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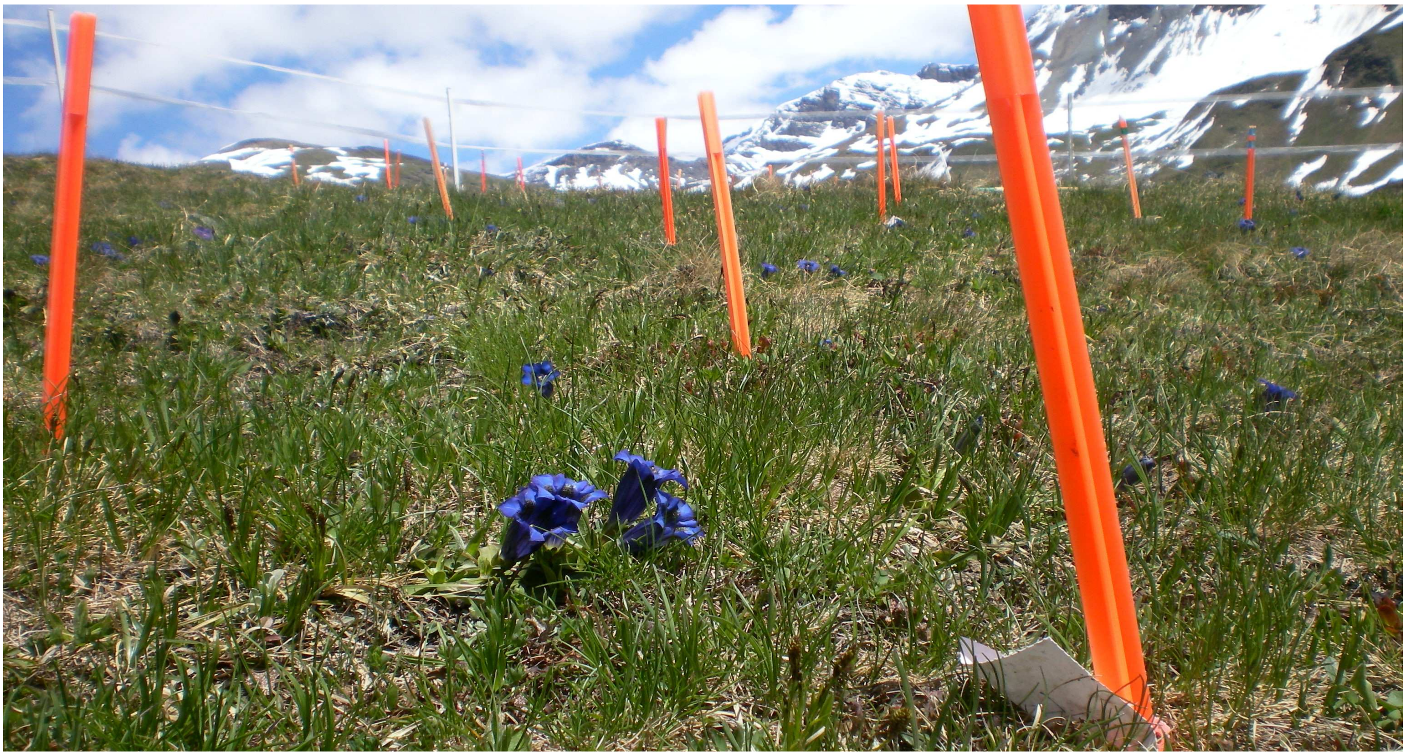
Effects on *Carex sempervirens* and other sedges in the inner Alps



Diploma Thesis

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Air-borne nitrogen in subalpine pastures:

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Abstract

Anthropogenically derived reactive nitrogen (N) compounds are known to affect several processes in terrestrial ecosystems including soil biogeochemistry and community diversity. Nutrient-poor habitats such as subalpine and alpine grasslands are thought to be especially susceptible to increased N input. In a free-air experiment examining the effects of elevated levels of air-borne N on subalpine pastures at Alp Flix, Grisons, Switzerland, a strong shift in species composition in favour of sedges (dominated by *Carex sempervirens* Vill.) was observed in plots receiving 50 kg N ha^{-1} $year^{-1}$ after three years of treatment. The present study was set up in order to examine the representativeness of findings of the Alp Flix experiment. Ten sites were selected in the adjacent valleys of Albula and Julia, matching conditions of the original site at Alp Flix with respect to elevation, exposition, inclination, management and presence of *C. sempervirens.* The only deliberately varying factor was soil pH (units between 4.5 and 6.8, Alp Flix: pH 5.2) since it was expected to influence the effect of N on plant growth. Between May and July 2008, three different treatments were applied to the vegetation: (a) Control, (b) 50 kg N ha^{-1} $year^{-1}$ as NH_4NO_3, (c) compound NPK fertiliser (50 kg N ha^{-1} $year^{-1}$ and a precast PK fertiliser). Total aboveground biomass, fraction of sedges and leaf length of C. *sempervirens* were recorded and analysed in linear regression for effects of treatments, pH and interaction of pH and treatments. After only one vegetation period total aboveground biomass production increased by 29% for N and 35% for NPK compared to the control plots. Although aboveground biomass of *C. sempervirens* was significantly stimulated by both treatments, the fraction of sedges only significantly increased with N deposition, and only at high pH units (interaction pH × N). These results suggest that, especially at non-acidic sites (pH > 5.5), sedges have a competitive advantage over non-sedges when N deposition increases, presumably due to their highly efficient nutrient utilisation. Matching this, leaf length of *C. simpervirens* equally increased in both treatments, and analysis of plant tissue of *C. sempervirens* revealed fairly constant concentrations of P across treatments. Together, the results imply that this sedge was predominantly limited by N and can thus be regarded especially susceptible to increased N supply. The present study confirms the results of the original Alp Flix experiment showing that increased N deposition causes pronounced changes in the species composition of subalpine pastures in favour of sedges. Moreover, such effects could be even stronger on more base-rich sites.

Zusammenfassung

Reaktive Stickstoffverbindungen (N) anthropogenen Ursprungs beeinträchtigen viele Prozesse in terrestrischen Ökosystemen, so z. B. Bodenprozesse und Biodiversität. Nährstoffarme Lebensräume wie subalpines und alpines Grasland gelten als besonders empfindlich gegenüber erhöhten N-Einträgen. Im Rahmen eines Freiluftexperiments auf der Alp Flix (Graubünden, Schweiz) werden derzeit Auswirkungen von erhöhten Konzentrationen von Luftstickstoff auf subalpine Weiden untersucht. Unter Einfluss von 50 kg N ha^{-1} a^{-1} wurde eine starke Veränderung der Artenzusammensetzung zu Gunsten von Seggen (dominiert von *Carex sempervirens* Vill.) beobachtet. Die vorliegende Studie dient der Untersuchung der Repräsentativität dieses Versuches. In den aneinandergrenzenden Tälern von Julia und Albula wurden zehn Standorte ausgewählt, die den Standortverhältnissen auf der Alp Flix im Hinblick auf Höhe, Exposition, Hangneigung, Nutzung und dem Vorkommen von *C. sempervirens* entsprachen. Da der pH möglicherweise die Wirkung von N auf das Pflanzenwachstum beeinflusst, wurden Flächen mit unterschiedlichen pH-Werten gewählt (4.5 bis 6.8; Alp Flix: 5.2). Von Mai bis Juli 2008 wurden drei unterschiedliche Behandlungen in der Vegetation ausgebracht: (a) Kontrolle, (b) 50 kg N ha^{-1} a^{-1} als NH_4NO_3, (c) Voll-Dünger (50 kg N ha^{-1} a^{-1} und ein PK-Fertigdünger). Erfasst wurden die oberirdische Gesamt-Biomasse, der Anteil der Seggen sowie die Blattlänge von *C. sempervirens* und in einer linearen Regression auf den Einfluss von Behandlung, pH und der Interaktion von pH und Behandlung analysiert. Nach nur einer Vegetationsperiode war die oberirdische Biomasse Produktion im Vergleich zu den Kontrollen um 29% (N) und um 35% (NPK) angestiegen. Obwohl die Biomasse von *C. sempervirens* durch beide Applikationen deutlich gefördert wurde, stieg der Anteil der Seggen an der Gesamtbiomasse nur unter N-Eintrag signifikant an, und zwar ausschließlich im höheren pH-Bereich (Interaktion pH × N). Die Ergebnisse zeigen, dass Seggen, besonders auf basenreicheren Standorten (pH > 5.5), bei steigendem N-Eintrag auf Grund ihrer sehr effizienten Nährstoffnutzung einen Konkurrenzvorteil gegenüber Nicht-Seggen haben. Die Ergebnisse von Blattlänge und P-Konzentration von *C. sempervirens* lassen auf eine N-Limitierung der Segge schließen weshalb sie als besonders empfindlich gegenüber erhöhter N-Versorgung einzustufen ist. Die vorliegende Studie bestätigt die Ergebnisse des Alp Flix Experiments, die gezeigt haben, dass erhöhte N Einträge in subalpinen Weiden starke Änderungen der Artenkomposition zu Gunsten von Seggen hervorrufen können, besonders unter basenreichen Verhältnissen.

