

Interaction of Carbon and Nitrogen Metabolisms in Alpine Plants

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9.1 Introduction

The importance of nitrogen (N) for plant growth has been well understood since the pioneering work of von Liebig (1840), which described the effect of individual nutrients on crops. Since this work, many studies have addressed plant nutrients in general and N in particular, leading to greater understanding of the coupling between N availability, carbon (C) and N fluxes, and whole plant growth.

Optimized whole plant growth requires a close relationship between C and N metabolisms. Although carbon fixation takes place in the leaves, its rate depends on leaf N content and thus on root N uptake, because chemical reactions are catalyzed by enzymes whose activities are based on the energetic substrate provided by photosynthetic C. Hence, the chemical composition of a plant in the different organs must be maintained in a narrow range, which therefore implies a balance between (1) N assimilation from the roots, (2) N allocation to the leaves and (3) C uptake of the leaves. This coupling is largely dependent on environmental constraints.

In alpine areas, the landscape-scale distribution of snow (which is closely related to the mesotopography) is a main driver of plant community composition and functioning. Through its effect on the length of the growing season, snow provides a complex ecological gradient affecting the seasonal course of temperature,

light, wind exposure, soil water content and nitrogen availability (Jones et al. 2000). Therefore, all temperature-dependent processes in alpine ecosystems are under the ultimate control of snow cover because it determines growing season length (i.e. the length of the favourable period), soil temperature and water and nitrogen availability (see Fig. 9.1). Typically, between late and early snowmelt locations, the delayed onset of the growing season can be particularly important, up to 40 days in the internal French Alps (Fig. 9.1). Besides, N availability in late snowmelt meadows is generally greater than in dry meadows, at least at the time of snowmelt (Baptist and Choler 2008; May and Webber 1982) and for some locations at all times of the year (Miller et al. 2009). This difference is reflected in all inorganic N pools, with gross and net N mineralization rates being systematically lower in early snowmelt locations compared to late snowmelt locations (Fisk et al. 1998; Miller et al. 2009). Given these constraints, whole plant growth and nutrient acquisition strategies vary greatly over very short distances within alpine areas.

According to the Intergovernmental Panel on Climate Change (IPCC 2007) and the European Environment Agency (EEA 2009), alpine plants will in future be exposed to enhanced CO₂ and temperature conditions. As described in more detail below, predicted temperature increases (IPCC 2007) are expected to have direct impact on plant performance. However, it should be also considered that temperature increases will have indirect effects in plants as a consequence of possible modifications of snow cover periods as well as shortages of N and water availability. In order to consider the effects of climate change on alpine plant growth and to identify potential synergistic and

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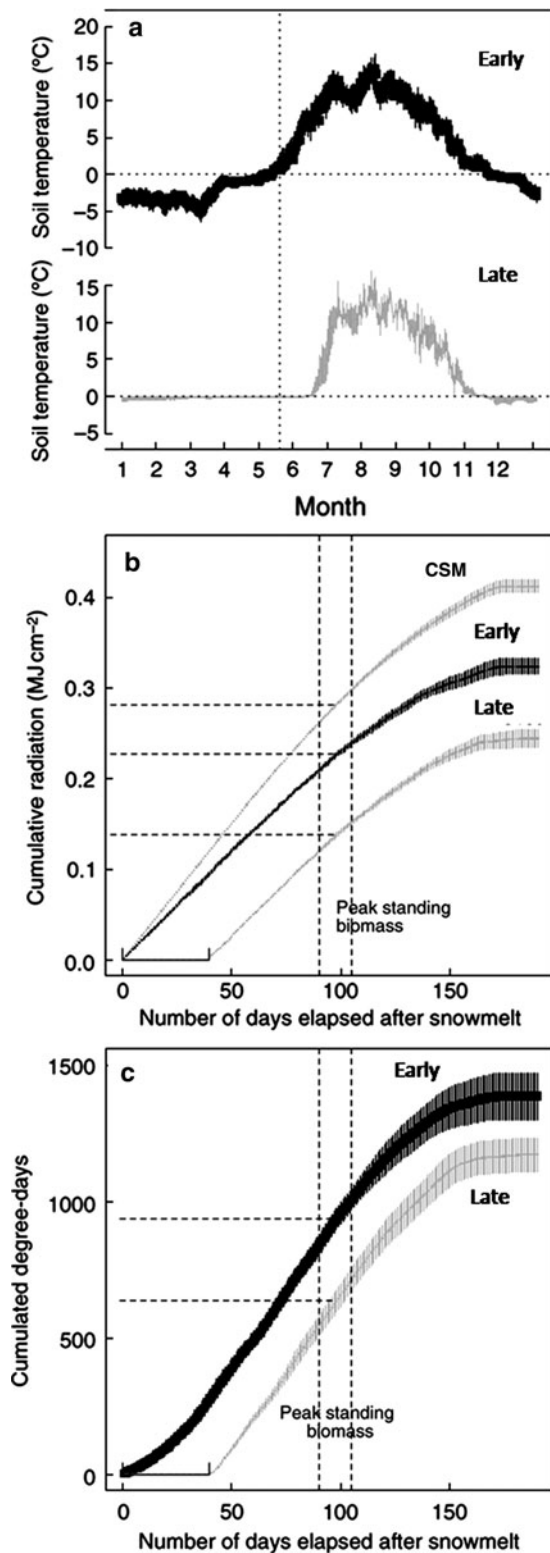


