Investigations on Spatial Heterogeneity of Humus Forms and Natural Regeneration of Larch (*Larix decidua Mill.*) and Swiss Stone Pine (*Pinus cembra L.*) in an Alpine Timberline Ecotone (Upper Engadine, Central Alps, Switzerland)

Bettina Hiller, Andreas Müterthies, Friedrich-Karl Holtmeier, Münster, Gabriele Broll, Vechta

1 Introduction and objective

The timberline ecotone, a transitional belt between the subalpine forest and the alpine zone, is characterised by a patchwork of different microsites (e.g. HOLTMEIER & BROLL 1992, BÜTLER & DOMERGUE 1997). The microtopography of the ecotone strongly affects most site factors, for example, snow cover, soil moisture and soil temperature, leading to different vegetation and soil properties between the microsites (BRAUN-BLANQUET et al. 1954). Both the site conditions and the general modes of seed dispersal (wind-mediated or by the European nutcracker (*Nucifraga caryocatactes caryocatactes*)) cause a heterogeneous regeneration of the main tree species reflected in the distribution of seedlings and saplings in the ecotone. The aim of this study is to analyse both the impact of the different site factors and their interaction on the altitudinal differentiation of the natural regeneration of the main tree species in the timberline ecotone. The humus forms, influenced by vegetation and soil organisms, as well as abiotic factors, like relief and climate, are investigated as to their suitability as indicators for potential successful natural regeneration of European larch (*Larix decidua Mill.*) and Swiss stone pine (*Pinus cembra L.*).

2 Study area

The study area is the north-west facing slope of the Piz da Staz (2847 m a.s.l.) in the Upper Engadine, Central Alps, Switzerland (Fig. 1). The study area has a slightly continental climate, characterised by relatively low precipitation and high solar radiation. Particularly due to alpine pasturage, which was stopped in the 50s, the timberline of the study area retreated to 2200 m a.s.l.. As reflected in the snow patterns of the timberline ecotone (located at about 2200 - 2400 m a.s.l.), the prevailing microclimatic conditions are strongly influenced by the locally varying microtopography. Talus deposits of gabbrodiorite, diorite and essexite make up the parent material (STAUB 1946). The topography is characterised by rocky outcrops, knolls and small ridges alternating with depressions. Leptosols, Cambisols and Podzols are common (MÜLLER 1983). In depressions, pedogenesis is often influenced by the accumulation of fine mineral and organic material. Swiss stone pine and European larch form the timberline. These trees also dominate the subalpine Larch-Stone pine forest (*Larici-Pinetum cembrae*) (KELLER et al. 1998). In the timberline ecotone the locally varying site conditions cause a mosaic-like vegetation pattern. Dwarf shrubs, like *Vaccinium gaultherioides* and *Vaccinium myrtillus*, are common. *Loiseleuria procumbens* and various lichen species are typical of wind-exposed locations. As the snow cover in depressions tends to last longer than on the surrounding area and due to the moist to wet conditions during the growing season, the vegetation of these areas is mostly dominated by sedges, grasses and mosses.

3 Material and methods

The study site, covering an area of 6 ha, extends over the whole timberline ecotone between 2200 m and 2400 m a.s.l.. The data presented in this paper were collected from six representative plots of 20 x 20 m. Plot 1, located at the treeline in the central part of the ecotone at 2300 m a.s.l., is chosen as an example. In 1997 and 1998, the following factors were mapped at the study site using a 10 m grid and recorded in detail on the six plots: microtopography, snow melt-out, vegetation, soil conditions and humus forms. Additionally, differences in soil conditions and humus forms between exposed sites and depressions were investigated on the basis of transects (20 m long). On the plots, microsites representing similar characteristics were defined. Microsite A represents an exposed site with melt-out before 22.05.1998, microsite B a depression with melt-out after 28.05.1998. The vegetation cover was estimated as a percentage of surface for three different categories at each microsite: vascular plants, lichens and mosses. Dendrochronological methods were used to determine the age and tree ring width of the examined trees. Samples were taken from trees with a diameter larger than five centimetres by an increment borer. For trees with a smaller diameter either an increment puncher was used (FORSTER et al. 2000) or discs were cut. Special attention was given to taking the discs and cores as close to the stem basis as possible. To establish missing and false tree rings and to date the years of germination and death of the examined trees, crossdating (DOUGLASS 1941) was

