The Effect of Bedrock on Plant Community Structure in the Swiss Alps

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Abstract

Alps are consisting of a huge variety of bedrock-types and microclimates. Bedrock types exert a selective action on plant life in diverse ways. This comparative study investigated the effect of two different kinds of bedrock (dolomite and gneiss) on the biomass of functional plant groups in an alpine valley (Val Piora, Switzerland). In a completely randomized block design, three sites in Val Piora were chosen, each comprising dolomite and gneiss bedrock. The aboveground biomass of a defined surface was sampled with 4 to 6 replicates per bedrock site per block. Total dry weight and the dry weight of the functional plant groups were measured.

Total biomass on gneiss was significantly higher than on dolomite bedrock. Grasses have been the dominant functional plant group followed by forbs and legumes. Proportion of plant functional groups was not significantly influenced by the bedrock, while grass percentage showed with 45% on dolomite and 55% on gneiss, a trend of higher proportion. Absolute biomass of grasses was significantly higher on gneiss than on dolomite. No effect was shown for forbs and legumes. Covariates as pH, slope and altitude influenced the proportion of the functional plant groups.

Keywords

Bedrock; Dolomite; Gneiss; Plant biomass; Plant functional group; Swiss Alps

基岩对瑞士阿尔卑斯山脉植物群落结构的影响

摘　要　阿尔卑斯山脉含有种类繁多的基岩类型和小气候，基岩类型通过不同的方式会对植物产生影响。该对比研究实验探讨了在瑞士阿尔卑斯高山山谷（Val Piora）里两种不同基岩类型（白云石和片麻岩）对不同功能群植物生物量的影响。在完全随机区组设计中，每个区组内的每种基岩类型中，有 4 到 6 个重复样方用于地上生物量的取样，并测定样品总干重和各功能群植物的干重。

结果显示，片麻岩上的植物生物量显著高于白云石上的。禾草是最主要的功能群，其次是非禾草草本植物，最后是豆科植物。基岩类型并没有显著影响植物功能群的比例，但是禾草在白云石上只占 45%，低于麻岩上的 55%。禾草在片麻岩上的绝对生物量则显著高于白云石上的生物量。对于非禾草草本植物和豆科植物，基岩类型没有显著影响。pH、坡度和海拔会影响植物功能群的比例。

关键词 基岩；白云石；片麻岩；植物生物量；植物功能群；瑞士阿尔卑斯山脉

Introduction

The Alps have been hotspots for the European scientific study (Guisan and Theurillat 2001; Mörschel, Arduino et al. 2004). The Alps are consisting of a huge variety of bedrock-types (Herwegh and Pfiffner 1999) and microclimates. That's one of the most important reasons why there exist lots of endemic species (Becherer 1960) and rare species.

Bedrock types exert a selective action on plant life in diverse ways, both direct and indirect. Frequently, especially where outcrops are exposed at the surface, they can act as direct substrates for plants. A lot of studies about the effect of outcrops on plants in America can be found (Baskin and Baskin 1988; Wiser, Peet et al. 1996; Ware 2002), but to our knowledge there is hardly any information about the European Alps.

Given bedrock type can be transformed into soil by weathering. The derived soil will bear the imprint of its parent material, as features of texture, clay content, water holding capacity, and the quality of the mineral ions themselves (Kruckeberg 1986). Therefore the vegetation of one special bedrock type is composed of unique assemblages of plant taxa, with many endemic or near-endemic species. However, there are a few cases where some plant species can distribute in a broad substrate. Such broad substrate distribution is usually accomplished by either wide physiological tolerance to soil chemistry or by ecotypic adaptation to substrate (Ware 1990).

Among various kinds of the bedrock types, gneiss and dolomite are quite common in the Swiss Alps (Steinmann, Chawla et al. 2010). Gneiss is a common and widely distributed type of rock formed by high-grade regional metamorphic processes from pre-existing formations that were originally either igneous or sedimentary rocks. In gneiss, feldspar is abundant and, together with quartz, forms the granular, lighter colored layers. Dolomite rock is a carbonate mineral, similar to limestone but contains an additional magnesium atom in its mineral composition, mainly $MgCaCO_3$ mineral. Dolomite rock is, compared to gneiss, easily eroded with acid water. The pH of the soil on the dolomite bedrock is higher than what on the gneiss. The key component to nutrient uptake is the chemical solubility of the ion that the plant requires and that solubility is highly dependent on soil solution pH (Gough, Shaver et al. 2000). For example, P availability will be highest in slightly alkaline soils.