Fig. 9.1 (a) Time course of daily mean (\pm standard error) soil temperature 5 cm below the ground surface and (b) cumulative

antagonistic phenomena (Valladares and Pearcy 1997), it is crucial to fully understand the coupling between N and C fluxes and pools taking into account variations in plant metabolism along environmental gradients.

In this chapter, we will begin by reviewing the coupling of C and N cycles at the whole plant level along the environmental snow cover gradient with a functional trait approach, before we move on to a more detailed understanding of C and N coupling for C/N uptake and storage in alpine plants. Finally, we will address the potential effect of climatic change (changes in air temperature, snow cover and CO₂ concentration) on C and N metabolisms and as a consequence on whole alpine plant growth.

9.2 Relation Between Resource Availability, Carbon and Nitrogen Assimilation, Tissue Composition and Whole Plant Growth

9.2.1 Carbon and Nitrogen Metabolisms for Resource Acquisition

Plants have several contrasting and complementary strategies for optimizing C and N uptake. However, these strategies do not occur randomly across terrestrial biomes, but partly follow soil N supply. Indeed, a growing body of theoretical (Grime 1977; Chapin 1980; Westoby 1998) and empirical work (Reich et al. 1999; Wright et al. 2004) points to the existence of a fundamental trade-off between rapid acquisition of resources and conservation of resources in plant species along fertility gradients. Cumulative radiation during the growing season in the C140 and C180 communities. The clear sky model is shown for comparison.

radiation during the growing season in the late (*grey*) and early (*black*) snowmelt communities. In (b), the Clear Sky Model (CSM) is shown for comparison, and means (\pm standard error) were calculated over the period 1999–2004. Data were recorded at Briançon (1,300 m a.s.l.), 30 km from the study site. The Clear Sky Model developed in the framework of the European Solar Radiation Atlas (Rigollier et al. 1999) was used to model the incoming global irradiance on a horizontal plane under cloudless sky cumulative degree-days in early and late-snowmelt locations. (c) Cumulative degree-days in early and late-snowmelt locations. Data were averaged over the period 1999–2005 and were recorded at two or three different sites, depending on the year, close to the Galibier pass (France). Modified from Baptist and Choler (2008)

Fast-growing species from fertile habitats maximize resource acquisition, whereas slow-growing species in infertile habitats maximize resource conservation. A series of quantitative traits have been associated with this fundamental trade-off in plant function (Reich et al. 1992; Grime 1997; Garnier et al. 1999). Fast-growing species usually have a combination of high Specific Leaf Area (SLA), high tissue N concentration, low tissue density, high rates of C and nutrient uptake, and short-lived leaves. These traits are basically associated with (1) higher rates of maximum photosynthesis because the large amount of leaf organic N is mostly allocated to the photosynthetic machinery (Evans and Seemann 1989) and (2) with short-lived leaves due to low C/N ratios and physically soft foliage. The opposite traits characterize species from nutrient-poor habitats in which the mean residence time of nutrients tends to be maximized through greater organ longevity (in particular leaves) and/or higher resorption of nutrients from senescing organs. Because these traits are easy to measure for a large number of species and sites, they can be considered as precious tools to understand whole plant functioning and to relate it to ecosystem processes.

