vascular plant species. For CCA and DCA data were transformed using square-root-transformation and rare species were downweighted.

Correlations between time since abandonment, Landolt indicator values of vascular plants, bryophyte vegetation and the cover of the herb layer were tested with Spearman Rho.

The permutation tests were carried out with the program VEGEDAZ (KÜCHLER 2009). CCA and DCA were carried out using the statistical software

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CANOCO 4.5 (BRAAK & ŠMILAUER 1998) and correlation analyses were performed with PASW Statistics 18.

The analyses revealed that the alkalinity of three plots was considerably higher compared to all the other plots. Due to the low number of total plots, these plots were not excluded from the analyses.

## 3. Results

Total plant cover differed markedly between sites (Table 2). It was highest at the first stage of abandonment (15 years) with a mean value of 98.6 %. At the pasture it was 76.0 %, at the site abandoned for 20-30 years 96.0 % and at the site abandoned for 30-40 years 67.0 %. At all sites total plant cover was mainly formed by the cover of the herb layer (Table 2, 3).

In total, 117 species were recorded. At the pasture the total number of species per relevé was significantly higher than at the abandoned sites. The mean number of species per 1 $m^2$ at the pasture was 32.8 (vascular plants: 24.4; bryophytes: 8.4). Within abandoned sites no significant differences regarding total species number were detected between the different stages of abandonment. Mean total species number at abandoned sites varied between 21.6 and 23.2 (vascular plants: 17.6 - 21.0; bryophytes: 2.2 - 4.0; Table 2, 3).

### 3.1. Bryophytes

The cover of bryophytes was significantly higher at the pasture than at the abandoned sites (Table 2). At the abandoned sites, cover tended to increase with time since abandonment. At the first two stages of abandonment (15 and 20-30 years), the cover of bryophytes was extremely low in many plots, often obtaining only 0.1 %. In two plots of the site abandoned for 15 years, no bryophytes could be found at all.

Bryophyte diversity was significantly higher at the pasture. The number of bryophyte species as well as the fraction of bryophyte species of total species number per 1 $m^2$ was significantly higher compared to abandoned sites. Within abandoned sites, these values tended to increase with time since abandonment. Regarding taxonomic groups, the fraction of acrocarpous mosses was higher at the pasture compared to the abandoned sites. A negative correlation was calculated between the number of acrocarpous moss species and time since abandonment (Table 4). For pleurocarpous mosses, no pattern could be detected. Liverworts were rare, i.e. they were present only within two plots. Only three species were recorded.

Tab. 2: Total plant cover and bryophyte vegetation at a pasture and three abandoned sites (abandonment of land-use since 15, 20-30 and 30-40 years). Permutation Tests (10.000*) for independent samples. Mean values (*m*) ± standard deviation and level of significance (*p*), *p*-values < 0.05 in bold.