Besides of the underlying substrate, soil types also result from a combination of altitude and the influence of the slope angle. Fewer gentle slopes are available at higher altitude (Baskin and Baskin 1988; Wiser, Peet et al. 1996). The soil is less fertilized in the higher altitude.

The aim of this study was to test whether the geological bedrock will affect the plant community in the Val Piora of the Swiss Alps by comparing the biomass of different functional groups on dolomite and gneiss bedrock. We hypothesized that bedrock will be the main factor influencing the biomass of plant functional groups. We expected the plant biomass on the dolomite to be higher than on the gneiss bedrock because of the higher soil pH and higher nutrient availability. The ratio of legumes should increase on dolomite for the same reasons.

Materials and Methods

Study area

The study site was located in the Val Piora, an alpine valley in the Swiss Alps (46°33'N, 8°43'E). The valley follows the so-called Piora zone which is a zone of sedimentary rocks wedged between two crystalline basement units, the Penninic Lucomagno Nappe to the South and the Gotthard Massif to the North (Dahl, Anbar et al. 2010). The underground of the valley comprises basic dolomite containing gypsum that is surrounded by acidic gneiss (metamorphic granite containing SiO_2).

The soil which has developed directly on a dolomite rock is a shallow lithic leptosol (Chawla, Steinmann et al. 2010). Soil on dolomite underground has an alkaline pH of 6.8-7.4, while soil shows acidic pH values ranging from 3.5-4.8 along the other side Val Piora (Steinmann, Chawla et al. 2010).

Experimental design and Sampling

The comparative study was designed in a completely randomized block design with three blocks comprising gneiss and dolomite closely together (Fig. 1). Sampling sites were not grazed. There were two kinds of bedrock sampling sites in each block, and 4-6 randomly chosen plots within each sampling site. Overall, per bedrock type 16 plots were sampled at altitudes between 2010 and 2250 m a.s.l.(Table 1). Each plot had an area of 0.5m×0.5m. Within each plot the total aboveground biomass of two squares (0.2m×0.2 m) on opposite sites was sampled.

Table 1. The altitude in each sampling site

Block	Block 1		Block 2		Block 3	
Sampling site	Site 1 A	Site 1B	Site 2A	Site 2B	Site 3A	Site3B
Bedrock	Dolomite	Gneiss	Dolomite	Gneiss	Dolomite	Gneiss
Altitude (m a.s.l.)	2010	2010	2030	2110	2250	2250

The biomass of each sample was mixed thoroughly and half of the fresh weight was taken to be divided into the functional groups (grasses, legumes, non-legume forbs, shrubs and mosses). The separated functional groups as well as the remaining unseparated half of the biomass were dried at 65°C for 48h. Then the dry biomass was weighed.

To determine the pH of each plot, four soil samples were taken and pooled. Ten grams of the pooled soil were mixed with 10 ml of tridest water and were shaken at 100 rpm for 1.5 hrs. After samples have settled for 30 min, the pH of the supernatant was measured with the pH meter "761 Calimatic" (Knick, Berlin, Germany). The pH-Values were defined as stabile when they did not change for 10 sec. The slope and the altitude were determined for every plot.