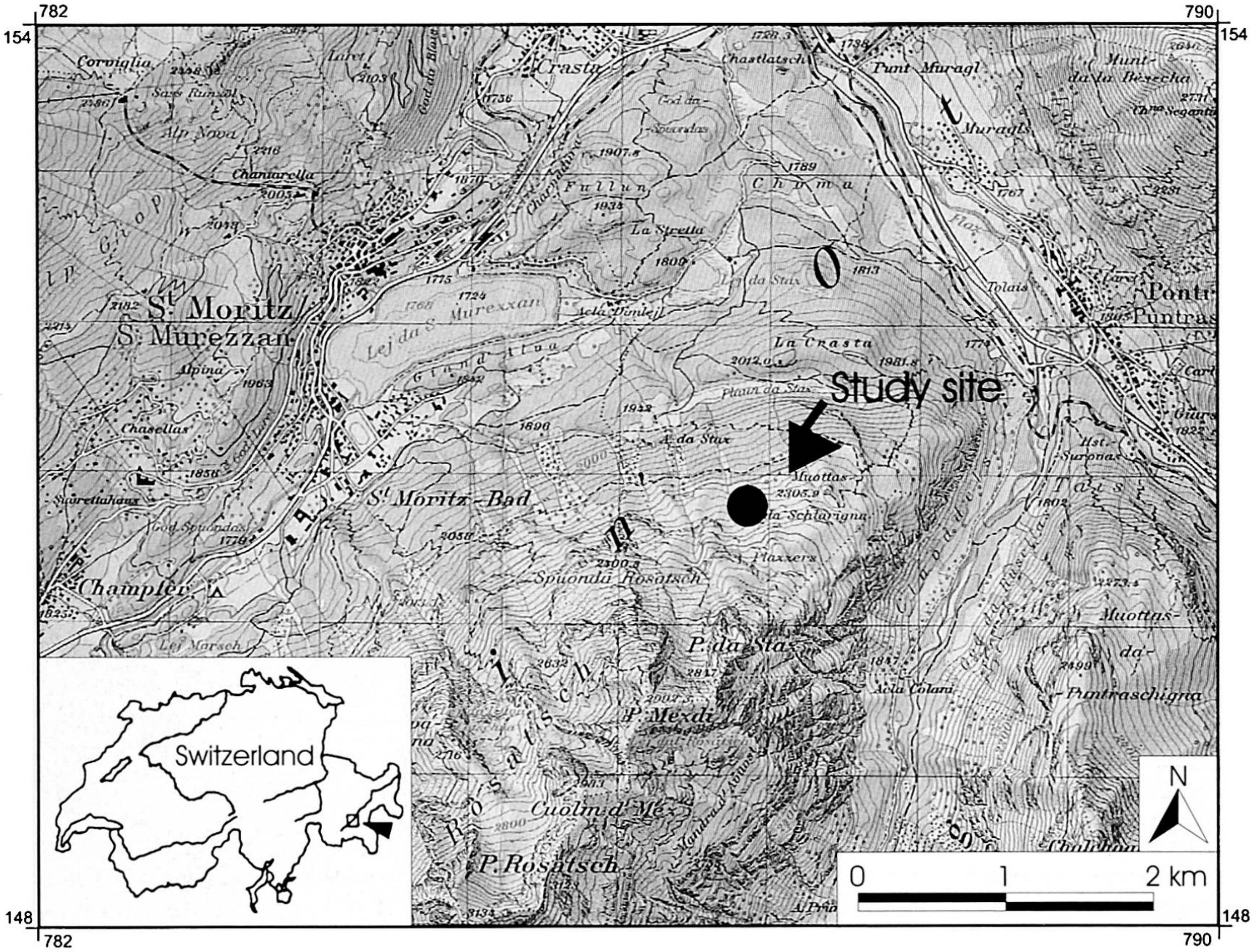

Fig. 1: Study area
Lage des Untersuchungsgebietes.
Situation de l'aire d'investigation
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done with TSAP (Time Series Analysis Program). Furthermore, height, basal area, number of whorls, growth form and damage were recorded for all examined trees. The humus forms of the study site were described and classified according to both Green et al. (1993) and the Swiss soil classification system (FAP 1992). The master organic horizons of the classification according to Green et al. (1993) correspond with the Swiss or German classification system for humus forms (FAP 1992, AK Standortskartierung 1996). Samples were taken from both the organic layer and the mineral topsoil from each perceived horizon. In situations where no horizon could be identified, samples were taken at 2 cm depth intervals. The soil temperatures were recorded with dataloggers (StowAway TidbiT) at a depth of 2.5 cm on two microsites from 26 May 1998 to 11 October 1998.

4 Results

The duration of snow cover on convex sites is usually shorter than on concave topography (Fig. 2 and 3). These differences are clearly reflected in the plant cover. Microsite A is dominated by dwarf-shrubs, such as *Vaccinium gaultherioides* and *Loiseleuria procumbens*, and lichens. The plant density is low, sometimes the bare mineral soil is exposed. At microsite B, the vegetation consists of sedges, grasses, mosses and herbs (mostly *Trichophorum caespitosum* and *Carex fusca*), indicating temporary moist site conditions. The plant density on these sites is markedly higher than on the more wind-exposed sites (Table 1).