Within alpine regions, recent studies have demonstrated that consistent shifts in specific richness (e.g. Komarkova and Webber 1978; Kudo and Ito 1992; Theurillat et al. 1994) and in plant functional diversity occur along mesotopographical gradients (Kudo et al. 1999; Choler 2005). A greater Leaf Nitrogen Content (LNC), a higher SLA and a predominance of horizontal leaves (i.e. trait values generally associated with a high capacity for resource acquisition) are common features of species from late snowmelt sites (Choler 2005). These traits ensure efficient carbon fixation at the leaf and canopy levels and are generally associated with higher root respiration rates and higher N uptake (Craine et al. 2002, 2005; Tjoelker et al. 2005). Typically, Bliss (1956) reported at the community level that values of above-ground net primary productivity varied from $0.4 \text{ g m}^{-2} \text{ d}^{-1}$ on a dry windy ridge to $1.9 \text{ g m}^{-2} \text{ d}^{-1}$ in a wet meadow, while above-ground production totalled 280 g m^{-2} in dry meadows, 410 g m^{-2} in moist meadows and 600 g m^{-2} in wet meadows (Fisk et al. 1998). These results underlie a clear reduction of above-ground production from early to late snowmelt locations. In parallel, below-ground productivity ($\text{g m}^{-2} \text{ d}^{-1}$) and total N uptake in semi-controlled conditions was more

than twice as high for the late snowmelt species compared to the early snowmelt species (Baptist et al. 2009a). Total N accumulation for production averaged 3.9 g m^{-2} in dry meadows, 5.4 g m^{-2} in moist meadows, and 6.8 g m^{-2} in wet meadows (Fisk et al. 1998) suggesting a higher total N uptake in late snowmelt locations. This tight coupling of C fixation and N uptake in late snowmelt locations allows plants to counterbalance the snow-induced reduction in the carbon uptake period and thus to complete their vegetative life cycle quickly.

Conversely, species from early snowmelt sites are characterized by upright and thick leaves and low SLA, i.e. trait values generally associated with nutrient conservation strategies (Wright et al. 2004). Increased leaf thickness along with reduced surfaces of alpine plants might protect tissues from being abraded by wind-transported particles and ensure structural photoprotection against photoinhibition (Valladares and Pugnaire 1999; Germino and Smith 2000).

Overall, these studies demonstrate the existence of a fundamental trade-off between rapid acquisition of resources and conservation of resources in plant species along snow cover alpine gradients that are regarded as adaptations for overcoming nutrient limitations and other environmental constraints (especially soil water content and fertility). Typically, they reveal a shift from energy-limited plants (i.e. light, because of short growing season) to nutrient and water-limited-plants.

9.2.2 Whole Plant Distribution of N-related Function and Compounds in Relation to Root/Shoot C Balance

Although still relatively unknown (Garnier 1991; Osonne et al. 2008), growth and carbon allocation patterns are largely affected by the distribution of N-related functions and compounds in plants. Several mechanisms exist including various patterns of biomass allocation and differences in the uptake, assimilation and/or storage of N mineral forms ($\text{NO}_3^-/\text{NH}_4^+$) and organic forms (amino acids) as well as the efficiency of using the assimilated nitrogen to produce new biomass. In order to be assimilated into organic nitrogen, NO_3^- must be reduced by nitrate reductase (NR) to NO_2^- and then by nitrite reductase (NiR) into NH_4^+ . Both reactions require electrons from

photosynthetic electron transport. At the leaf level, NH_3 is converted into amino acids by the GS/GOGAT enzyme reaction and carbon skeletons provided by the organic acids derived from the tricarboxylic acid cycle in the mitochondria. These C-skeletons used for amino acid biosynthesis are derived from glycolysis, photosynthetic carbon reduction, the oxidative pentose phosphate pathway and the citric acid cycle, and ATP for the GS/GOGAT reaction is generated by photosynthesis and respiration (Lawlor 2002). Accordingly, the site of NO_3^- reduction (roots and shoots) may have a substantial impact on the C demand for NO_3^- assimilation. For example, species that reduce NO_3^- predominantly in their shoots may have the advantage of being able to use the excess reductant produced in photosynthesis (Pate 1983). By contrast, species that reduce NO_3^- mainly in the roots must obtain their reductants from glycolysis and the oxidative pentose phosphate pathway (Oaks and Hirel 1986). Depending on the plant species and growing conditions, nitrate reduction may be predominantly in the shoot or the root, or there may be some intermediate strategy (Pate 1983; Andrews 1986).