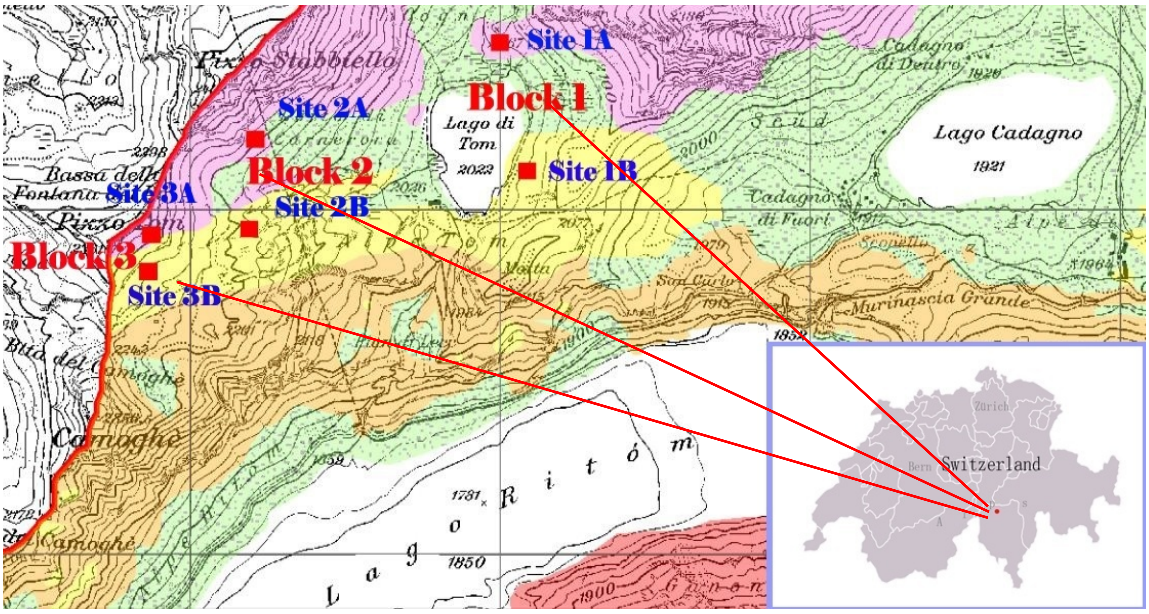

Fig. 1. Map of the study area showing sampling site locations (small red squares). The pink zone corresponds to the gneiss bedrock, and yellow zone corresponds to the dolomite bedrock. Capital letters indicate the positions of the studied blocks. Block 1 contained 4 plots for each bedrock site, while block 2 and block 3 contained 6 plots for each bedrock site.

Data analysis

Total dry weight of each sample was calculated by summing the dry weight of the unseparated half of the sample and the dry weights of all the functional groups.

Statistical analyses were carried out using R 2.12.2(R Development Core Team 2011). Means were considered to differ significantly at a type-I error level of $\alpha < 0.05$.

To test the influence of the bedrock on the total biomass and the biomass of the plant functional groups, a linear model was used with block and bedrock as the source of variation and slope, pH and altitude as covariates. The effect of bedrock types on the percentage of the plant functional group biomass was assessed using a linear model with block and bedrock and their interaction as main source of variation, as well as slope, pH and altitude as covariates. To judge whether the pH was determined by the type of bedrock, it was assessed using a linear model with block and bedrock as the source of variation. In order to improve homoscedasticity in the data, log transformations were used for the assessment of grasses biomass. For graphical presentation, only untransformed data were used.

Results

Soil pH

The mean value of the soil pH on the dolomite bedrock was 6.74±0.13, significantly (P=<0.0001) higher than the pH on the gneiss bedrock with the mean value of 5.53±0.07 (Fig. 2).

The effect of bedrock on total plant biomass

The total aboveground biomass on dolomite bedrock was 362.92±19.01 g/m^2, the one on gneiss bedrock comprised 419.67±29.09 g/m^2 (Table 2, Fig. 3). Total biomass on dolomite is significantly lower by 13.52% (P=0.024) compared to gneiss. A high variation of total plant biomass between blocks can be found, partial with opposite trends concerning the biomass on gneiss and dolomite bedrock (Fig. 4).