Microtopography and snow cover also influence the soil conditions and humus forms of these two micro-

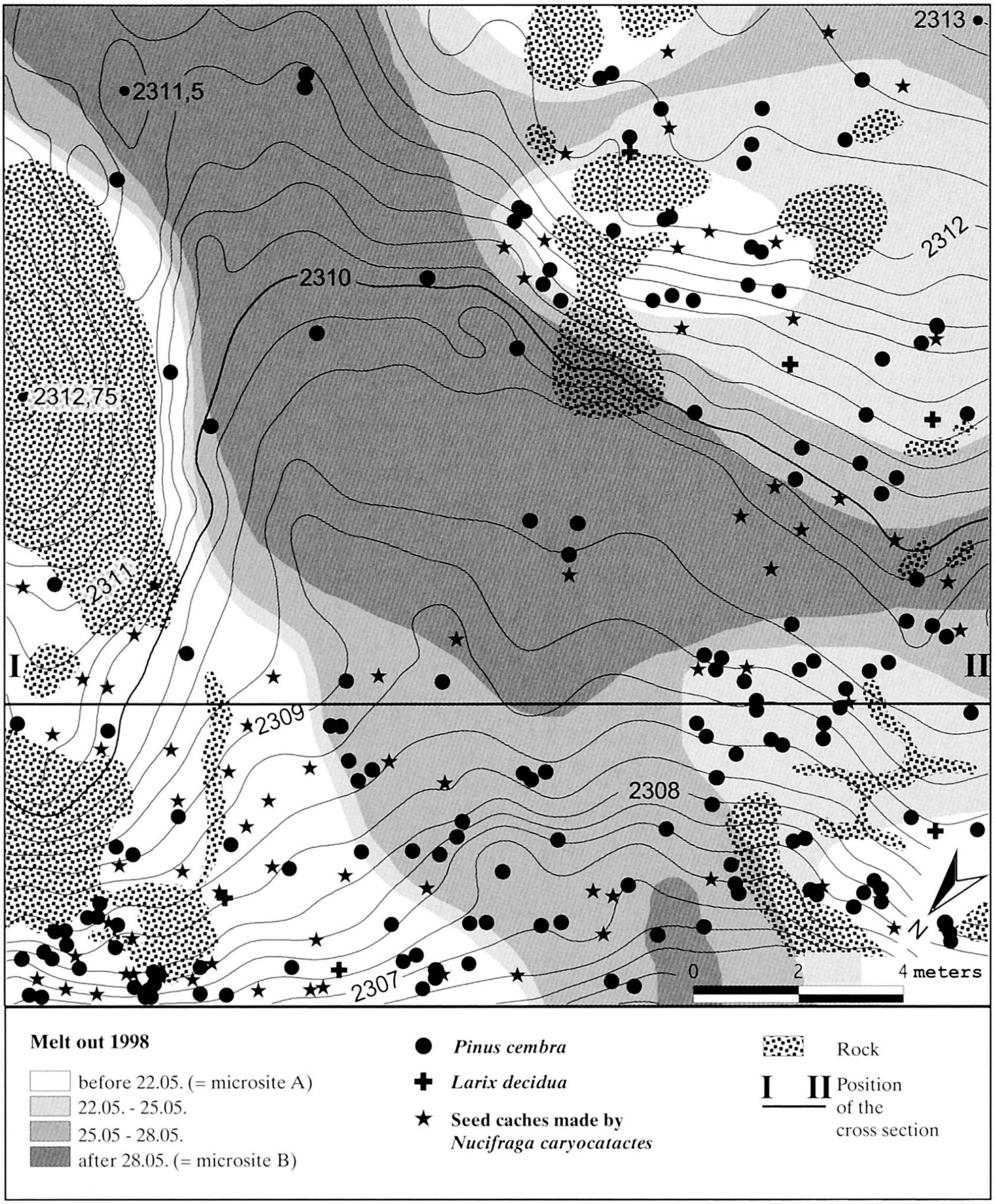


Fig. 2: Snow cover and natural regeneration of *Larix decidua Mill.* and *Pinus cembra L.* on plot 1
Schneebedeckung und natürliche Regeneration von «Larix decidua Mill.» und «Pinus cembra L.» auf der Aufnahmefläche 1
Couverture neigeuse et régénération naturelle des «Larix decidua Mill.» et «Pinus cembra L.» sur l'aire d'observation 1