Introduction

Over the last century emissions of anthropogenically derived reactive nitrogen (N) have substantially increased (Galloway & Cowling 2002) resulting in elevated background concentration of N compounds not only in source areas but on a global scale (Matson *et al.* 2002). N is mostly released as nitrogen oxides (NO_x) and ammonia (NH_3), with NO_x deriving from combustion processes (mainly traffic) and NH_3 released by agriculture, especially intensive livestock farming (Galloway & Cowling 2002). Partly, these emissions are transported over long distances and released far from their sources in untouched areas (Malberg 2007). In Switzerland, current ambient depositions in remote areas occur at the rate of around 5 kg N ha^{-1} y^{-1} but in regions with intensive agriculture they reach up to 60 kg N ha^{-1} y^{-1} (Rihm & Kurz 2001).

As a key nutrient, increased N depositions can influence ecosystems by altering carbon (C) and N cycling, enhancing productivity (Vitousek *et al.* 1997) and changing biodiversity (Bobbink *et al.* 1998; Stevens *et al.* 2004; Suding 2005). The impacts of air-borne N are suggested to be especially severe in N-limited systems (e.g. Chapin 1980; Tamm 1991). Such ecosystems are generally very diverse (Stevens *et al.* 2004) as they shelter a variety of highly specialised species, which in turn are suggested to disappear first under increased N deposition (Clark & Tilman 2008). Alpine and subalpine grasslands belong to the most species-rich plant communities of the temperate zone (Ellenberg 1996; Dietl & Jorquera 2007). Plants growing at high elevations are subject to a combination of stress factors such as low temperatures, high radiation, and a short vegetation period (Körner 2003). Moreover, due to low mineralisation rates alpine ecosystems are mostly N-limited (e.g. Bobbink *et al.* 1998). They are highly balanced systems composed of various interactions among species, soil and environmental traits, which are especially susceptible to external interference such as elevated N deposition (Rusek 1993).

Numerous studies have examined the effects of air-borne N (e.g. Verhoeven *et al.* 1990; Bobbink 1991; van den Berg *et al.* 2005; Remke *et al.* 2009, in press), with several experiments investigating responses of (sub-) alpine vegetation (e.g. Bowman *et al.* 1993; Paal *et al.* 1997; Soudzilovskaia & Onipchenko 2005; Brancaleoni *et al.* 2007). Most experiments found the vegetation to alter in composition (decreased diversity) and biomass (increased), but in some studies vegetation did not respond at all. The sensitivity of subalpine pastures to N deposition is currently being studied in a free-air experiment at Alp Flix, 2000 m asl in Central Grisons, Switzerland. Five levels of N deposition (+0, 5, 10, 25, 50 kg N ha^{-1} y^{-1} added as NH_4NO_3) were applied to 180 grassland monoliths from a *Geo-Montani-Nardetum* growing on slightly acidic soil (mean pH 5.2) (for detailed information refer to Bassin *et al.* 2007). In 2006, after three years of N application, total biomass production was stimulated by 30%, while the functional group of sedges, dominated by *Carex sempervirens* Vill., has more than doubled from 14% in the control plots to 31% in the highest N treatment (Bassin *et al.* 2007).

In many experiments graminoids (sedges and grasses) benefit disproportionately from extra N (e.g. Jones *et al.* 2004; Soudzilovskaia & Onipchenko 2005), often at the cost of other species over the long term (e.g. van den Berg *et al.* 2005). Such exclusions are usually of competitive nature, favouring nitrophilous species and discriminating against specialised and characteristic ones (Bobbink *et al.* 1998). The advantage of graminoids can be found in adaptation to low phosphorus (P) levels by efficiently recycling P from senescing leaves (Güsewell 2004) or, as suggested by Grime (2001), in the formation of hairy cluster roots. When more N is available, co-limitation by other nutrients, such as P, becomes more important (Bobbink 1991, Soudzilovskaia 2005). As nutrient availability is largely controlled by pH (lesser influences include soil water content and soil texture), mainly due to buffering systems (Schachtschabel *et al.* 1998; Blum 2007), it is likely that soil pH plays an important role with respect to the effect of N. Solubility of many nutrients is impeded at low pH units (*ca.* < 4) and peaks close to neutrality (*ca.* pH 6) before decreasing again at values above *ca.* pH 7.5 (Larcher 2003). Consequently, under nutrient-poor conditions at extreme pH values, the response to N would be weaker or even absent in plants that are co-limited by other, non-available nutrients (e.g. P) (Gordon *et al.* 2001). Such pH-dependent co-limitations could be revealed by introducing an additional treatment with compound fertiliser (NPK), which should produce consistent growth stimulation across the whole range of pH. Only under severely nutrient limited conditions, when binding sites to soil particles exceed the incoming amount of nutrients, might the response to NPK fail to appear (Opitz von Boberfeld 1994). Directly or indirectly, pH also affects other processes such as solubility of toxic substances (aluminium), N-cycling (Schachtschabel *et al.* 1998) and aboveground biomass yield (Gough *et al.* 2000), the latter being higher at acidic sites. Nevertheless, the relation between pH and N input has remained largely unstudied until today. Some experiments investigated the effect of liming together with fertilisation (e.g. Silvertown 1980; Chapin *et al.* 2004; Spiegelberger *et al.* 2006); however, no study could be found treating the original site pH as a factor influencing responses to N addition. In consideration of the contradictory results of the different field studies in alpine environments and regarding the importance of soil pH in view of potential co-limitations by other nutrients on the effect of N deposition, two questions arise: (a) Are findings of the Alp Flix experiment representative for subalpine pastures of comparable situation in the inner Alps? (b) Is the response of sedges, focussing on *C. sempervirens*, to N addition influenced by soil pH? To illuminate these issues, this study examined ten sites in central Grisons, corresponding to the conditions at Alp Flix with respect to elevation, exposition, inclination, management and presence of *C. sempervirens*, but differing in soil pH values (4.5 to 6.8). Concordant with the Alp Flix experiment, the dominant sedge was *C. sempervirens* at all sites. This evergreen sedge is bound to alpine and subalpine environments and equally occurs in *Seslerion*- and *Nardion*-communities on base-rich to moderately acidic soils (Hegi 1980; Gigon 1971). At each site twelve plots were established, of which four each received one of the following treatments: Control, N and compound fertiliser (NPK). The study focussed on the effects of treatments, pH and the interaction of pH and treatments on (a) total aboveground biomass, (b) proportion of sedges to total biomass and (c) leaf length of *C. simpervirens* as an indicator of growth stimulation. Hypotheses of the experiment were:

1. Fertilisation with N and NPK stimulates total aboveground biomass production, increases fraction of sedges to total biomass (in keeping with observations at Alp Flix) and promotes leaf length of *C sempervirens*. The effect of NPK is stronger for all three variables.

2. pH interacts with N input so as to stimulate N-induced growth rates at sites characterised by extreme pH values.

Materials and Methods

Study area

The study area is located in the valleys of Julia and Albula (Grisons) in the Swiss Central Alps (Fig. 1, Appendix, Map 1). The climate in this region is characterised by cold winters with permanent snow cover and short summers with a growing season from April to October. Mean annual temperature is 2.8°C, with the highest monthly average temperatures occurring in July and August (11.3 and 10.8°C) (meteorological station in Davos [1590 m asl], measuring period 1961 – 1990, Meteoswiss). Precipitation peaks in summer with ~140 mm per month and adds up to ~1100 mm *per annum*. N depositions in the study area are 3-4 kg N ha^{-1} y^{-1} (Bassin *et al.* 2007). Geologically, the region is characterised by a high variety of bedrocks resulting from the thrusting of the Austroalpine over the Penninic nappes (Labhardt 2005).

Study sites

Site selection

Ten study sites were selected, each comparable with the reference site (free air experiment at Alp Flix, Bassin *et al.* 2007) in terms of elevation (2000-2250 m asl), exposition (south- to westwards), inclination (moderate), management (subalpine pasture with cattle grazing), and presence of the sedge *C. sempervirens* (Tab. 1). The only deliberately varying factor was the pH value of the uppermost soil layer, which ranged between 4.5 and 6.8 across sites. Sites with soil pH < 5.5 were defined as acidic, while non-acidic soils had pH values > 5.5 (Soil taxonomy survey 1999). Further details are listed in Table 1 and 2.
Sites were selected by means of a geographic information system (GIS) in combination with *in situ* inspections. Maps used were: digital simplified geotechnical map (BWG & BUWAL 1990), digital terrain model (Swisstopo 2001), digital community and canton borders (BFS & Swisstopo 2004) and digital and analogue plane survey sheets (Swisstopo 2005).