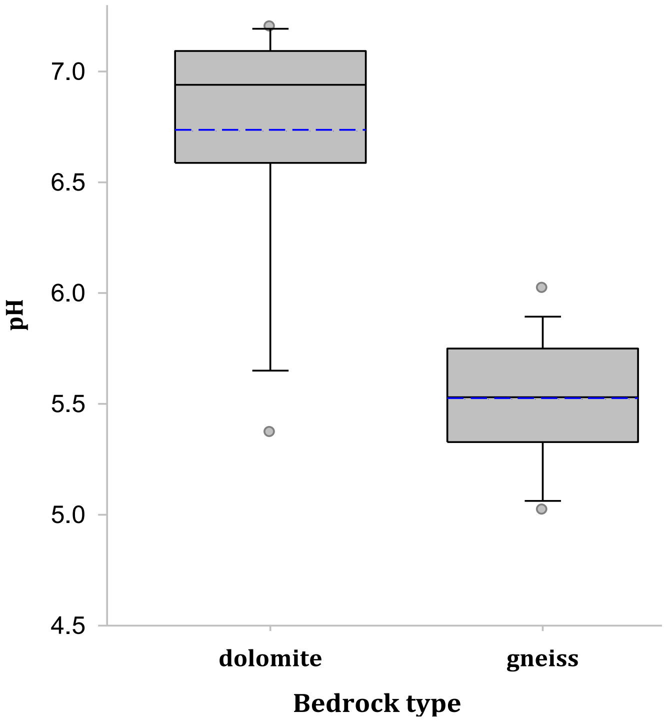

Fig. 2. Soil pH on dolomite and gneiss bedrocks. Data of 16 replicates per bedrock are shown. Blue dashed line represents the mean value of the pH in each bedrock type. The pH between the different bedrocks differs significantly (P<0.0001).

Table 2. Results of the linear model testing for the effects of bedrock and block on the plant biomass.

Source of variation	Df	total biomass P value	legumes P value	log(forbs) P value	log(grasses) P value
block	2	0.00028	0.9937	0.0377	0.00055
bedrock	1	0.02435	0.2817	0.7991	0.0330
block:bedrock	2	0.12473	4.8808	0.0003	0.5314
Residuals	25				

Prior to analysis data of non-legume forbs and grasses biomass were log transformed.

Table 3. Total aboveground biomass and percentage of functional plant groups on two different bedrocks. Data represent means±standard errors of 16 replicates. The P value of a linear model for the percentage of functional plant group biomass with block and bedrock and their interaction as the source of variation is shown.

Bedrock	Total biomass (g/m^2)	Grasses (%)	Legumes (%)	Non-legume forbs (%)
Dolomite	362.92±19.01	45.31±4.10	7.01±1.70	22.90±3.8
Gneiss	419.67±29.09	55.24±4.97	7.28±1.45	26.86±5.3
P value		0.1101	0.6402	0.6999

The effect of bedrock on the proportion of plant functional groups

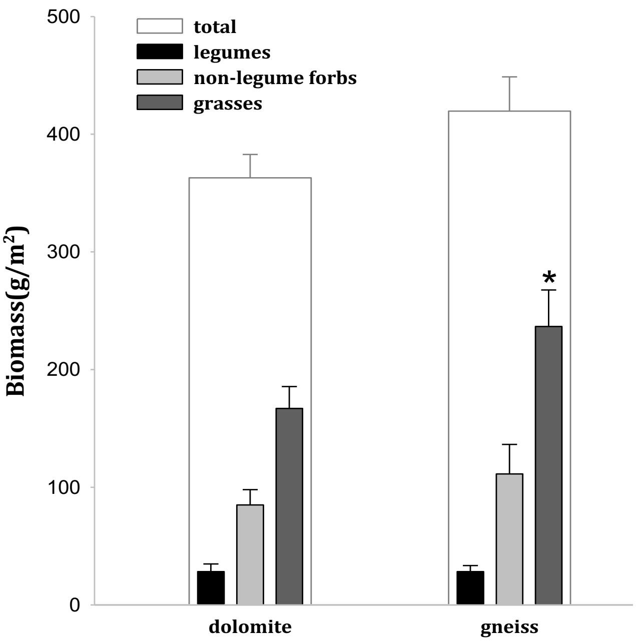

Fig. 3. Aboveground biomass of functional groups and total plants on dolomite and gneiss bedrock. Data represent means ± SE for 16 replicates per bedrock type. Significance levels of the F-test are indicated as: *P < 0.05

For both types of bedrock, the grasses had the highest biomass, 45.3% of the total biomass on the dolomite bedrock and 55.2% on the gneiss bedrock. The legumes had the lowest biomass, only 7% and 7.28% of the total biomass on the dolomite and gneiss bedrock respectively. The non-legume forbs comprised 22.9% and 26.9% of the total biomass on the dolomite and gneiss bedrock respectively (Fig. 3). None of the percentages of functional plant groups was significantly affected by the bedrock (Table 3), but biomass data showed a trend of a higher proportion of the grasses on gneiss bedrock. Grass percentage was affected by slope and block, legume percentage by pH and shrub percentage was influenced by altitude and block.