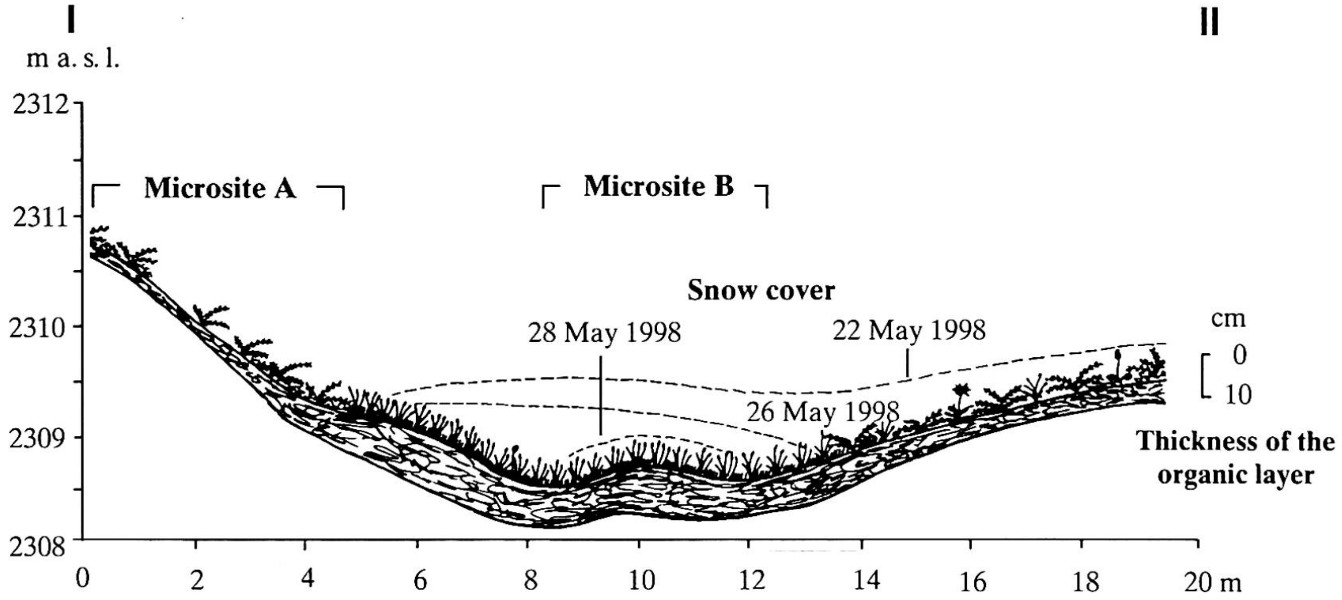


Fig. 3: Cross section (I - II) of plot 1
Transekt (I - II) auf der Aufnahmefläche 1
Coupe transversale (I-II) – Aire d'observation 1

sites. The humus form of microsite A can be defined as a Tenuic Humimor (GREEN et al. 1993) or as a «typischer feinhumusreicher Rohhumus» (FAP 1992) with a very thin organic layer (Fig. 4). The L-layer is composed of *Vaccinium* and *Loiseleuria* leaves. A few fungal mycelia were observed. Faunal droppings could not be found. The H-horizon (about 2 cm thick) contains finely dispersed organic matter and mineral particles. The underlying A-horizon is affected by podzolization (Fig. 4). The humus form of microsite B

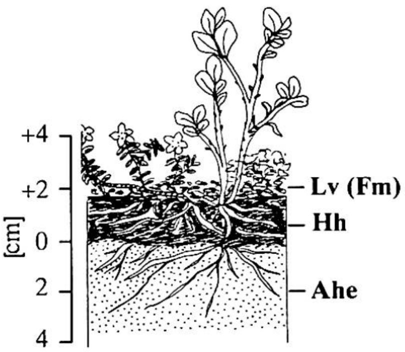
		Microsite A			**Microsite B**	
Vegetation cover [%]						
Total vascular plants		65			95	
Total lichens		20			-	
Total mosses		5			25	
Bare ground		30			-	
Total vegetation		90			120	
Temperature [°C] (2.5 cm depth)		Minimum	Maximum		Minimum	Maximum
	9.2	1.3	20.0	8.2	-0.5	17.0

Tab. 1: Soil temperatures at a depth of 2.5 cm (May to October 1998) and vegetation cover of microsites A and B on plot 1
Vegetationsbedeckung und Temperaturen in 2.5 cm Tiefe unterhalb der Geländeoberfläche (Mai bis Oktober 1998) auf den Kleinstandorten A und B auf der Aufnahmefläche 1
Couverture végétale et températures à 2,5 cm de profondeur (de mai à octobre 1998) sur les microsites A et B de l'aire d'observation 1

Microsite A

Elevation: 2310 m a.s.l.
Vegetation: dwarf shrubs (*Vaccinium gaultherioides, Vaccinium myrtillus, Loiseleuria procumbens*) and lichens

Humus form: Tenuic Humimor (GREEN et al. 1993)
Typischer feinhumusreicher Rohhumus (FAP 1992) with a very low thickness



+3 - 2 cm **L (Fm)**
dry; dark brown and dark grey (discoloration); *Vaccinium* and *Loiseleuria* leaves; single particle, seldom compact; loose; very few fungal mycelia

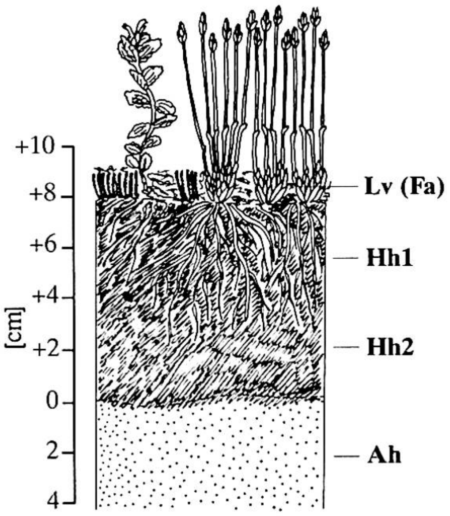
+2 - 0 cm **Hh**
moist; 10YR 2/1; moderate, granular; friable; greasy; plentiful fine roots and few medium roots; no visible biota; slightly humified