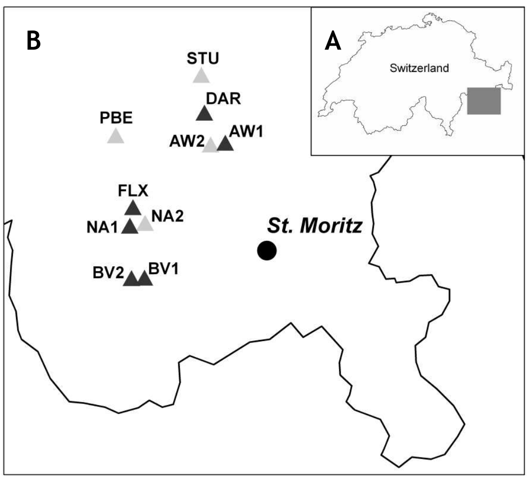

Figure 1. (**A**) Location of the study area in Switzerland, and (**B**) location of the study sites in the study area: Light-grey triangles indicate non-acidic (pH > 5.5), dark-grey triangles acidic sites (pH < 5.5). Abbreviations for site names are explained in Tab. 1.

Site and soil characteristics

At each site, elevation, exposition, and inclination were measured *in situ* using altimeter and compass. Soil parameters, namely soil nutrient availability, soil temperature and soil water content were recorded several times during the vegetation period in 2008. Mixed soil samples were taken from the top 12 cm of each site before the first fertilisation event in May (randomly from all over the site) (n = 10), and after the harvest in July of each site and treatment (from plot margins) (n = 30). Nutrient analysis was carried out following the reference methods of the Swiss Federal Agricultural Research Institutions. Fresh soil samples were analysed for N_{min} via flow injection spectrometry (Skalar Segmented Flow Analyser, SAN^{plus} System, Skalar Analytical B.V., Breda, Netherlands). To measure P, potassium (K), pH and carbonates samples were oven-dried at 40°C for 48 hours, sieved to 2 mm and extracted with CO_2-saturated water (except for carbonates). P was analysed photometrically as molybdenum blue (Photometer Helios Gamma, Thermo Scientific, Sysmex Corporation, Kobe, Japan), K via emission spectrometry (Varian SpectraAA 220 FS, Varian Inc., Palo Alto, USA), pH in aqueous solution (Metrohm 855 Robotic Titrosampler, Metrohm AG, Herisau, Switzerland) and carbonates by adding hydrochloric acid (HCl) to the dried soil and converting the exhausted volume of CO_2 to the content of carbonates. To analyse total C and total N, samples were dried at 105°C for 48 hours, ground to fine powder with a ball mill (Mixer Mill, Retsch MM301, Haan, Germany) and measured after combustion with an elemental analyzer (Euro EA 3000, Hekatech, Wegberg, Germany). Soil organic carbon content (C_{org} [%]) was calculated from carbonates and total C.
All mentioned pH values relate to aqueous solution. If in the literature they referred to CaCl-solution, they were converted by subtracting 0.6 pH units (after Blum 2007).

Climate and phenology

Temperature loggers (HOBO Pendant, Onset, Bourne, USA), registering temperature every 30 minutes, were buried 10 cm below the soil surface in the centre of each site. Soil temperature was averaged for the period between 20 May and 20 July.

Before each fertiliser application, soil water content was recorded at ten sampling points per site using a Time Domain Reflectrometer (TDR) (TRIME-EZ/-HD, Imko, Ettlingen, Germany) and averaged per site. Since drought is one of the limiting factors to plant growth (Körner 2003), the three measuring dates with lowest soil humidity were used to characterise sites.

The ten sites varied widely in snow melt timing, with a span of over two weeks separating the first and last sites to become snow-free. After 9 May, snow cover was removed from sites where it still remained, namely Alp Weissenstein 1 (AW1), Bivio 1 and 2 (BV1, BV2), Alp Flix (FLX) and Alp Natons 1 (NA1). To account for this microclimatic divergence, date of first flowering of *Gentiana acaulis* was recorded to describe phenological development of the vegetation (bound to dates when sites were visited).

Experimental design and fertilisation treatments

In late summer 2007, four blocks containing three plots of 60 × 60 cm each were laid out in homogeneous parts of the vegetation where *C. sempervirens* was present (Fig. 2). Distances between plots were at least 4 m in the slope line and 60 cm along the contour lines. In cases where these distances could not be met, plastic boards of 12 cm height were buried at ground level between plots, to prevent nutrient fluxes. The following three treatments were randomly assigned to the plots of each block: (a) a control which received only water, (b) 50 kg N ha^{-1} year^{-1} as ammonium nitrate (NH_4NO_3) to simulate atmospheric N deposition (amount corresponding to the Alp Flix experiment), (c) a compound NPK fertiliser as a combination of 50 kg N ha^{-1} year^{-1} as NH_4NO_3 and a precast PK fertiliser (Ferty® Basis 1, Planta Düngemittel GmbH, Regenstauf, Germany) in the corresponding quantities of 10 kg P and 51.6 kg K ha^{-1} year^{-1}. N/P and N/K ratios were set according to the recommendations for grassland fertilisation (KTBL 2005). These annual amounts were separated into five additions of 600 ml of a solution of the respective nutrients with water, applied every eleventh day, starting on 21 May, when the last site was snow-free. Last treatment event was carried out between 4 and 6 July.

In fall 2007, cover of sedges (sum of *C. sempervirens* and *Carex* spp.) was estimated for each plot (Fig. 3). Then, plots were mown and biomass was removed. Cattle and possibly game were excluded by electric fences.

Vegetation measurements

Vegetation was clipped from the inner 40 x 40 cm of each plot at peak season growth in mid July 2008. Biomass was stored at 4°C before being sorted into three groups (a) *C. sempervirens*, (b) *Carex* ssp. and (c) non-sedges (grasses, forbs and legumes), and subsequently ovendried at 60°C for 72 hours. Dry weight was recorded for each group and plot. Vegetation type was defined by relevés (after Braun-Blanquet 1964) carried out in early July.

Leaf length of *C. sempervirens* was measured right before harvest on the three longest leaves of three tussocks in each plot. Values were averaged per tussock and plot. Aboveground plant tissue of *C. sempervirens* was

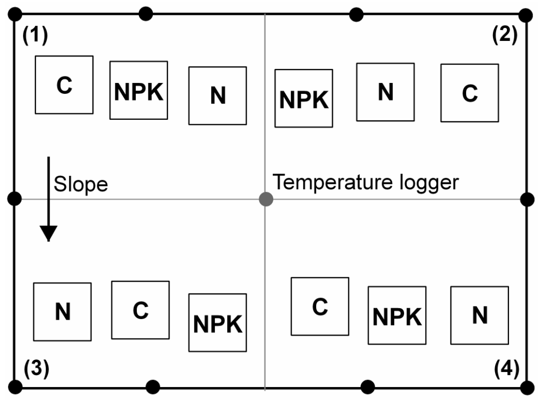

Figure 2. Experimental design used for each study site. Blocks (1-4), plots, slope direction and location of the temperature logger are displayed. Treatments were randomly assigned to the three plots in each block (C = control, N = nitrogen fertilisation, NPK = compound fertiliser). Area of sites varied between 40 and 100 m²according to site conditions.

ground with a Cyclotec mill to 2 mm (Cyclotec 1093 Sample mill, FOSS, Hillerød, Denmark) for analysis of nutrient content (N and P). N was measured via flow injection analysis (Skalar Segmented Flow Analyser, SAN^{plus} System, Skalar Analytical B.V., Breda, Netherlands); after incineration at 600°C, P was analysed photometrically as molybdenum blue (Photometer Helios Gamma, Sysmex Corporation, Kobe, Japan). Samples were pooled per treatment and site (n = 30).

Statistical analysis

Effects of abiotic variables on total aboveground biomass, on fraction of sedges and on leaf length of *C. sempervirens* were tested with linear mixed regressions. Explanatory variables were pH, fertilisation treatment, and the interaction of pH with treatment. The block effect entered the models as a random variable. Cover of sedges in 2007 was used as a covariable to account for the great variability of fraction of sedges between the plots and the ten sites. Model comparisons were carried out to examine the relevance of a variable to the model: To do so, a model with the respective variable was tested against the model without the variable, and with $P > 0.1$, variables were excluded. With $P \leq 0.1$ variables were considered as showing a trend, with $P \leq 0.05$ they were considered significant. If necessary, transformations (log, arcsin-sqrt) were applied to meet the assumptions of linear regression (normal distribution and homogeneity of residual variance). Further, Pearson's correlation coefficients between site-describing variables such as pH, soil temperature, soil water content, C/N-ratio and availability of N_{min}, P and K were calculated. Treatment effects on leaf nutrient content (N, P and N:P ratio) of *C. sempervirens* were tested in a one-way ANOVA followed by a Tukey post-hoc test, or in a Kruskal-Wallis rank sum test followed by a Wilcoxon signed rank test where residuals were not normally distributed. All analysis was performed using the statistics software R (R Development Core Team 2007).