| | | | Years since abandonment | | |
|---|---|---|---|---|---|
| | | **pasture** | **15** | **20-30** | **30-40** |
| **Total plant cover [%]** | *m* | 76.0 ± 17.1 | 98.6 ± 2.2 | 96.0 ± 4.2 | 67.0 ± 10.9 |
| | *p* | **0.044** | **0.005** | **0.049** | **0.003** |
| **Cover of bryophyte layer [%]** | *m* | 4.40 ± 3.5 | 1.28 ± 2.6 | 1.86 ± 2.4 | 2.68 ± 5.8 |
| | *p* | **0.020** | 0.107 | 0.450 | 0.302 |
| **Diversity [number of species]** | | | | | |
| Bryophytes | *m* | 8.4 ± 1.1 | 2.2 ± 2.3 | 3.2 ± 1.6 | 4 ± 2.7 |
| | *p* | **0.000** | **0.037** | 0.190 | 0.375 |
| Acrocarpous mosses | *m* | 5 ± 1.0 | 0.8 ± 1.1 | 0.8 ± 0.8 | 1 ± 0.0 |
| | *p* | **0.000** | 0.070 | 0.119 | 0.260 |
| Pleurocarpous mosses | *m* | 3.2 ± 0.8 | 1.4 ± 1.3 | 2.4 ± 1.7 | 2.6 ± 2.1 |
| | *p* | 0.087 | 0.059 | 0.440 | 0.385 |
| Liverworts | *m* | 0.2 ± 0.4 | 0 ± 0.0 | 0 ± 0.0 | 0.4 ± 0.9 |
| | *p* | 0.440 | 0.552 | 0.557 | 0.242 |
| **Fraction of bryophytes in % of the total species number** | *m* | 26 ± 3 | 9 ± 8 | 15 ± 15 | 18 ± 13 |
| | *p* | **0.006** | **0.022** | 0.322 | 0.498 |
| **Fraction of taxonomic groups in % of total bryophyte species number** | | | | | |
| Acrocarpous mosses | *m* | 59 ± 6 | 18 ± 25 | 27 ± 30 | 41 ± 36 |
| | *p* | **0.009** | **0.034** | 0.260 | 0.392 |
| Pleurocarpous mosses | *m* | 38 ± 10 | 42 ± 43 | 73 ± 30 | 53 ± 32 |
| | *p* | 0.074 | 0.301 | 0.055 | 0.372 |
| Liverworts | *m* | 2 ± 6 | 0 ± 0 | 0 ± 0 | 5 ± 11 |
| | *p* | 0.436 | 0.541 | 0.546 | 0.256 |

Tab. 3: Functional groups and life forms of vascular plants at a pasture and three abandoned sites (abandonment of land-use since 15, 20-30 and 30-40 years). Permutation Tests (10.000*) for independent samples. Mean values (*m*) ± standard deviation and level of significance (*p*), *p*-values < 0.05 in bold.

| | | Years since abandonment | | | |
|---|---|---|---|---|---|
| | | **0 (pasture)** | **15** | **20-30** | **30-40** |
| **Cover [%]** | | | | | |
| Herb layer | *m* | 75.0 ± 18.4 | 98.6 ± 2.2 | 96.0 ± 4.2 | 67.0 ± 10.9 |
| | *p* | **0.046** | **0.004** | 0.050 | **0.004** |
| Graminoids | *m* | 19.8 ± 3.3 | 17 ± 9.6 | 21.8 ± 8.4 | 21.6 ± 5.9 |
| | *p* | 0.454 | 0.087 | 0.253 | 0.286 |
| Herbs | *m* | 52 ± 5.5 | 35 ± 4.6 | 23 ± 7.0 | 25.4 ±11.1 |
| | *p* | **0.000** | 0.310 | **0.013** | 0.054 |
| Dwarf shrubs | *m* | 0.0 ± 0.0 | 7.6 ± 4.4 | 13.4 ± 6.3 | 4.4 ± 3.2 |
| | *p* | **0.000** | 0.213 | **0.003** | 0.410 |
| **Fraction of functional groups** | | | | | |
| Graminoids | *m* | 20 ± 2 | 21 ± 11 | 27 ± 11 | 25 ± 7 |
| | *p* | 0.297 | 0.132 | 0.191 | 0.215 |
| Herbs | *m* | 54 ± 04 | 61 ± 9 | 43 ± 5 | 49 ± 10 |
| | *p* | 0.182 | **0.011** | **0.003** | 0.284 |
| Dwarf shrubs | *m* | 0 ± 0 | 10 ± 3 | 15 ± 8 | 7 ± 2 |
| | *p* | **0** | 0.079 | **0.022** | 0.420 |
| **Diversity [number of species]** | | | | | |
| Total (including bryophytes) | *m* | 32.8 ± 3.1 | 23.2 ± 4.7 | 22.6 ± 4.8 | 21.6 ± 6.2 |
| | *p* | **0.000** | 0.249 | 0.116 | 0.129 |
| Vascular plants | *m* | 24.4 ± 2.5 | 21 ± 3.5 | 19.4 ± 5.2 | 17.6 ± 6.2 |
| | *p* | **0.024** | 0.468 | 0.211 | 0.110 |
| **Fraction of life forms in % of** | | | | | |
| Dwarf shrubs | *m* | 0 ± 0 | 14 ± 5 | 22 ± 11 | 11 ± 5 |
| | *p* | **0.000** | 0.108 | **0.022** | 0.484 |
| Herbaceous chamaephytes | *m* | 6 ± 1 | 4 ± 3 | 0 ± 0 | 0 ± 0 |
| | *p* | **0.005** | 0.120 | **0.049** | 0.052 |
| Hemicryptophytes | *m* | 84 ± 4 | 79 ± 6 | 78 ± 11 | 87 ± 4 |
| | *p* | 0.342 | 0.121 | 0.241 | 0.070 |
| Cryptophytes | *m* | 3 ± 4 | 3 ± 4 | 0 ± 0 | 0 ± 0 |
| | *p* | 0.173 | 0.178 | 0.288 | 0.274 |
| Annuals | *m* | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| | *p* | 1 | 1 | 1 | 1 |
| Biennials | *m* | 7 ± 2 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| | *p* | **0.000** | 0.190 | 0.197 | 0.193 |