The effect of bedrock on the absolute biomass of plant functional groups

The biomass of grasses on gneiss (236.66±30.94 biomass/m^2) was significantly higher than on the dolomite (166.97±18.6 g biomass/m^2) (P=0.005) (Fig. 3). The pH was also shown to be a main factor influencing the grass biomass (P=0.0056) as well as the block. No significant effect of bedrock on the absolute biomass of legumes (28.27±6.46 on dolomite and 28.33±5.09 biomass/m^2 on gneiss) and non-legume forbs (84.93±12.99 on dolomite and 111.27±25.13 biomass/m^2 on gneiss) could be detected, but forbs seem to produce more biomass on gneiss (Fig. 3). Taking the ratio of the forbs to grasses biomass into account, the grasses biomass was affected by the abundance of forbs (P=0.00016). No significant effect of the covariates slope and altitude on the absolute biomass of the functional groups could be detected. The ratio of the forbs biomass to grasses biomass tended to be higher on gneiss than on dolomite, but statistical analysis failed to prove it.

The biomass production of single functional plant groups varied strongly between blocks (Fig. 4), partially showing contrasting trends of the effect of the bedrock. For instance, forbs biomass tended to be lower on gneiss compared to dolomite in block one and two, but block three depicted a converse relation.

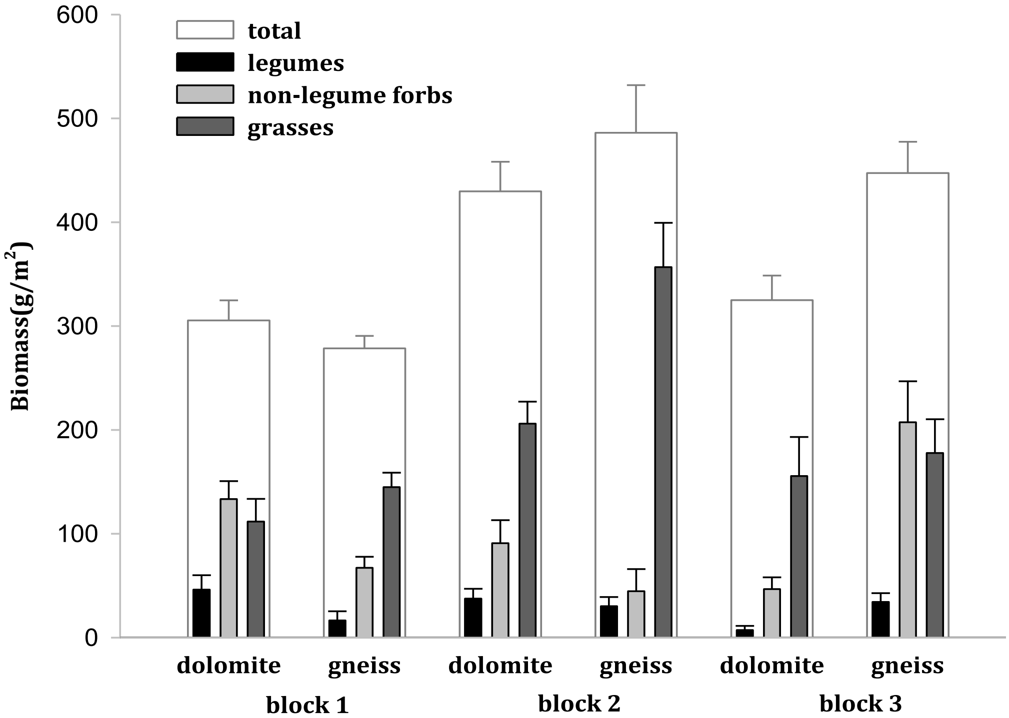

Fig. 4. Aboveground biomass of different functional plant groups and total plant on dolomite and gneiss bedrock in different blocks. Data represent means, and error bars represent SE for 4 or 6 replicates.