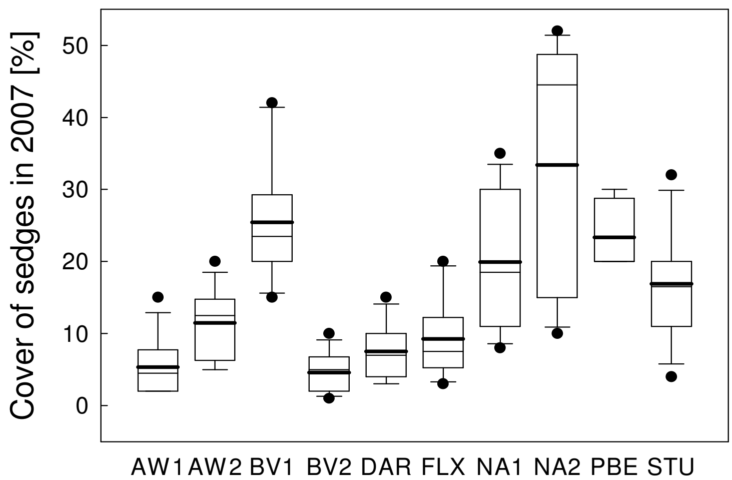

Figure 3. Boxplots of cover of sedges [%] estimated in 2007 at the different sites displayed in order of increasing soil pH. Means are displayed in boxplots as thick lines. For corresponding pH values and abbreviations of site names see Tab. 1.

Table 1. Elevation [m asl], exposition, and inclination [°] of the ten study sites located in the Swiss Central Alps. Vegetation characteristics (vegetation type, phenology, biomass production [g m^{-2}], fraction of sedges [%], and cover of sedges in 2007 [%]) are listed.

Site	Full name	Elevation [m asl]	Exposition	Inclination [°]	Vegetation type [1]	First date of flowering of *Gentiana acaulis* [2]	Total biomass 2008 [g m^{-2}]	Fraction of *Carex* 2008 [%]	Cover of *Carex* in 2007 [%]
AW1	Alp Weissenstein 1	2230	SW	10	*Hypochaero-Nardetum*	3 June	153.8 ± 8.8	9 ± 2.2	5 ± 1.1
AW2	Alp Weissenstein 2	2200	SSW	15-25	*Seslerietum*	3 June	126.5 ± 9.9	6 ± 1.1	12 ± 1.3
BV1	Bivio 1	2100	S	10-15	*Hypochaero-Nardetum*	17 June	116.0 ± 9.3	28 ± 2.3	25 ± 2.5
BV2	Bivio 2	2100	–	0	*Hypochaero-Nardetum*	17 June	188.7 ± 18.2	8 ± 2.1	5 ± 0.7
DAR	Alp Darlux	2080	SSW	30-45	*Hypochaero-Nardetum*	23 May	271.5 ± 14.4	10 ± 1.4	7 ± 1.1
FLX	Alp Flix, Salategnas	2125	SW	5-10	*Hypochaero-Nardetum*	2 June	162.1 ± 12.0	15 ± 2.1	9 ± 1.5
NA1	Alp Natons 1	2125	SSW	10-15	*Hypochaero-Nardetum*	2 June	245.8 ± 15.3	22 ± 2.6	20 ± 2.7
NA2	Alp Natons2	2170	SW	10	*Seslerietum*	2 June	182.9 ± 11.6	35 ± 3.8	34 ± 5.0
PBE	Plang Begls	2190	SSW	5-10	*Seslerietum*	21 May	201.5 ± 15.7	25 ± 1.8	23 ± 1.3
STU	Alp da Stugl	2050	S	8	*Seslerietum*	3 June	173.0 ± 11.1	17 ± 3.2	17 ± 2.1

[1] after Dietl & Jorquera 2007
[2] Sites were visited every 10th day at the least.

Table 2. Characteristics of the top soil layer of the ten study sites: bedrock type, pH, soil water content [% by volume], soil temperature [°C], NH_4^+ content [mg kg^{-1}], NO_3^- content [mg kg^{-1}], available P [mg kg^{-1}], available K [mg kg^{-1}], C/N ratio, C_{org} content [%].

Site	Bedrock [1]	pH [2,3]	Soil water content [4] [% by volume]	Soil temperature [5] [°C]	Soil NH_4^+ [3] [mg kg^{-1}]	Soil NO_3^- [3] [mg kg^{-1}]	Soil P [3,6] [mg P_2O_5 kg^{-1}]	Soil K [3,6] [mg K_2O kg^{-1}]	Soil C/N ratio [3]	Soil C_{org} [3] [%]
AW1	siliceous	4.90	35.2 ± 0.98	11.4	7.31	0.0003	1.33	8.01	11.4	6.05
AW2	calcareous	6.16	34.8 ± 0.94	10.6	4.45	0.0179	1.18	5.85	12.2	6.70
BV1	calcareous	5.36	34.7 ± 2.00	10.2	5.44	0.0003	0.60	11.63	12.8	6.81
BV2	siliceous	4.53	34.3 ± 1.93	10.0	6.40	0.0003	8.74	47.88	12.6	6.13
DAR	siliceous	5.37	23.7 ± 1.43	11.5	10.27	0.0003	1.25	23.66	13.4	7.48
FLX	siliceous	4.93	34.1 ± 1.56	11.0	8.29	0.0002	1.08	13.23	12.4	8.22
NA1	siliceous	4.80	26.3 ± 1.50	no data	9.68	0.0003	0.85	13.06	11.4	7.86
NA2	calcareous	5.94	43.1 ± 1.58	10.5	9.04	0.1027	2.20	51.01	10.4	18.32
PBE	calcareous	5.88	35.9 ± 1.71	10.6	7.93	0.0002	1.21	33.90	13.2	8.06
STU	calcareous	6.79	43.1 ± 2.68	10.7	18.34	0.0413	17.18	143.09	10.8	15.65

[1] Information from Swiss Geological Data.
[2] Measured in aqueous solution.
[3] Measured in May 2008.
[4] Average from the three dates with lowest soil water content.
[5] Mean from 20 May to 23 July (last day of harvest). Data Logger of NA1 collapsed.
[6] Extracted with CO_2-saturated water

Results

Total aboveground biomass

Both elevated N deposition and fertilisation with NPK strongly stimulated production of total aboveground biomass at the ten sub-alpine grassland sites (Tab. 1, Fig. 1 and 2). On average, it increased by 29% for N (193.52 ± 10.27 g m^{-2}) and 35% for NPK (200.19 ± 9.30 g m^{-2}) compared to the control plots (152.34 ± 8.92 g m^{-2}). The difference between the two fertilisation treatments was not significant (N *vs.* NPK, $P = 0.347$). However, NPK-induced growth stimulation tended to be less pronounced with higher pH (interaction pH × NPK treatment ($P = 0.056$)). No interaction between pH and N deposition could be observed.

Table 3. Results of linear mixed regression of total biomass (log-transformed) against pH and two fertilisation treatments (N and NPK). The estimates are given for a mean pH of 5.47.

Variable	Estimate (log)	Df effect	Df residuals	*t* value	*P* value
Control (Intercept)	4.957	1	76	92.68	< 0.001
pH	-0.021	1	38	-0.26	0.322
N (*versus* C)	0.254	1	76	5.45	< 0.001
NPK (*versus* C)	0.300	1	76	6.41	< 0.001
pH × N	-0.009	1	76	-0.13	0.895
pH × NPK	-0.134	1	76	-1.94	0.056

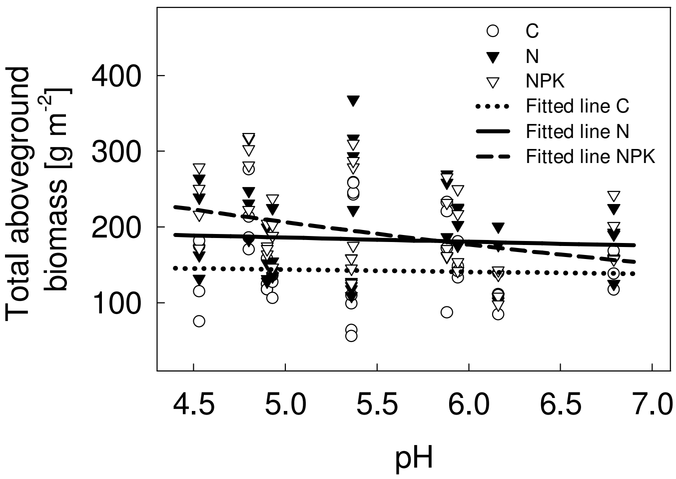

Figure 4. Total aboveground biomass [g m^{-2}] as a function of pH for control (circles), N deposition (black triangles), and NPK fertilisation (white triangles). Fitted lines are based on linear mixed regression (variables are listed in Tab. 3).