Tab. 4: Spearman RHO correlation analysis between bryophyte vegetation (cover, number of species and fraction of taxonomic groups), time since abandonment and the cover of the herb layer at a pasture and three abandoned sites (abandonment of land-use since 15, 20-30 and 30-40 years). B bryophytes, A acrocarpous mosses, P pleurocarpous mosses, L liverworts, T species total (including vascular plants); *p*-values < 0.05 in bold.

| | Cover | No. B | No. A | No. P | No. L | Fraction B/T | Fraction A/B | Fraction P/B | Fraction L/B |
|---|---|---|---|---|---|---|---|---|---|
| **Time since abandonment** | | | | | | | | | |
| Coefficient of correlation | -.301 | -.422 | -.536 | -.075 | .022 | -.272 | -.228 | .359 | .022 |
| *p* (2 sided) | .197 | .064 | **.015** | .754 | .926 | .247 | .335 | .120 | .926 |
| N | 20 | 20 | 20 | 20 | 20 | 20 | 20 | 20 | 20 |
| **Cover of herb layer** | | | | | | | | | |
| Coefficient of correlation | -.216 | -.454 | -.428 | -.359 | -.121 | -.395 | -.433 | .009 | -.121 |
| *p* (2 sided) | .360 | **.044** | .060 | .121 | .611 | .084 | .057 | .971 | .611 |
| N | 20 | 20 | 20 | 20 | 20 | 20 | 20 | 20 | 20 |

The total number of bryophyte species recorded in the plots at the pasture was 14, comprised of seven acrocarpous mosses, six pleurocarpous mosses and one liverwort. At the sites abandoned for 15 and 20-30 years the total number of species was nine. In each case three of them were acrocarpous mosses and six were pleurocarpous mosses. At the stage abandoned for 30-40 years two acrocarpous mosses, five pleurocarpous mosses and two liverworts (nine species in total) were recorded. At the pasture, bryophyte species contributed 26 % to the total number of plant species whereas at the site abandoned for 15 years, they added only 9 % (Table 2).

The number of bryophyte species was negatively correlated with the cover of the herb layer. The number of acrocarpous mosses and the ratio of acrocarpous mosses to total bryophyte species were marginally negatively correlated with the cover of the herb layer (Table 4).

The CCA based on abundance data of bryophyte species clearly separated the pasture site from the abandoned sites along the first ordination axis (Fig. 2). The different stages of abandonment were not clearly grouped. The plots six and seven which show high soil reaction values were separated along the second axis.

The composition of the bryophyte vegetation differed considerably between the pasture and abandoned sites (Fig. 3). One group of species, including many short-living acrocarpous mosses like *Weissia controversa, Bryoerythrophyl-*

*lum recurvirostrum* or *Dicranella varia*, was present only at the pasture whereas other species were limited to the abandoned sites. Most species limited to the abandoned sites were layer-, cushion- or bank-forming mosses including many pleurocarpous mosses like *Rhytidiadelphus triquetrus, Hylocomium splendens, Brachythecium velutinum, B. starkei.* Only four out of 29 species were recorded at the pasture as well as at the abandoned sites: *Brachythecium glareosum, B. salebrosum, Fissidens dubius* and *Plagiomnium rostratum. B. salebrosum* and *P. rostratum* were frequent in all plots at the pasture whereas at abandoned sites they occurred only in a few plots; in three respectively two plots out of 15. *B. glareosum* occurred in one plot at the pasture and in two plots at abandoned sites, *F. dubius* occurred in one plot at the pasture and in one at abandoned sites.