0 - 4 cm **Ahe**
moist; 10YR 4/1; moderate, granular; friable, gritty; common fine roots and few medium roots; no visible biota

Microsite B

Elevation: 2308 m a.s.l.
Vegetation: dominated by sedges, grasses, mosses and herbs *(Carex fusca, Trichophorum caespitosum)*

Humus form: Rhizic Leptomoder (GREEN et al. 1993)
Typischer feinhumusreicher Moder (FAP 1992)



+11 (9) - 8 cm **L (Fa)**
moist; yellow-brown to grey (discoloration); leaves and stems of grasses, few dwarf shrub leaves; non-compact matted

+8 - 4 cm **Hh1**
wet; 10YR 2/1; moderate, granular; pliable; fibrous; abundant fine roots and very fine roots, mat-like structure, very few medium roots; well humified

+4 - 0 cm **Hh2**
wet; 10YR 3/1; moderate, granular; pliable to firm; mushy and fibrous; common fine and very fine roots, and very few medium roots; well humified

0 - 4 cm **Ah**
wet; 10YR 3/1; moderate, granular; friable; fibrous; gritty; few to common fine and very fine roots, and very few medium roots

Fig. 4: Humus forms on the microsites A and B of plot 1
Humusformen der Kleinstandorte A und B auf der Aufnahmefläche 1
Formes d'humus des microsites A et B de l'aire d'observation 1

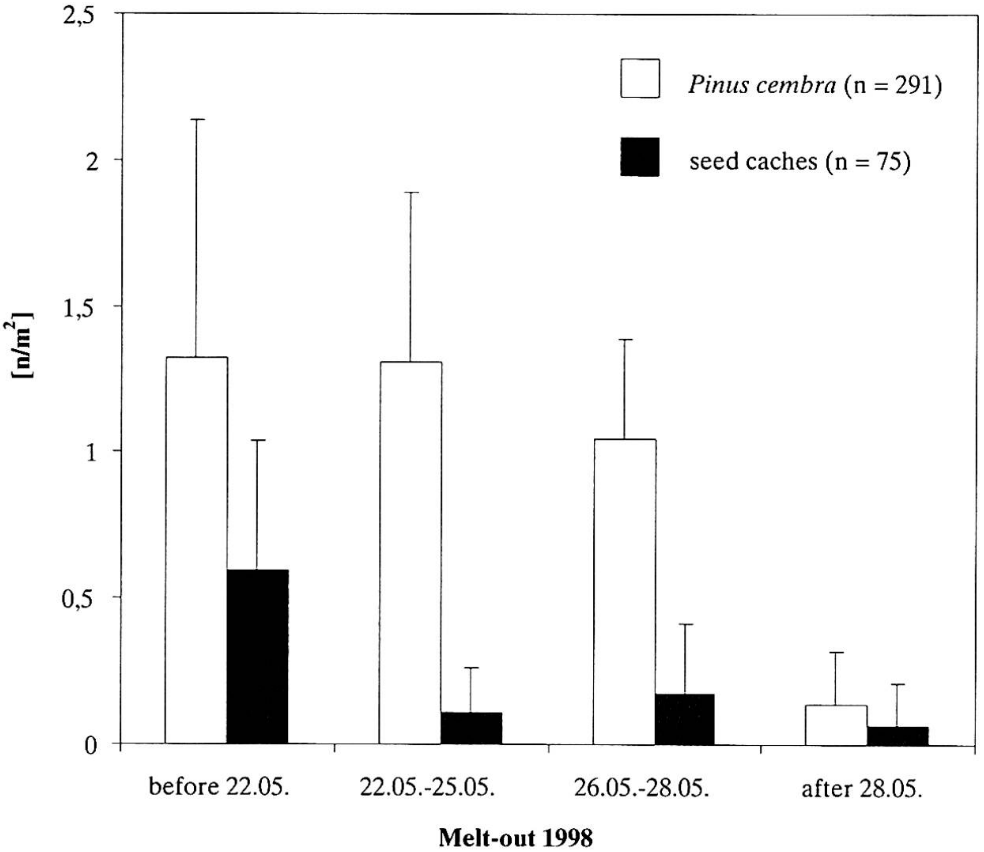


Fig. 5: Number of *Pinus cembra L.* and seed caches opened by the nutcracker per m^2 in relation to the date of melt-out for plot 1
Anzahl von «Pinus cembra L.» und der vom Tannenhäher geöffneten Samendepots pro m^2 in Abhängigkeit vom Ausaperungszeitpunkt auf der Aufnahmefläche 1
Nombre de «Pinus cembra L.» et de dépôts de semences/m^2, ouvertes au casse-noisette (aire d'observation 1) lors de la fonte de la couverture neigeuse