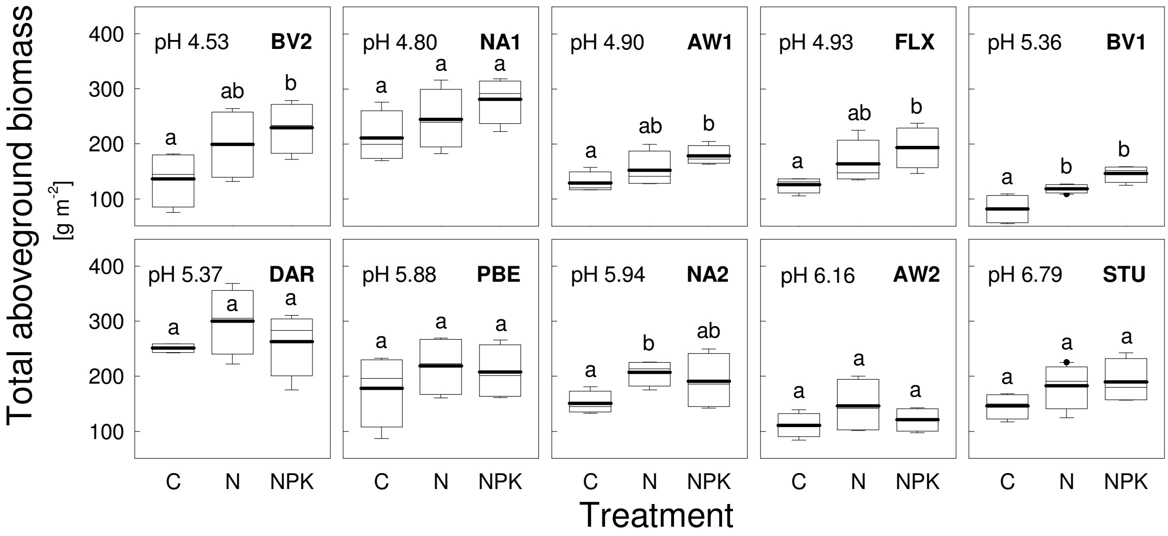

Figure 5. Total aboveground biomass production [g m^{-2}] separated by site and fertilisation treatment (C = control, N = nitrogen, NPK = compound fertiliser). Site specific pH values of the upper soil layer are indicated. Means are displayed in boxplots as thick lines. Different letters above boxes indicate significant differences. Abbreviations for site names are explained in Tab. 1.

Aboveground biomass and fraction of sedges

Absolute biomass of sedges responded strongly to both fertilisation treatments (P = 0.008 for N and P < 0.001 for NPK, Tab. 4, Fig. 4). It increased from 25.55 ± 3.7 [g m^{-2}] in the control plots by 30% to 33.18 ± 4.11 g m^{-2} with N deposition and by 46% to 37.24 ± 4.26 g m^{-2} in the NPK fertilised plots. Interactions between pH and treatments were not significant. The over-all effect of both fertilisation treatments caused no significant change in sedges' contribution to total biomass (5% in N, 12% in NPK fertilised plots). However, with increasing pH, the fraction of sedges responded more strongly to N deposition: Interaction of pH and treatment was significant for the N application (P = 0.01) (Tab. 2, Fig. 3). A test examining the N effect at higher pH units, using the pH of the most alkaline site (STU, pH = 6.79), revealed that for this pH the N treatment was significant (P = 0.009) (Tab. A1). The NPK treatment showed neither significant differences to N deposition nor an interaction with pH.

Table 4. Results of linear mixed regression of absolute biomass of sedges [g m^{-2}] against pH and two fertilisation treatments (N and NPK). Cover of sedges in 2007 has been used as a covariable to correct for the sedges cover in the preceding year. The estimates are given for a mean cover of sedges in 2007 of 16% and a mean pH of 5.47.

Variable	Estimate (log)	Df effect	Df residuals	*t* value	*P* value
Control (Intercept)	2.789	1	75	22.72	< 0.001
Cover Carex 07	5.054	1	75	7.07	< 0.001
pH	-0.220	1	38	-1.15	0.258
N (*versus* C)	0.357	1	75	2.73	0.008
NPK (*versus* C)	0.465	1	75	3.56	< 0.001
pH × N	0.291	1	75	1.48	0.143
pH × NPK	-0.028	1	75	-0.14	0.887

Table 5. Results of linear mixed regression of fraction of biomass of sedges (arcsin-sqrt-transformed) against pH and two fertilisation treatments (N and NPK). Cover of sedges in 2007 has been used as a covariable to correct for the cover of sedges in the preceding year. The estimates are given for a mean cover of sedges in 2007 of 16% and a mean pH of 5.47.

Variable	**Estimate (arcsin-sqrt)**	**Df effect**	**Df residuals**	***t* value**	***P* value**
Control (Intercept)	0.390	1	75	24.36	< 0.001
Cover Carex 07	1.143	1	75	12.35	< 0.001
pH	-0.563	1	38	-2.26	0.030
N (*versus* C)	0.013	1	75	0.67	0.504
NPK (*versus* C)	0.026	1	75	1.31	0.193
pH × N	0.079	1	75	2.67	0.009
pH × NPK	0.026	1	75	0.91	0.367

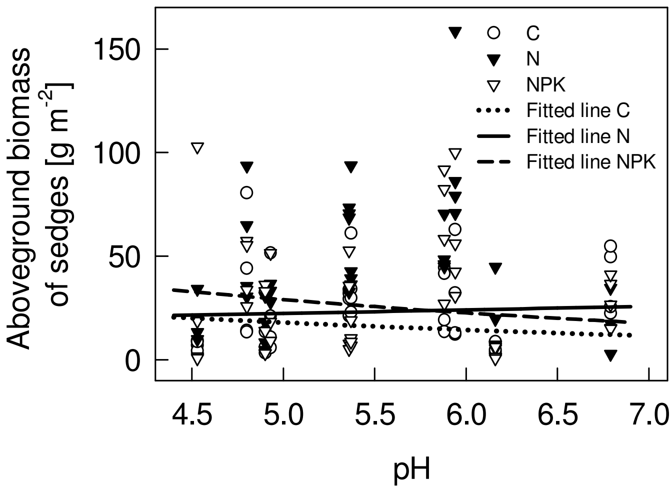

Figure 6. Absolute aboveground biomass of sedges [g m^{-2}] as a function of pH for control (circles), N deposition (black triangles), and NPK fertilisation (white triangles). Fitted lines are based on linear mixed regression (variables are listed in Tab. 4). Cover of sedges in 2007 has been used as a covariable to correct for the sedges cover in the preceding year.

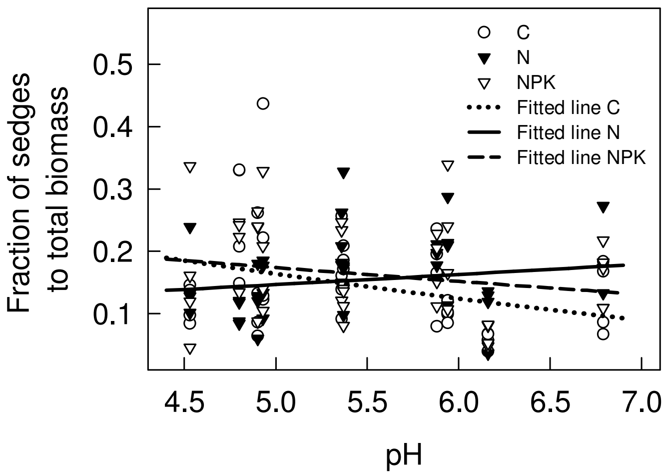

Figure 7. Fraction of aboveground biomass of sedges to total biomass as a function of pH for control (circles), N deposition (black triangles), and NPK fertilisation (white triangles). Fitted lines are based on linear mixed regression (variables are listed in Tab. 5). Cover of sedges in 2007 has been used as a covariable to correct for the sedges cover in the preceding year.

Leaf length and nutrient content of Carex sempervirens

Leaf length

Both treatments (N and NPK) stimulated longitudinal growth of leaves of *C. sempervirens* compared to the control (Fig. 8 and 9). Average leaf length was 13.71 ± 0.62 cm. Overall, leaf length increased on average by 21% to 16.53 ± 0.57 cm with N deposition ($P < 0.001$, Tab. 6), while leaves in NPK fertilised plots gained 20% resulting in 16.41 ± 0.57 cm ($P < 0.001$). The difference between N and NPK treatment was not significant ($P = 0.852$). Leaf length decreased significantly by *ca.* 11% per unit with increasing pH ($P = 0.009$), though the interaction between pH and treatments was not significant ($P = 0.231$).

Table 6. Results of linear mixed regression of leaf length of *Carex sempervirens* against pH and two fertilisation treatments (N and NPK). The estimates are given for a mean pH of 5.47.