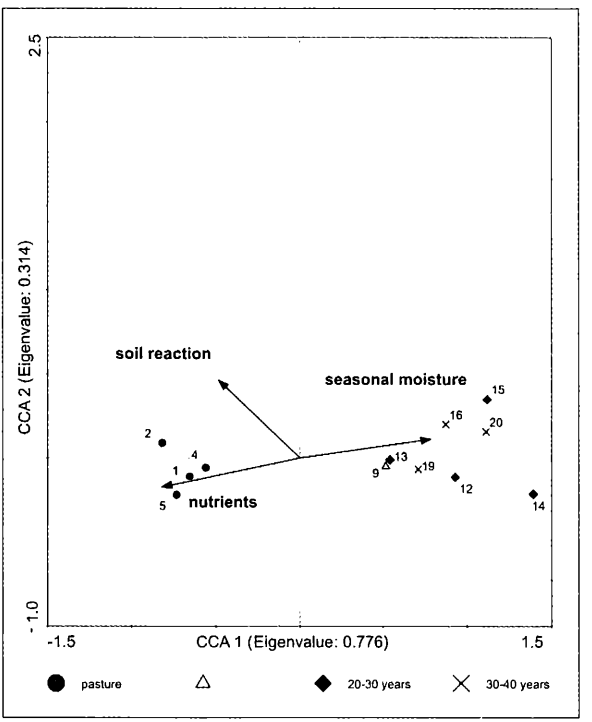


Fig. 2: CCA ordination diagram of 18 plots examined at a pasture and three abandoned sites (abandonment of land-use since 15, 20-30, and 30-40 years) based on the abundance of bryophyte species. The environmental variables are based on the Landolt indicator values of vascular plants.

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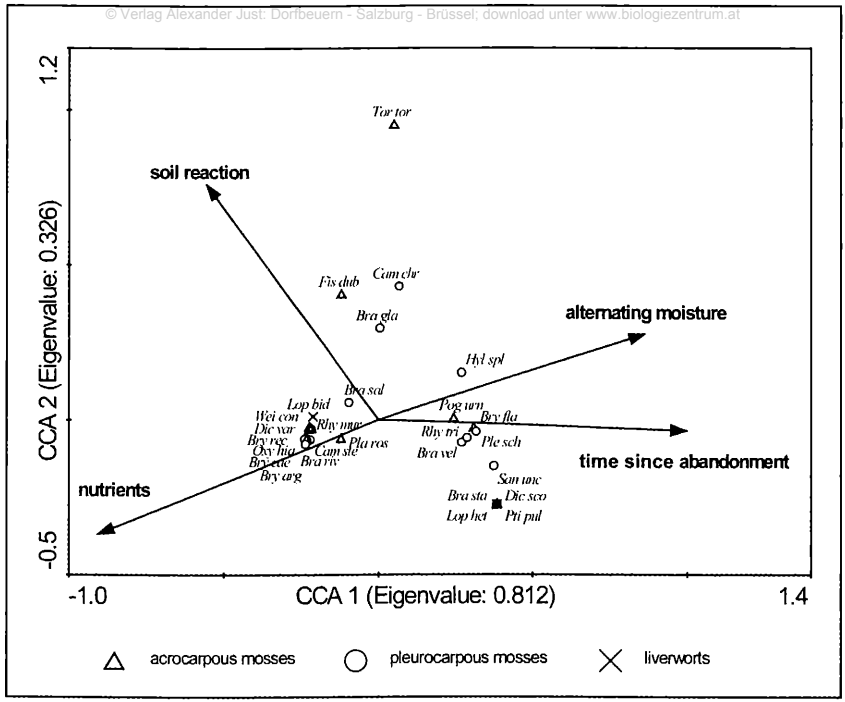