can be described as a Rhizic Leptomoder (Green et al. 1993) or as a «typischer feinhumusreicher Moder» (FAP 1992). Being 9 to 11 cm deep, the thickness of the organic layer of microsite B exceeds that of microsite A. The L-layer contains mainly leaves and grass stems. Only a few dwarf shrub leaves are to be found. The litter is «non-compact matted». The underlying H-horizons contain predominantly finely dispersed organic matter. The numerous fine and very fine roots with a mat-like structure in the first 2 cm of the H-horizon are striking. The root density decreases in the lower horizons (Fig. 4). Results of soil temperature monitoring at a depth of 2.5 cm between May and October 1998 likewise reflect differences between microsites A and B. The average temperature at microsite A is 1 °C higher than at microsite B. Not only does microsite A have the highest temperatures, the lowest temperatures were also recorded on this site (Table 1).

The density of young stone pines and the number of seed caches established by the European nutcracker correspond to the duration of the snow cover in a given area (Fig. 5). Microsite A has a density of 0.55 seed caches per square meter, whereas at microsite B the density is only 0.07 caches per square meter. The number of Swiss stone pines germinating from these caches amounts to 1.3 per square meter for microsite A and 0.15 for microsite B. The correlation coefficient (Spearman) between the date of melt-out and the number of Swiss stone pines is 0.5. The same holds true for the correlation between the date of melt-out and the number of seed caches. The age structure of Swiss stone pines on plots 1-6 indicates that the survival rate of seedlings decreases with increasing duration of the snow cover (Fig. 6).

5 Discussion

The microtopography is an important factor controlling spatial distribution and growth of natural tree regeneration in the alpine timberline ecotone. For

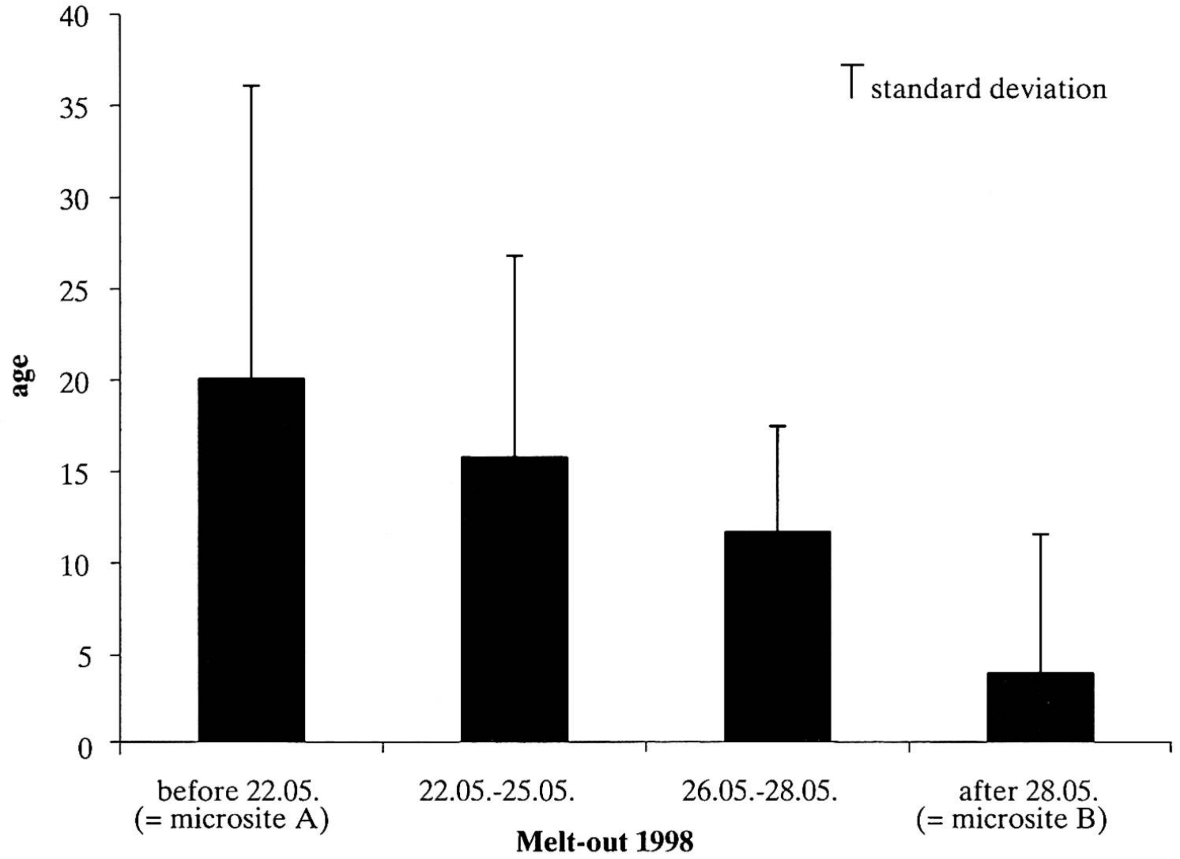


Fig. 6: Age structure of the *Pinus cembra L.*-stand from plots 1 - 6 in relation to the date of melt-out (n = 192)
Altersstruktur des «Pinus cembra L.»-Bestandes der Standorte 1 - 6 in Abhängigkeit vom Ausaperungszeitpunkt
Structure d'âge du «Pinus cembra L.» (aires d'observation 1 - 6), en relation avec n = 192 (lors de la fonte de la couverture neigeuse)