According to Scheurwater et al. (2002) and Andrews (1986), under optimum nutrient availability conditions, shoots are the main site of whole plant NO_3^- reduction in both fast- and slow-growing grasses. However, the mechanisms underlying such a shoot versus root pattern of N reduction may display large interspecific variability in non-optimal environmental conditions. For example, a recent study conducted by Baptist et al. (2009a) with fast (*Carex foetida*) and slow (*Kobresia myosuroides*) growing alpine plants showed that fast-growing species displayed improved photosynthetic capacity and decreased N reduction capacity in leaves, which was compensated by the preferential C allocation to root growth and/or storage. These plants increased the translocation of reduced N to above-ground organs so as to compensate for the lower N assimilation capacity. The high C flux allocated to the below-ground compartment in *C. foetida* promoted significant levels of NO_3^- reduction in the roots (Pate 1980). Hence, although these results cannot be generalized, they suggest that an allocation-based balance between root N reduction and leaf CO_2 assimilation is involved in growth strategies of alpine species growing under short, energy-limited vegetation periods. This coupling between C and N fluxes was less apparent in

the case of slow growing species that experienced higher N reduction in the leaves.

Depending on nutrient acquisition strategies, preferential N uptake (mineral, organic) might be expected in order to adapt to N form availability and to optimize uptake and reduction costs especially in the alpine areas. Indeed, approximately 81% of the energy required to synthesize protein with nitrate as the source of nitrogen is used in reducing nitrate and synthesizing amino acids, however when nitrogen is supplied as ammonium, only 2% of the energy involved in protein synthesis is required to synthesize the constituent amino acids. Hence, the conversion of nitrate into amino acids in the cell is a process that consumes large amounts of energy and carbon. Plant roots also display high-affinity uptake systems for amino acids and therefore amino acids can be readily catabolized or used without additional costs.

Numerous studies have addressed the functional significance of the uptake of various forms of N by alpine plants and have generally indicated that all species were capable of taking up organic nitrogen (Chapin et al. 1993; Kielland 1994; Raab et al. 1999; Miller and Bowman 2003), some even equalling or exceeding inorganic N uptake (Raab et al. 1999; Xu et al. 2006). However, relative concentrations of N at the sites of plant sampling did not correspond to patterns of N uptake among species. Instead, species from the same community varied widely in their capacity to take up NH_4^+ , NO_3^- and glycine, suggesting the potential for differentiation among species in resource (N) use and also during the growing season. For example, while *Festuca eskia* mainly used NH_4^+ early and NO_3^- late in the growing season, the reverse was observed for *Nardus stricta* (Pornon et al. 2007). Besides, according to Miller and Bowman (2003), soils from late snowmelt locations and from mid-gradient locations characterized by high amino acid concentration do not support species that exhibit a high capacity for glycine uptake. By contrast, Baptist et al. (2009a) indicated that *Carex foetida*, which grows in late snowmelt locations, displayed higher amino acid uptake compared to species from early snowmelt locations (i.e. *Kobresia myosuroides*). Hence, along snow cover gradients, contrasting and complementary strategies exist for increasing N uptake efficiency, and/or for broadening the options of N uptake from resources of different chemical composition. Although soil N fertility plays an

important role in species' distribution and abundance, it is therefore a relatively poor predictor of plant N preferences. Rather, these patterns may favour the potential for species coexistence in a given habitat and might allow plants to adapt to N-form seasonal variations.

9.3 Carbon and Nitrogen Storage in Alpine Plants

The acquisition and the allocation of resources are dependent on the build-up of stored carbohydrate and nutrients. This function is particularly important in mountain environments characterized by harsh and constraining conditions (i.e. long, cold winters and short growing seasons) as it gives plants: (1) the support of vegetative regrowth following dormancy (Menke and Trlica 1981), (2) the ability to bridge temporal gaps that exist between resource availability and resource demand (Chapin et al. 1990), (3) the support for sexual or vegetative reproduction during the absence of photosynthesis and (4) the ability to survive calamities such as defoliation, shading or frost. Moreover, the mobilization of stored nitrogen and carbon reserves facilitates competing sinks and permits successful completion of reproduction before the onset of the winter season. Finally, the occurrence of a large concentration of soluble proteins may be important in the low temperature conditions of alpine regions (Öncel et al. 2004). It was typically the case of the leguminous alpine herb, *Oxytropis sericera*, or of members of the Caryophyllaceae that vegetative and reproductive growth was partly supported from stored reserves at least in its earlier stages (Wyka 1999).