Fig. 3: CCA ordination diagram based on the abundance of bryophyte species from 20 plots from four sites. The four sites represent a successional gradient: a pasture and three abandoned sites (abandonment of land-use since 15, 20-30, and 30-40 years). The environmental variables are based on the Landolt indicator values of vascular plants. Species: *Bra gla Brachythecium glareosum, Bra riv Brachythecium rivulare, Bra sal Brachythecium salebrosum, Bra sta Brachythecium starkei, Bra vel Brachythecium velutinum, Bry rec Bryoerythrophyllum recurvirostre, Bry arg Bryum argenteum, Bry cae Bryum caespiticium, Bry fla Bryum flaccidum, Cam chr Campylium chrysophyllum, Cam ste Campylium stellatum, Dic var Dicranella varia, Dic sco Dicranum scoparium, Fis dub Fissidens dubius, Hyl spl Hylocomium splendens, Lop bid Lophocolea bidentata, Lop het Lophocolea heterophylla, Oxy hia Oxyrrhynchium hians, Pla ros Plagiomnium rostratum, Ple sch Pleurozium schreberi, Pog urn Pogonatum urnigerum, Pti pul Ptilidium pulcherrimum, Rhy mur Rhynchostegium murale, Rhy tri Rhytidiadelphus triquetrus, San unc Sanionia uncinata, Tor tor Tortella tortuosa, Wei con Weissia controversa.*

### 3.2. Vascular plants

The cover of the herb layer differed markedly between sites, being extremely high (98.6 %) at the site abandoned for 15 years and decreasing at the older successional stages. At the pasture, the value was 75.0 %. The cover of herbs was significantly higher at the pasture. The value was 52.0 % at the pas-

ture compared to 35.0, 23.0 and 25.4 % at the sites abandoned since 15, 20-30 and 30-40 years. Concerning the cover of graminoids no differences could be detected: the value ranged around 20 % at all sites. Dwarf shrubs were only present at the abandoned sites. The cover of dwarf shrubs was highest at the site abandoned for 20-30 years with a mean value of 13.4 % (Table 3).

At the pasture, the mean number of vascular plant species was significantly higher than at abandoned sites. No differences regarding the number of species were detected between the different stages of abandonment.

Herbaceous chamaephytes and cryptophytes were recorded only at the pasture and at the site abandoned for 15 years, biennial species only at the pasture. The fraction of hemicryptophytes of total number of vascular plants did not differ considerably between sites. No annual species were found at any site. For details see Table 3.

Fig. 4 shows the DCA ordination diagram of the plots based on the abundance data of vascular plant species. The analysis clearly separated the pasture from abandoned sites along the first ordination axis. The plots no. 6, 7 and 8 were separated along the second axis.