Variable	Estimate	Df effect	Df residuals	*t* value	*P* value
Control (Intercept)	13.708	1	78	24.63	< 0.001
pH	-1.741	1	38	-2.77	0.009
N (*versus* C)	2.825	1	78	4.53	< 0.001
NPK (*versus* C)	2.707	1	78	4.34	< 0.001

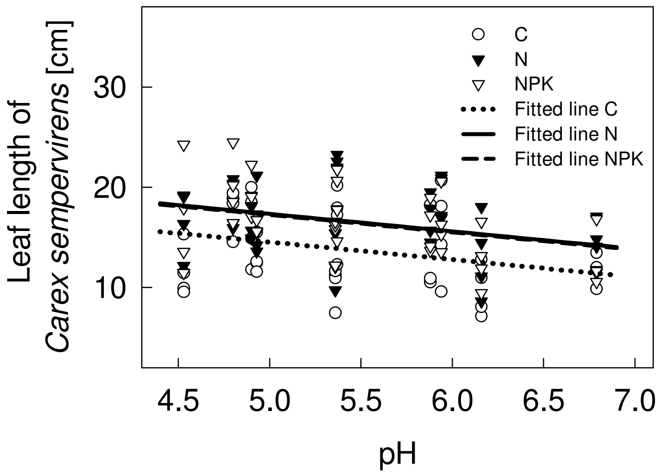

Figure 8. Leaf length of *Carex sempervirens* as a function of pH for control (circles), N deposition (black triangles), and NPK fertilisation (white triangles). Fitted lines are based on linear mixed regression (variables are listed in Tab. 6).

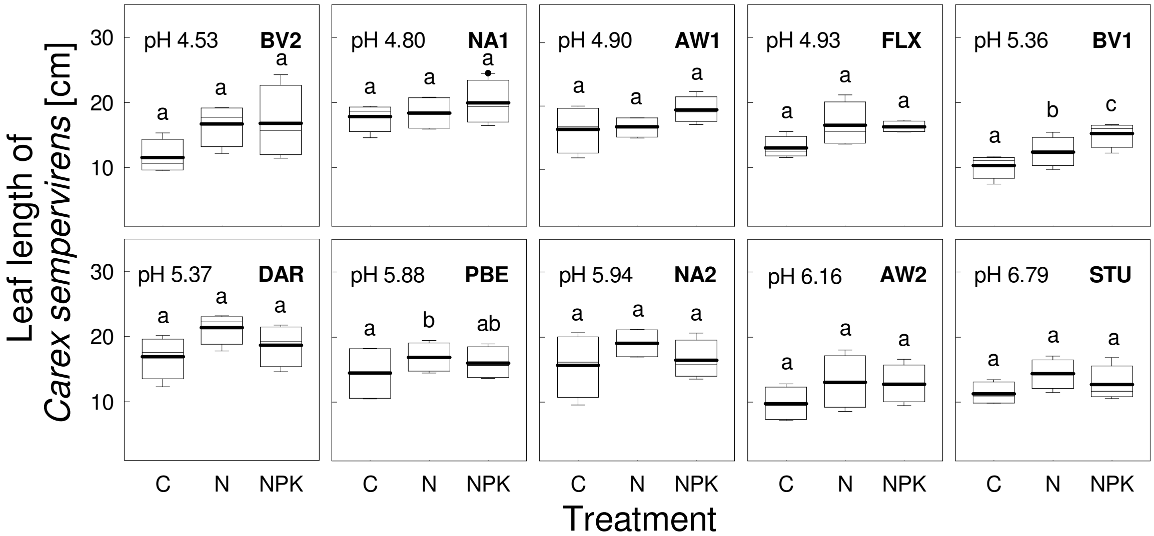

Figure 9. Leaf length of *Carex sempervirens* separated by site and fertilisation treatment (C = control, N = nitrogen, NPK = compound fertiliser). Site specific pH values of upper soil layer are indicated. Means are displayed in boxplots as thick lines. Different letters above boxes indicate significant differences. Abbreviations for site names are explained in Tab. 1.

Nutrient content

Concentrations of N [N] in aboveground plant tissue of C. *sempervirens* were on average significantly higher in both treatments compared to the control (19.50 ± 0.39 mg g^{-1}) (both $P < 0.001$), increasing by 18% with N deposition and by 15% in NPK fertilised plots to 23.13 ± 0.48 mg g^{-1} and 22.37 ± 0.54 mg g^{-1}, respectively (Fig. 10). N and NPK treatment did not differ significantly ($P = 0.065$). Shoot P concentration [P] did not significantly change in the three treatments ($P = 0.118$); however, there was a very slight decrease from the average of 1.24 ± 0.08 mg g^{-1} in controls to 1.15 ± 0.06 mg g^{-1} with N deposition and to 1.21 ± 0.05 mg g^{-1} in NPK fertilised plots (-7% and -2% compared to controls, respectively). The average N:P ratio in control plots was 16.53 ± 1.17. It increased significantly when N ($P < 0.001$) and NPK ($P = 0.006$) were applied, by 25% (N) to a value of 20.67 ± 1.16 and by 14% (NPK) to 18.83 ± 0.88 compared to control plots. The difference between both treatments was not significant ($P = 0.062$).

Significant positive correlations across treatments were detected for pH and [N] (Pearson's correlation coefficient R = 0.20, Tab. 7) and pH and N:P ratio (R = 0.48) whereas pH and [P] correlated negatively (R = -0.37). Testing treatments separately revealed weaker or non-significant correlations.

Table 7. Correlations of pH with plant tissue [N], [P] and N:P ratio across and separated by treatments. Displayed is Pearson's correlation coefficient R and its significance level (* < 0.05, ** < 0.001, *** < 0.0001).

Variable	pH (all treatments)	pH (C)	pH (N)	pH (NPK)
plant tissue [N]	0.20 *	0.33 *	0.32 *	0.23
plant tissue [P]	-0.37 ***	-0.25	-0.39 *	-0.57 **
plant tissue N:P	0.48 ***	0.43 *	0.48 *	0.76 ***

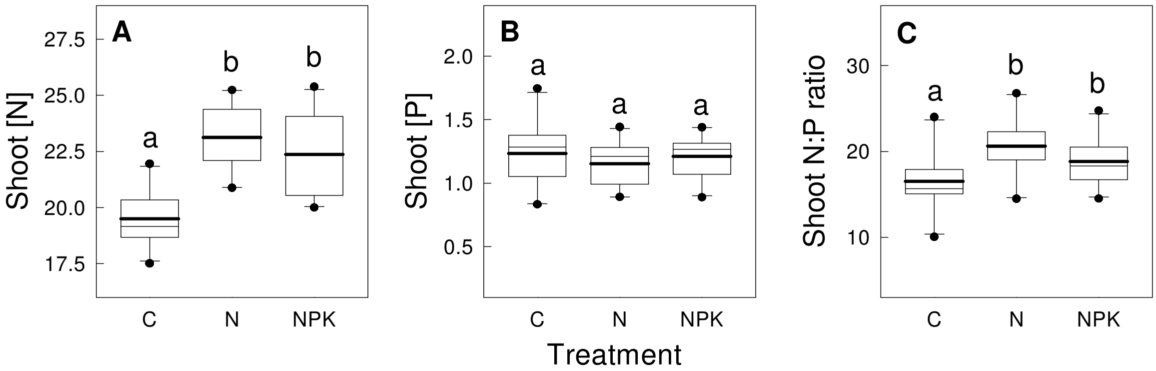

Figure 10. Aboveground plant tissue concentration of *Carex sempervirens* for (**A**) N [mg g^{-1} dry substance], (**B**) P [mg g^{-1} dry substance] and (**C**) N:P ratio [mg N/ mg P] separated by fertilisation treatment (C = control, N = nitrogen, NPK = compound fertiliser). Means are displayed in boxplots as thick lines. Different letters above boxes indicate significant differences.

Table 8. Correlation cross tabulation of pH, soil temperature, soil water content, C/N-ratio and the soil nutrients N_{min}, P and K. Displayed is Pearson's correlation coefficient R and its significance level (* < 0.05, ** < 0.001, *** < 0.0001).

	pH	Soil temperature	Soil water content	C/N-ratio	Soil N_{min}	Soil P
Soil temperature	0.324					
Soil water content	0.110	-0.412 ***				
C/N-ratio	-0.313 **	0.232	-0.601 ***			
Soil N_{min}	0.492 ***	0.044	0.402 ***	-0.400 ***		
Soil P	0.432 ***	0.144 *	0.484 ***	-0.379 ***	0.807 ***	
Soil K	0.616 ***	0.164	0.579 ***	-0.458 ***	0.873 ***	0.935 ***

Correlations between site specific factors

Of the site specific factors, soil pH correlated positively with dissolved nutrients (N_{min}, P and K) in the soil solution and negatively with soil C/N-ratio (Tab. 8). Soil nutrients (N_{min}, P, K) correlated positively with each other, and with soil water content, but negatively with the C/N-ratio. Soil water content showed negative correlation with soil temperature. Correlations between soil pH and other factors did not change direction when outliers were ignored (e.g. for the correlation of pH and P: omission of STU and BV2; data not shown).