example, the distribution of stone pine-seed caches is strongly influenced by the microtopography. The larger number of caches observed on microsite A (Fig. 2 and Fig. 5) may be explained by the nutcracker's seed caching behaviour. The bird prefers for different reasons exposed sites with little or no snow cover (HOLTMEIER 1966, MATTES 1982, KAJIMOTO et al. 1998). It appears obvious that the nutcracker would need to make the least effort looking for seed at sites with little or no snow, thus saving energy. The bird's success rate in finding seed is also higher at such sites (MATTES 1982), not only because of little snow cover but also due to better orientation. It may also be easier for the nutcracker to establish seed caches on microsite A because of the lower plant cover alternating with patches of bare mineral soil (Table 1). The higher temperatures registered at this site probably encourage a greater germination rate of conifer seeds than at microsite B (Table 1). On the other hand, snow accumulation at microsite B protects young trees and seedlings from climatic injuries (frost, desiccation, ice particle abrasion) during the winter months. Although Swiss stone pines are comparatively frost resistant, younger pines are susceptible to frost during the growing season (TRANQUILLINI 1979). The duration of the snow cover can also negatively affect the number of stone pines in an area. *Phacidium infestans*, a fungus infecting the needles and shoots of pines covered too long by snow (ROLL-HANSEN 1989), is responsible for the greater mortality of pines on microsite B.

The accumulation of the wind-dispersed seeds of European larch may be higher in surface depressions due to lower wind speeds, but the ability of this species to germinate successfully at such sites is low. One reason for the low germination rate is the dense plant cover which prevents the light larch seeds from reaching a suitable seed bed. Usually, larch seeds need bare mineral soil for germination (AUER 1947). Possibly for this reason the number of young larches at the study site is low, particularly as the density of vegetation increased after pasture abandonment at the study site in the early fifties.

Moder and Mor humus forms are very common in the timberline ecotone of the Alps (NEUWINGER & CZELL

1961, Bochter et al. 1983), as were also found on the study site in the Upper Engadine. The microtopography is an important factor for the humus form development in the timberline ecotone (Lüscher 1991, Bednorz et al. 2000). Due to particular site microtopography and snow cover duration, the properties of the organic layers and the topsoil at microsites A and B on plot 1 differ, too. The temperatures during the growing season at a depth of 2.5 cm are higher on microsite A than on microsite B. The temperatures are influenced by microtopography, vegetation and the overlying organic or mineral material. Under the scattered dwarf shrubs and lichens of microsite A, the upper 2.5 cm of soil contain slightly humified organic material, while at microsite B, the dense vegetation, mostly sedges, grasses and mosses, leads to a high content of well humified organic matter and abundant fine roots. The differences in the morphology of the organic layers of microsite A and B also influence the soil moisture conditions. The well humified organic material of microsite B enhances the water holding capacity of the soil, resulting in moist to wet soil conditions during the growing season. Moreover, during snow melt the snow-rich microsite B receives additional melt water from adjacent slopes. The temporary moist to wet soil conditions during the growing season are also reflected in the vegetation by the dominance of *Carex fusca* and *Trichophorum caespitosum*. The conditions at microsite A are different as dryness may occur in summer caused by a well-drained substrate and the lower water holding capacity of the slightly humified organic material. A vegetation dominated by dwarf shrubs favours an increase of the soil acidity and the development of Mor humus forms, thus leading to the occurrence of podzolization processes as indicated by an Ahe horizon. However, the Mor humus forms at the study site in the timberline ecotone have a thinner H and F horizon (Tenuic Mor or «Hagerhumus» after AK Standortskartierung 1996) than the humus forms of the montane belt. In particular, the translocation of litter and organic fine material by wind and water prevents the development of thick Mor layers at these exposed sites. Both the humus form and the occurrence of podzolization in the mineral topsoil indicates that the content of plant available nutrients is probably lower at microsite A than at microsite B. As the natural regeneration of Swiss stone pine is greater on the nutrient poor microsite A, it may be presumed that the nutrient content of a soil is less important than the other dominating factors: date of melt-out, vegetation cover and soil temperature.