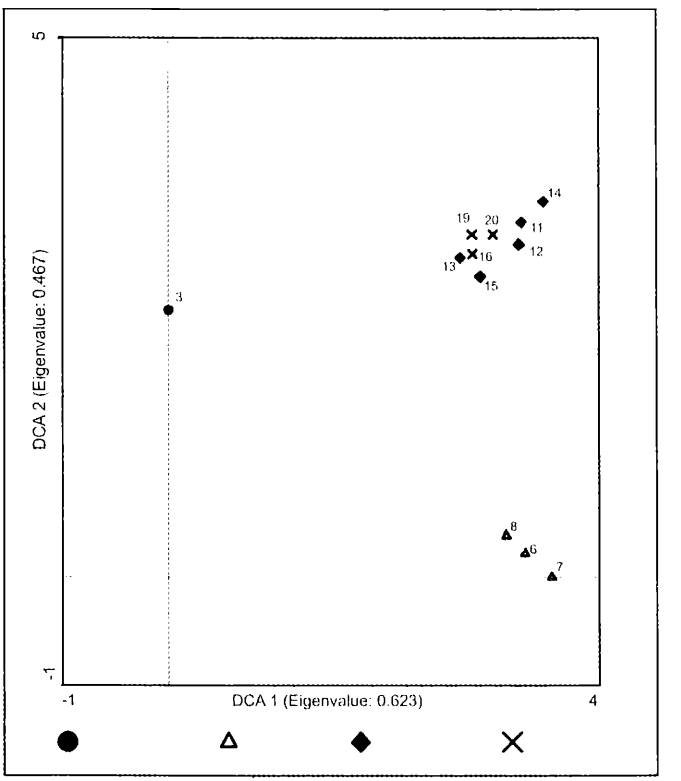


Fig. 4: DCA ordination diagram of 20 plots examined at a pasture and three abandoned sites (abandonment of land-use since 15, 20-30, and 30-40 years) based on the abundance of vascular plant species.

### 3.3. Landolt indicator values

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No significant differences in moisture values of vascular plants could be detected (Tables 5, 6). Seasonal moisture values were higher at abandoned sites compared to the pasture, being highest at the site abandoned for 20-30 years. Nutrient values were significantly higher at the pasture compared to abandoned sites. They tended to decrease with time since abandonment. Soil reaction values varied significantly between all sites and were highest at the site abandoned for 15 years (Table 5). Three of the plots of this site had considerably higher values (3.71, 3.87, and 3.81) than all other plots. The distinctness of these plots (no. 6, 7, and 8) was also detected by CCA and DCA analyses (Fig. 2, 4).

Correlation analysis revealed negative correlations between nutrient and soil reaction values and time since abandonment. Regarding seasonal moisture, a positive correlation with time since abandonment was found (Table 6).

Tab. 5: Landolt indicator values of vascular plants at a pasture and three abandoned sites (abandonment of land-use since 15, 20-30 and 30-40 years). Permutation Tests (10.000*) for independent samples. Mean values (*m*) ± standard deviation and level of significance (*p*), *p*-values < 0.05 in bold.

| **Landolt indicator value** | | **Years since abandonment** | | | |
|---|---|---|---|---|---|
| | | **0 (pasture)** | **15** | **20-30** | **30-40** |
| moisture | *m* | 2.75 ± 0.07 | 2.57 ± 0.26 | 2.79 ± 0.06 | 2.78 ± 0.08 |
| | *p* | 0.393 | 0.168 | 0.207 | 0.340 |
| seasonal moisture | *m* | 0.12 ± 0.04 | 0.31 ± 0.04 | 0.36 ± 0.06 | 0.32 ± 0.06 |
| | *p* | **0.000** | 0.288 | **0.028** | 0.233 |
| nutrients | *m* | 2.87 ± 0.17 | 2.27 ± 0.28 | 2.24 ± 0.10 | 2.19 ± 0.04 |
| | *p* | **0.001** | 0.057 | 0.304 | 0.153 |
| soil reaction | *m* | 2.88 ± 0.06 | 3.37 ± 0.59 | 2.50 ± 0.21 | 2.49 ± 0.19 |
| | *p* | **0.044** | **0.013** | **0.027** | **0.023** |

Tab. 6: Spearman RHO correlation analysis between Landolt indicator values of vascular plants and time since abandonment at a pasture (time since abandonment = 0) and three abandoned sites (abandonment of land-use 15, 20-30 and 30-40 years); *p*-values < 0.05 in bold.

| Landolt indicator value | moisture | nutrients | seasonal moisture | soil reaction |
|---|---|---|---|---|
| **Years since abandonment** Coefficient of correlation | .183 | -.535 | .602 | -.698 |
| *p* (2 sided) | .441 | **.015** | **.005** | **.001** |
| N | 20 | 20 | 20 | 20 |

## 4. Discussion

### 4.1. Bryophytes

The bryophyte vegetation was strongly affected by abandonment of land use. The cover of bryophytes was found to be reduced at abandoned sites. Previous studies revealed comparable effects. PEINTINGER & BERGAMINI (2006) showed that the bryophyte biomass was twofold lower in abandoned than in mown montane fens in Switzerland. HUHTA et al. (2001) found an increase in the cover of bryophytes on a formerly grazed, abandoned meadow after restorative mowing. Similar responses to restorative mowing were observed by BILLETER et al. (2007) on mountain fen meadows in Switzerland.