Although starch and sucrose are considered as the major storage compounds for cereals and grasses (grains filled with starch) other carbohydrate stores can be metabolized, e.g. fructans in *F. paniculata*, a subalpine species, or cyclitol in some Caryophyllaceae. While *B. bistortoides* relies almost entirely on glucose, fructose and sucrose, *Castilleja puberula* produces high concentrations of mannitol, and *Trifolium nanum* contains high concentrations of cyclitols. According to Monson et al. (2006), in alpine fellfields two groups emerged: the first constituted by *Trifolium sp.* and *Artemisa scopulorum*, which maintain a majority of the soluble carbohydrate as cyclitols, whereas the monocots *Carex* and *Luzula* exhibited little cyclitol

and maintained a majority of soluble carbohydrate as sucrose. The selective advantage of fructan or cyclitol as storage carbohydrates is commonly based on the idea that the utilization of the vacuole as a storage compartment would allow plants to exploit constraining environments where periods of positive carbon balance are short and net mobilization of reserves is required to sustain growth (Pollock and Cairns 1991; Monson et al. 2006). Indeed, by maintaining supplies of fructose and sucrose and other ready-to-use C-compounds in vacuoles, these species obviate the need for transport of carbohydrate over distance as in starch storing species (Bloom et al. 1985; Hendry 1987). Besides, in subalpine and alpine ecosystems, plant growth starts, depending on species, either 10 days before and after snowmelt, which largely sensitizes plants to freezing events leading to the loss of tissue (Körner 1999; Inouye 2000, 2008). The presence of such C stores in the stem base and leaf vacuole might offset possible damaging effects associated with frost events (Bloom et al. 1985).

Several studies in controlled environments and field conditions have demonstrated that the availability of N reserves, and particularly the concentration in vegetative storage proteins, is closely related to shoot growth potential (Avicé et al. 1996; Justes et al. 2002; Meuriot et al. 2005). However, to our knowledge, no studies have identified patterns of N storage along alpine gradients. The species that possess the highest protein concentration and level of vegetative storage protein (VSP) accumulation consequently exhibit the fastest bud growth, the greatest rate of expansion in leaf area index and the highest shoot production in spring (Justes et al. 2002). This increase in N reserves in perennial organs (taproot), especially in the form of VSPs, can be an important adaptive trait towards tolerance to unpredictable events in alpine environments, to sustain growth at the beginning of the growing season or to withstand processes of cold hardening, which is fundamental in alpine habitats. For example, *Eriophorum vaginatum* reached its maximum growth rate early in the season supported entirely by N stored in the stem at a time when the roots were still frozen in the soil (Shaver et al. 1986). By contrast, according to Jaeger and Monson (1992) and Lipson et al. (1996), rather than using N stores to start its growth earlier in the season, *Bistorta bistortoides* used them to support the high demand for resources encountered during the growing season when leaves competed for substrate

that could not be supplied adequately by soil uptake alone. Hence, although the storage organ of *B. histortoides* accommodates luxury uptake of N, the major function of the rhizome seems to retain a pool of mobile nitrogenous compounds to accommodate predictable seasonal variation in N supply and demand rather than to capitalize on unpredictable events. Similarly, Kleijn et al. (2005) demonstrated that reserves allow *Veratrum album* to complete the above-ground growing cycle as fast as possible and thus reduce the exposure to stochastic events such as frosts. Hence, higher nutrient concentrations and important N stores permit the refilling of carbohydrate stores used to promote growth during the growing season, and to support maintenance metabolism during the winter season. However, according to the literature, most of the studied plants rely primarily on soil N-resources for their seasonal growth rather than on N stores. Hence, a reduction in soil N availability due to lower snow precipitations may result in a reduction of C stores and therefore (1) decreased allocation to growth and reproduction and (2) a lower ability to cope with hazardous events.

9.4 Effect of Climatic Changes on Carbon–Nitrogen Interactions in Alpine Plants

9.4.1 Global Climate Change in Alpine Areas

The EU White Paper on Adaptation (EEA 2009) names the Alps as among the areas most vulnerable to climate change in Europe, although much uncertainty still exists as to the possible effects of such changes on vegetation communities and ecosystem properties (Theurillat and Guisan 2001). After the industrial revolution, as a consequence of human activity, atmospheric [CO₂] has steadily increased from an estimated 280–379 μmol mol⁻¹ in 2005 with a current average increase of 1.9 μmol mol⁻¹ per year (Alley et al. 2007). According to the predictions of the IPCC (2007), at the end of the present century this concentration may be around 700 μmol mol⁻¹, i.e. 2.5 times the preindustrial value. As a consequence, the global mean surface temperature has risen by 0.74°C ± 0.18°C over the last 100 years (1906–2005), and Europe has become warmer than the global average especially in