Discussion

Effect of treatments

Effect on total aboveground biomass

Deposition of N and application of compound fertiliser both strongly stimulated productivity across sites for total aboveground biomass, NPK slightly more than N alone (35% and 29%, respectively) (see Tab. 3, Fig. 4 and 5). This is in agreement with the initial hypothesis and common knowledge about fertilisation to promote plant growth (e.g. Bobbink 1991; Crawley *et al.* 2005), and it corresponds to the oldest fertilisation-experiment in subalpine pastures at Schynige

Platte, Switzerland (Spiegelberger *et al.* 2006). Although the difference between N and NPK was not significant, the study sites must be considered as not only limited by N but slightly co-limited by P, K or both. Interestingly, the response to NPK interacted significantly with pH: It considerably promoted plant growth on acidic sites but the effect weakened with increasing pH. With the effect of N deposition being invariant across sites, this resulted in higher biomass at non-acidic sites with N deposition compared to the NPK treatment. This contradicts general assumptions that a broader supply in nutrients combined with an equal amount of N would stimulate productivity more intensely (e.g. Soudzilovskaia & Opnichenko 2005). Only at sites where nutrients are being adsorbed to ions or soil particles immediately (e.g. P by calcium (Ca) or iron) might such an effect be revealed (Opitz von Boberfeld 1994). Yet, in this study, this could be true for both ends of the pH-gradient (4.5 – 6.8) as sites with pH > 6.8 were buffered by carbonates and sites with pH 4.5 – 4.8 by iron (Blum 2007). Additionally, this approach conflicts with the response to N deposition which did not differ across pH units and was consequently not constrained by adsorption.

The second hypothesis, claiming the effect of N being stronger at extreme pH values due to lower nutrient-availability (Schachtschabel *et al.* 1998), was disproved by the present results. Little literature is available describing the effect of fertilisation combined with pH. The few studies did not find interactions between fertilisation treatments and pH (e.g. Pieterse & Rethman 2002) and only some studies treated compound fertiliser (Spiegelberger *et al.* 2006). However, for untreated arctic tundra, Gough *et al.* (2000) described aboveground biomass to decline with increasing pH, which is in line with a very slight (but not significant) decrease in the control plots of the present experiment. Along with the unexplained interaction of pH and NPK treatment, the weak decrease in controls with increasing pH could be a product of the specific conditions at the selected sites which arise from a combination of factors which can not be elucidated with the present dataset.

Effect on fraction of sedges

This study focussed on the response of fraction of sedges (with *C. sempervirens* dominating) to increased levels of air-borne N input. Indeed, across sites aboveground biomass of sedges gained 29% with N deposition and 45% with application of NPK (see Tab. 4, Fig. 6) matching the hypothesis that fertilisation promotes productivity of sedges. Concordant with these results, a positive response of sedges to N deposition was observed by Theodose & Bowman (1997) and Soudzilovskaia & Onipchenko (2005) in alpine environments, whereas Gigon (1971) did not find responses of *C. sempervirens* to N fertilisation in pot experiments. However, in values relative to total aboveground biomass, a significant increase could only be found with N deposition at the highest pH unit (6.8) (interaction of pH and N for proportion of sedges) (see Tab. 5 and A1, Fig. 7). While the N effect produced a steep increase for fraction of sedges with higher pH, the response to NPK was rather constant across sites, corresponding to the response of total aboveground biomass to application of N. Thus, it seems that at higher pH values, sedges had a competitive advantage over non-sedges with respect to use of N or other nutrients. In turn, with broader nutrient supply (NPK) they were apparently edged out by non-sedges, which enhanced productivity clearly in the NPK treatment (data not shown). The assumption that sedges possess beneficial traits concerning nutrient cycling is sustained by several studies: Sedges are known to efficiently recycle P from senescing leaves (Güsewell 2004) and to be capable of P acquisition from compounds not available to all plants (Pérez-Corona *et al.* 1996), thus not depending on the presence of P-solubilising root fungi (Haselwandter and Read 1982). As well, they have been found to regulate their P-uptake independently of N-supply and N-source (Choo & Albert 1999a, b; Choo *et al.* 2002). In line with this, several experiments reported sedges to perform their full growth response with N input, indicating marginal co-limitation by other nutrients (Pauli *et al.* 2002; Soudzilovskaia & Onipchenko 2005). Although most studies did not treat *C. sempervirens* but sedges in general, they seem to be applicable to this experiment. Together, these traits affirm the assumption that sedges have an essential advantage over other species with respect to N input under P-limited conditions, allowing them to respond to extra N while the reaction of other plants is constrained.

Why was the effect of the N deposition on fraction of sedges influenced by pH? The few studies investigating alpine or subalpine vegetation did not treat differences in the effect of N deposition or fertilisation along a gradient of pH. One possible explanation could be the masking of pH by soil water content: Theodose & Bowman (1997) found N deposition to stimulate growth of sedges in wet but not in dry habitats. Yet, in this study pH was not correlated with soil water content (Tab. 8). The interaction could also be bound to the ecological optimum of the dominant sedge *C. sempervirens* which preferably grows on slightly acidic to base-rich soils (Oberdorfer 2001), although estimations of cover of sedges in 2007 did not show any consistent pattern with respect to pH (Fig. 3) and despite the decrease of fraction of sedges in control plots in 2008 with ascending pH (Fig. 7). In some way, the success of sedges at sites with higher pH units was probably related to nutrient solubility; however, in this study, sites with higher soil nutrient content did not match sites where sedges were successful. There must be other, undetected factors controlling this interaction. Although several site and soil characteristics were recorded, the present dataset was apparently not sufficient to answer this question satisfactorily, pointing to the need for further research.

With the stimulating effect of extra N on proportion of sedges, the present study can be added to a considerable number of experiments which recorded a positive impact of N deposition on productivity of sedges: In sand dune ecosystems on *Carex arenaria* (van den Berg *et al.* 2005; Jones *et al.* 2004; Remke *et. al.*, 2009 in press) and in montane fens, alpine tundra and alpine heath on various sedges (Pauli *et al.* 2002; Theodose & Bowman 1997; Soudzilovskaia & Opnichenko 2005). Sedges' prosperity is often attributed to their successful competition for light (e.g. Grime 1973) and/ or, as described above, to their ability to cope with decreased nutrient (especially P) supply. Increases in biomass and productivity of one or several nitrophilous species in lowland communities often lead to shifts in species composition accompanied by decreasing diversity (Bobbink *et al.* 1998; Bowman 2000; Zavaleta *et al.* 2003; Clark & Tilman 2008). However, in alpine communities the decreasing diversity effect did not occur (Soudzilovskaia & Opnichenko 2005; Bowman *et al.* 2006; Bassin *et al.* 2007). This might be due to limited competition for light in sparse alpine canopies (Körner 2003) which allows non-responsive and responsive species to coexist (Bassin *et al.* 2007). How vegetation in the current experiment will develop under longer-term N input requires further investigation.

Effect on leaf length and nutrient content of Carex sempervirens

The positive effect of N deposition and NPK application on biomass of sedges is reflected in the response of leaf length of *C. sempervirens*: Both treatments had an overall stimulating effect on longitudinal growth, producing practically the same increase in leaf length (21% and 20%, respectively; Tab. 6, Fig. 8 and 9) which partly contradicts the first hypothesis. Yet, it supports the above-mentioned studies revealing growth of sedges being primarily N-limited owing to their excellent P-uptake and -utilisation (Haselwandter & Read 1982; Pérez-Corona *et al.* 1996). No interaction between N and pH could be observed for leaf length, invalidating the second hypothesis. However, in line with the stimulation of longitudinal growth, N deposition substantially increased plant tissue [N] in *C. sempervirens* while the response to NPK was slightly weaker (Fig. 10). In both treatments, [N] was positively correlated with pH (Tab. 7). Plant tissue [P] correlated negatively with pH and was hardly affected by any of the treatments. This caused on the one hand enhanced N:P ratios in fertilised plots and on the other hand increasing N:P ratios with increasing pH. As wider N:P ratios (> 20) usually indicate increasing limitation by P (Güsewell 2004) these observations again underpin the sedges' extraordinary ability to acquire and use N despite low levels of P (Choo *et al.* 2002; Pauli *et al.* 2002) and reflect the increase of fraction of sedges at non-acidic sites.

Leaf length of *C. sempervirens* decreased consistently across pH units and treatments, contrasting observations of Gigon (1971) who recorded leaves to be longer at non-acidic sites. However, considering the positive correlation of leaf elongation and biomass suggested by di Renzo (2000), it matches findings of Gough *et al.* (2000) reporting biomass to decline with increasing pH and the decreases of sedges (relative and absolute) in control and NPK fertilised plots observed in this study (Tab. 4 and 5, Fig. 6 and 7). Conflictive is, however, the positive response to N deposition of fraction of sedges with increasing pH (interaction *vs.* no interaction of pH and N). This discrepancy might have been influenced by the exclusive measurements of leaf length of *C. sempervirens* since a slight increase in fraction of *Carex* ssp. with increasing pH was recorded (data not shown), or by changes in leaf thickness and number of leaves per tussock which remained unidentified in this study, but contribute to increases in biomass (Schulze *et al.* 2002).