The crucial factor limiting bryophyte growth at abandoned sites might be light. BERGAMINI et al. (2001) found that bryophyte biomass decreased with increasing vascular plant biomass, indicating that bryophyte growth is light-limited. The same was shown by MAYER et al. (2009) in subalpine and alpine grasslands after seven years of grazing exclusion. Equally BILLETER et al. (2007) suggested that in mown plots, bryophytes benefit from improved light conditions compared to unmanaged plots. The accumulation of death plant material is a second factor responsible for reducing light intensity at the soil surface. Pronounced litter accumulation at abandoned sites compared to managed grassland at the study area has already been reported by BITTERLICH et al. (1999), which coincides with my observations in the field. The crucial influence of litter on bryophyte density has been shown by PEITINGER & BERGAMINI (2006).

Summing up, the cover of bryophytes on mountain grasslands seems to be positively affected by management due to improved light conditions caused by the removal of vascular plant material. Moisture might play an additional role since soils at abandoned sites compared to pastures are characterized by higher water conductance and lower water storage capacity (BITTERLICH et al.

1999, SALCHNER 1997), leading to faster and stronger dehydration of upper soil layers (SALCHNER 1997).

The diversity of bryophytes was significantly reduced at abandoned sites. The number of bryophyte species as well as the fraction of bryophyte species of total species number were highest at the pasture and increased with time since abandonment. These results coincide with studies performed in mountain fen meadows where equally the diversity was highest at managed sites, considerably lower at abandoned sites but increasing in the older successional stages (PEINTINGER & BERGAMINI 2006). Likewise HUHTA et al. (2001) found a decrease in bryophyte diversity in a six year-abandonment experiment on a meadow in the boreal vegetation zone.

Contrasting results revealed by two previous studies should however, not be neglected: MASKOVA et al. (2009) recorded a slight increase of bryophyte diversity in mountain meadows of the Czech Republic after 10 years of abandonment (10 species at a fallow compared to eight at a mown site). Furthermore, in a five year long sheep-grazing exclusion experiment in the low alpine zone of Norway bryophyte species richness was reported to be unaffected (AUSTRHEIM et al. 2007). Nonetheless, in the latter study a certain level of disturbance was maintained due to rodent grazing. The positive effects of disturbances caused by management on bryophyte diversity have already been ascertained by various studies (e.g. BERGAMINI et al. 2001). PRESTON et al. (2009) demonstrated an increase of bryophyte diversity caused by disturbance considering also other forms of impacts.

In this study, special habitats like stones, wet hollows or tree trunks were excluded, thus only α-diversity was considered. Overall diversity of the sites is expected to be by far higher when such frequent habitats of mountain grasslands are included.

At the abandoned sites, the diversity of bryophytes and the diversity of vascular plants showed opposing trends. Bryophyte diversity increased in the older stages whereas vascular plant diversity tended to decrease. Bryophytes, especially woodland species, have lower compensation points than vascular plants (FRAHM 2001), consequently at older successional stages they benefit from reduced vascular plant cover within the herb layer caused by shading trees. Due to the dispersion by spores and small propagules the typical forest species are able to recolonize abandoned areas quickly. Moreover at special habitats of the pasture, e.g., in the vicinity of stones I noticed some of the typical forest species (e.g. *Hylocomium splendens*) which were not present within the plots.

Regarding species composition, high species dynamics were detected. Only four out of 29 species occurred both at the pasture and at the abandoned sites. PEINTINGER & BERGAMINI (2006) reported high species dynamics comparing mown and abandoned fen meadows. In other studies regarding shorter time intervals since abandonment, species dynamics were less pronounced and the

changes were partly limited to the frequency and abundance level of the species (AUSTRHEIM et al. 2007, HUHTA et al. 2001, MASKOVA et al. 2009).