6 Conclusions

As has been shown, the establishment, distribution pattern and development of larch and stone pine and the occurrence of different humus forms are controlled by microtopography influencing other site factors such as snow cover duration, soil temperature and soil moisture. At an exposed site, as represented by microsite A, the vegetation, dominated by dwarf shrubs and lichens, and an early snow melt lead to the formation of a Mor humus form. The abundant natural regeneration of Swiss stone pine at this site may also be attributed to these factors. Due to the dense sedge and moss vegetation of a relief depression, represented by microsite B, and the closely related late melt-out corresponding with moist soil conditions, a Moder humus form developed on microsite B. These factors are also responsible for the low natural regeneration of Swiss stone pine and a high tree mortality at this site. Therefore, humus forms probably correspond with the site quality for natural regeneration of seedlings and saplings. Further detailed investigations of chemical and physical soil properties should help to better define site quality for natural regeneration of trees at the timberline. The classification system for humus forms according to Green et al. (1993) is best suited for describing and classifying the humus forms of mountain ecosystems in general (Bednorz et al. 2000). The classification can be used in the alpine belt where Moder humus forms are very common. It may also be applied to closed forests where Mor humus forms prevail. However, a more detailed differentiation of the humus forms, especially of the Mor order, in the timberline ecotone is necessary due to the extreme patchiness of site conditions.

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Abstract: Investigations on Spatial Heterogeneity of Humus Forms and Natural Regeneration of Larch (*Larix decidua Mill.*) and Swiss Stone Pine (*Pinus cembra L.*) in an Alpine Timberline Ecotone (Upper Engadine, Central Alps, Switzerland)

The north-west facing study area in the Upper Engadine (Central Alps, Switzerland) encompasses the whole timberline ecotone between 2200 m and 2400 m a.s.l.. By dendroecological methods, clear differences concerning quantity and age structure of the natural regeneration of the main tree species Swiss stone pine (*Pinus cembra L.*) and larch (*Larix decidua Mill.*) at different sites could be detected. The differing site conditions, closely linked to the microtopography, determine distribution and age structure of natural tree regeneration, as well as humus forms. On exposed sites characterised by Tenuic Humimors, an intensive natural regeneration of, in particular, Swiss stone pine occurs. In depressions with a Rhizic Leptomoder, the density of tree regeneration is low and a high tree mortality could be observed. The results indicate that the site conditions most important for the natural regeneration of trees in the timberline ecotone are reflected in the site-specific humus form.

Zusammenfassung: Untersuchungen zur räumlichen Variabilität von Humusformen und natürlicher Regeneration von Lärche (*Larix decidua Mill.*) und Arve (*Pinus cembra L.*) im Waldgrenzökoton (Oberengadin, Zentralalpen, Schweiz)

Auf einer nordwest-exponierten Untersuchungsfläche im Oberengadin, die den gesamten Bereich des Waldgrenzökotons zwischen 2200 m und 2400 m ü. NN umfasst, wurden mit Hilfe dendroökologischer Methoden deutliche Unterschiede hinsichtlich Anzahl und Altersstruktur der natürlichen Regeneration der waldbildenden Baumarten Arve (*Pinus cembra L.*) und Lärche (*Larix decidua Mill.*) festgestellt. Die in Abhängigkeit vom Mikrorelief kleinräumig wechselnden Standortbedingungen bestimmen Verteilung und Mortalität des Baumwuchses sowie die Humusformen. Während auf exponierten Standorten mit der Humusform Tenuic Humimor eine intensive Verjüngung insbesondere von *Pinus cembra L.* zu beobachten ist, zeichnen sich Muldenlagen mit längerer Schneebedeckung, auf denen ein Rhizic Leptomoder ausgebildet ist, durch eine geringe Verjüngungsdichte und eine hohe Mortalität aus. Die Ergebnisse deuten darauf hin, dass die für die natürliche Regeneration der waldbildenden Baumarten wesentlichen Standortbedingungen sich in den Humusformen widerspiegeln.

Résumé: Recherches sur la variabilité spatiale des formes d'humus et sur la régénération du mélèze (*Larix decidua Mill.*) ainsi que du *Pinus cembra L.* dans le domaine de l'écotone de bordure forestière (Engadine supérieure, Alpes centrales, Suisse)
Sur une aire d'étude exposée au nord-ouest de l'Engadine supérieure (dans les Alpes centrales suisses), qui englobe la totalité de l'ensemble de l'écotone de la bordure forestière étagée entre 2200 et 2400 m d'altitude, il a été possible d'observer, à l'aide de méthodes dendro-écologiques, des différences notoires, en ce qui concerne le nombre et la structure d'âge, parmi les principaux arbres forestiers *Pinus cembra L.* et *Larix decidua Mill.* soumis à la régénération naturelle. L'évolution des rapports de dépendance réciproque entre des aires exiguës et le micro-relief détermine la répartition et la mortalité des arbres, ainsi que les formes d'humus. Alors qu'il est notamment possible d'observer un rajeunissement intense du *Pinus cembra L.* sur les aires à humus Tenuic Humimor, les aires de dépression à couverture neigeuse prolongée sur lesquelles se développe le Rhizic Leptomoder, se caractérisent par une faible régénération et une mortalité élevée. Les résultats obtenus témoignent du fait que les principales conditions d'une régénération naturelle de ces types d'arbres forestiers se reflètent dans les caractéristiques de l'humus.

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