Representativeness of the Alp Flix experiment

Overall, stimulation of N application increased proportion of sedges by 5%. Although considerably weaker, this reflects results of the experiment at Alp Flix where in the first year (2004) fraction of sedges increased by 27% (Bassin *et al.* 2007). The differing responses were possibly caused by climatic conditions (considerably higher precipitation in spring 2008 than 2004 [Meteo swiss] inducing a snow melt-delay of about one month in 2008 and delayed plant development). Yet, variations in system responses can as well be caused by soil conditions, plant composition or duration of fertiliser application (e.g. Gough *et al.* 2000; Fremstad *et al.* 2005). As the studied sites differed not only in pH but also in other parameters (soil nutrient content, soil temperature, soil humidity, productivity), the extrapolation of findings of the Alp Flix experiment must be considered as being limited by certain factors. However, it is unlikely that correlations between pH and soil parameters (see Tab. 8) masked the effect of pH since they are in agreement with common knowledge about soil processes (Schachtschabel *et al.* 1998; Blum 2007). Thus, even in consideration of site-specific limitations, the N-induced change in species composition observed in the Alp Flix experiment can be regarded representative for subalpine pastures in the inner Alps. With respect to the interaction of pH and treatment, the stimulating effect of N deposition on sedges might even be stronger at non-acidic sites.

Conclusions

This study examined the effect of air-borne deposition of reactive N compounds on species composition in subalpine pastures at ten different sites with respect to changes in biomass of sedges, specifically *C. sempervirens*. After only one season, total aboveground biomass had increased by 29% and 35% with the N and the NPK treatments, respectively, suggesting that the vegetation at the sites was primarily limited by N, but slightly co-limited by other nutrients. Sedges were stimulated in both treatments in terms of aboveground productivity; however, their contribution to total biomass only substantially increased with N deposition (although restricted to high pH values). This suggests that sedges were advantaged over non-sedges at elevated N deposition, possibly due to their extraordinary capabilities to uptake and utilize other soil nutrients. In fact, leaf length of

C. sempervirens was equally stimulated by both the N and the NPK treatment. Together with analysis of plant tissue of *C. sempervirens* revealing fairly constant concentrations of P across treatments, this implies that this sedge species was predominantly limited by N and can thus be considered especially susceptible to increased N supply.

Consequently, this study revealed that the increased productivity as well as the change in species composition recorded in the Alp Flix experiment in response to elevated N deposition can be considered representative for comparable subalpine pastures in the central Alps, and that the response might be even stronger on more base-rich sites. With respect to the results of Alp Flix, where the fractional biomass of sedges tripled after only three years of addition of 50 kg N ha^{-1} y^{-1}, increased N deposition must be regarded as a major threat to today's composition of subalpine pastures. It is to be expected that in the long term, increasing deposition of air-borne N will lead to dramatic changes in species composition of subalpine pastures, especially in favour of sedges.

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Davos: Diagramme of the measuring period 1961 – 1990 http://www.meteoswiss.admin.ch/web/de/klima/klima_schweiz/klimadiagramme/dav.html

Davos: Precipitation and temperature data: 1866 – 2008 http://www.meteoswiss.admin.ch/web/de/klima/klima_heute/homogene_reihen.Par.0025.DownloadFile.ext.tmp/davos.txt

Appendix

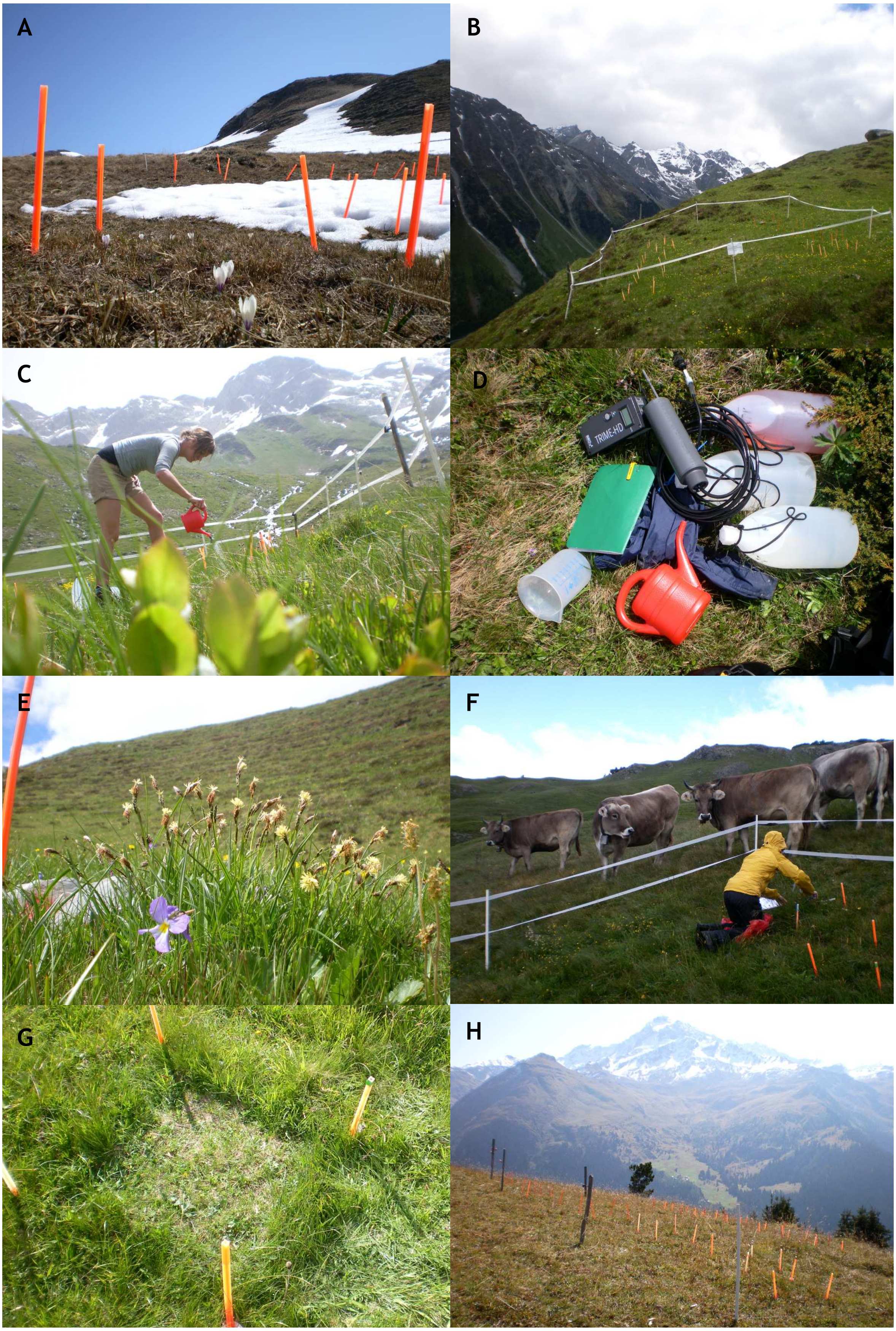
Tables

Table A1: Results of linear mixed regression of fraction of biomass of sedges (arcsin-sqrt-transformed) against pH and two fertilisation treatments (N and NPK) calculated for a pH of 6.79 (=STU). Cover of sedges in 2007 has been used as a covariable to correct for the sedges cover in the preceding year. The estimates are given for a mean cover of sedges in 2007 of 16% and a pH of 6.79.

Variable	Estimate (arcsin-sqrt)	Df effect	Df residuals	*t* value	*p* value
Control (Intercept)	0.316	1	75	8.61	< 0.001
Cover Carex 07	1.142	1	75	12.35	< 0.001
pH max	-0.563	1	38	-2.26	0.030
N (*versus* C)	0.117	1	75	2.69	0.009
NPK (*versus* C)	0.061	1	75	1.41	0.164
pH × N	0.079	1	75	2.67	0.009
pH × NPK	0.026	1	75	0.91	0.368

Plate 1. The course of field work: (**A**) A plot with melting snow at Alp Natons (NA1) in mid-May. (**B**) Full view of the site Alp Weissenstein (AW1) in June. (**C**) Fertilizer application at Bivio 2 (BV2) in June. (**D**) Field equipment: TDR, bottles with treatment solutions, watering can, measuring can, field book, rain coat. (**E**) Flowering *Carex sempervirens* tussock at Alp Weissenstein (AW1) in June. (**F**) Harvest at Alp Natons 1 in mid-July. (**G**) Plot after harvest. (**H**) View of, and from Plang Begls (PBE) after fence removal in September.

Color plates



Declaration

I affirm that this thesis, including the inserted figures, tables and map, was produced by me alone. It was accomplished by no means but those indicated. All passages originating from other acts, literally or analogous, are indicated with their references.

Münster, December 23rd ,2008

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