The current study revealed a significant decrease of acrocarpous mosses at abandoned sites. It is suggested that this is due to the fact that a high portion of acrocarpous mosses consists of short-living species with good colonizing abilities (*r*-strategists sensu OKSANEN & RANTA 1992, colonists sensu DURING 1992). In contrast most pleurocarpous mosses are persisting long-lived species (*K*-strategists sensu OKSANEN & RANTA 1992, perennials sensu DURING 1992). *r*-strategists depend on disturbance and are thus favoured by management. The most frequent pleurocarpous mosses at the pasture *Brachythecium salebrosum* and *Oxyrrhynchium hians* also belong to this functional group. Following the classification of DURING (1992), they are pioneer colonists whereas the most frequent pleurocarpous mosses at abandoned sites *Rhytidiadelphus triquetrus, Pleurozium schreberi* and *Hylocomium splendens* are competitive perennials (DIERßEN 2001). HUHTA et al. (2001) found comparable effects. In a restorative mowing experiment species with good colonizing abilities increased whereas cover-, cushion- or bank-forming mosses decreased in mown plots. However, partly contrasting results were observed under harsh environmental conditions. In the low alpine zone of Norway short-lived colonizers were favoured by the exclusion of sheep grazing (AUSTRHEIM et al. 2007) whereas typical forest species were favoured by exclusion in accordance with the results of this study.

### 4.2. Vascular plants

The effect of abandonment of mountain pastures and meadows on vascular plant vegetation has been broadly studied and discussed in many publications. Hence, the results regarding vascular plants will not be discussed in detail. The main effects observed are in line with previous studies. Abandoned sites are characterized by the appearance of dwarf shrubs and a reduction in diversity (CERNUSCA et al. 1992, NIEDRIST 2006, SPATZ et al. 1978, TASSER et al. 2001, TASSER et al. 1999). Light demanding and weakly competitive species disappear whereas competitive species with mainly clonal propagation become dominant (MASKOVA et al. 2009, NIEDRIST 2006, SPATZ 1994, TAPPEINER & CERNUSCA 1993, TASSER & TAPPEINER 2002, TASSER et al. 2001, ZOLLER et al. 1984).

### 4.3. Landolt indicator values

The decrease of nutrient values at abandoned sites reflects the fact that in contrast to the pasture, abandoned sites are not fertilized. KLEIN (2010) and TASSER et al. (1999) also reported a decrease of nutrient values at abandoned sites in comparison with managed grassland. On abandoned sites, nutrient supply mainly depends on litter decomposition (TASSER et al. 1999). Litter quality is

lower (higher proportion of hardly decomposed material) at abandoned areas compared to managed grasslands (BITTERLICH et al. 1999, TASSER et al. 2001). Hence, the decomposition of dead plant material is slow (CERNUSCA et al. 1992) leading to litter accumulation (BITTERLICH et al. 1999, TASSER et al. 2001).

Regarding indicator values for soil reaction, previous studies reported that they clearly decrease with abandonment (KLEIN 2010, TASSER et al. 1999). Decreasing alkalinity at abandoned areas is also supported by pH-measurements of soils (BITTERLICH et al. 1999, TASSER et al. 2001). Except for the site abandoned for 15 years this pattern could also be proven by the current study. The site abandoned for 15 years is the side closest and most exposed to the calcareous strata located above the study area. It is suggested that a higher input of alkaline rock material is responsible for the considerably higher soil reaction values observed at this site, especially within the plots no. 6, 7 and 8.

No differences in moisture values between the pasture and the abandoned sites were detected. However, KLEIN (2010) reported marginally lower values at abandoned sites compared to meadows and pastures at the Kaserstattalm.

The seasonal moisture value was significantly increased at abandoned sites. Compared to meadows and pastures, soils at abandoned areas have more air and water conducting large pores due to lower mechanical impact and an increase of root biomass (BITTERLICH et al. 1999, GISI et al. 1990). As a consequence, water is quickly transported to lower strata. Furthermore, soils of abandoned areas are characterised by lower water storage capacity and fewer medium-sized pores (TASSER et al. 2001, BITTERLICH et al. 1999). Hence, soils are less capable of storing water available for plants. These properties lead to faster and stronger dehydration of the upper soil layers (SALCHNER 1997) which is suspected to be the reason for the observed increase of species indicating seasonal moisture at abandoned sites.

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