Discussion

Bedrock effect on the plant biomass

Our results did not agree with the hypothesis which predicted higher biomass on the dolomite bedrock (Fig. 3). The results suggest that more biomass is produced on the gneiss than the dolomite bedrock (Table 3). This effect is mainly due to an increased grass biomass (Fig. 3). An increase in forbs biomass could be proven statistically.
In accordance with the absolute biomass data, the percentage of grass relative to the total biomass is higher on gneiss (Table 3). Regarding the biomass, grasses dominate the meadows of the Piora valley, followed by forbs and legumes.
Steinmann et al. (2010) mentioned in his paper that the leptosol which has developed directly on a dolomite rock is quite shallow along the Val Piora and thus nutrient supply will be limited. The low nutrient availability will result in a low total biomass and furthermore will be a disadvantage for grasses in competition with legumes and herbs. Furthermore, leptosols are characterized by a poor water holding capacity (Schütt 2004). An insufficient and irregular water supply will be reflected in reduced plant growth.
Statistically, only the difference of the absolute biomass of grasses between dolomite and gneiss underground could be proven. We suppose, increasing the sample sites would manifest the trend that forbs and grass biomass is higher on gneiss than on dolomite bedrock. The chosen blocks have been close together which is not ideal for taking a representative sample. Furthermore, sampling plots within each block have been spatially separated by bedrock type thus not being randomly distributed. Due to the unbalanced design results are not well-defined, and the study should be repeated in a larger scale.

Soil pH and functional groups

Soil pH had a close correlation with the bedrock (Fig. 1). Soil on dolomite was shown to be alkaline, whereas soil on gneiss was slightly acidic. Bedrock defines soil pH. Therefore, soil pH also had a significant effect on the grass biomass as well as bedrock. Gough et al. (2000) provided evidence that pH is related directly to species richness regardless of the driving force behind soil acidity or base content. They found a stronger correlation with species richness than species density (Gough, Shaver et al. 2000). They discovered that most of the differences in species richness among sites are due to increased numbers of relatively sparse forbs species on non-acidic sites, while the dominant species at acidic sites tend to be still present but less abundant at non-acidic sites. Looking at Val Piora, the ratio of the forbs biomass to the grasses biomass tended to be higher on the dolomite bedrock. This indicates that dolomite bedrock might promote small forbs low in biomass to the detriment of grasses producing higher biomass. To illuminate this issue an analysis of the plant species diversity would be necessary.
Although there are specific endemic plants on bedrock, Some species might accomplish the occupation of different substrates by either broad ecological tolerance (substrate indifference) or by ecotypic adaptation to each of the substrates (Ware 1990). Many of

the endemic plant species are not restricted to a single geological substratum, and they grow equally well, or better, on other bedrock soil. But if the competition is fierce, they would choose the less competition sites. The soil pH on the gneiss maybe not as good as what on the dolomite, but there seems to be less competition and suit for the grasses.

Effect of other factors on the plant biomass

From table 1, we could see that besides of the bedrock effect, block had a big effect on the plant biomass. There may exist other factors influencing the plant biomass that we did not measure on the block level. Baskin (1988) evaluated the roles of the edaphic, genetic and light factor on plants in relation to the proximal causes of endemism of the endemic plants rock outcrop of unglaciated eastern United States. They found the requirement for a high level of light is the most important (Baskin and Baskin 1988).
Proportion of grass was influenced by slope, proportion of forbs by altitude. An effect of altitude is surprising as it varies only between 2010 and 2250 m a.s.l. The slope ranges between 12.16°-32.88°. Study design should exclude the influence of covariates like slope and altitude, but was not possible in this case.

Conclusion

Bedrock is a driving force of plant productivity and community structure in the Alps and thus should be taken into consideration when studying Alpine ecology. Management of alpine meadows will differ between sites of different underground and artificial nutrient input and grazing periods should be adjusted to the prevailing soil conditions. To gain a clearer picture of the effect of bedrock on plant productivity and plant community structure, large scale comparative studies should be accomplished including more response variables as plant diversity.

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