the south-west, the north-east and mountain areas (IPCC 2007). Besides, according to Dye and Tucker (2003), between 1972 and 2000 the duration of the snow-free period in northern hemisphere land areas increased by 5–6 days per decade, and earlier snow cover disappearance in spring has been observed to have increased by 3–5 days per decade. Moderate future climate scenarios predict a temperature rise of 3.9°C up to the end of the twenty-first century for the Alps, with stronger warming during the second half of the century (European Environment Agency 2009; Beniston 2003; Noguès-Bravo et al. 2007) associated with an alpine-wide decline of snow-covered days (see Stewart 2009 for a review). As a consequence, the observed and projected impacts include changes in the hydrological cycle of mountain regions and changing water availability in elevated and surrounding regions, a decline in glacier cover, and a reduction in permafrost, increasing hazards and damage to high-mountain infrastructure and northward and uphill distribution shifts of many European plant species (60% of mountain plant species may face extinction by 2100) (Auer et al. 2007; Beniston 2003; Noguès-Bravo et al. 2007). As a result of the changing precipitation patterns, there will also be a change in the incidence of dry periods. The enhancement of temperature will lead to increased rainfall, less snowfall during the winter, and consequently water availability limitation during the growing season (EEA 2009).

9.4.2 Effect of Increasing Temperature and Decreasing Snow Cover Duration on Plant Performance

As mentioned above, warmer conditions and decreased snow cover are expected in the Alps (IPCC 2007, Figs. 9.2 and 9.3), which has the potential to alter individual plant performance by influencing the growing season length and soil microclimate. Warmer conditions are very likely to increase productivity and the biomass of alpine plant communities (Theurillat and Guisan 2001), however, this question has mainly been addressed through modelling approaches. Typically, Riedo et al. (1997) showed that a seasonally uniform temperature increase by 2°C raised net primary production by 50% in an alpine landscape by modelling the productivity of managed grasslands in the Swiss Alps. Similarly, Baptist and

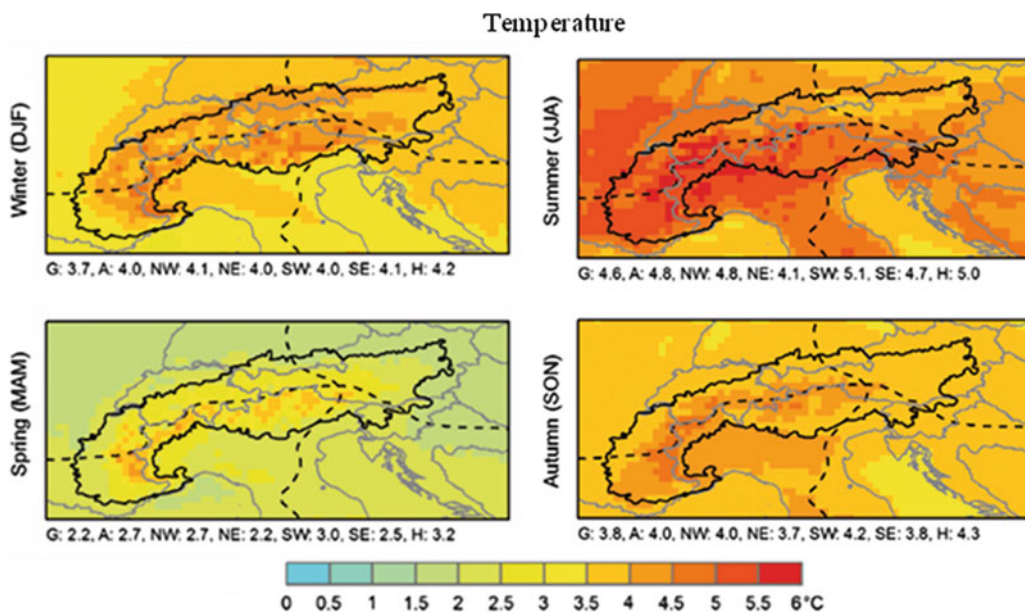


Fig. 9.2 Seasonal changes in precipitation and temperature up to the end of the twenty-first century, according to CLM scenario A1B. Figure adapted from the European Environment Agency, Regional Climate Change and Adaptation (2009)

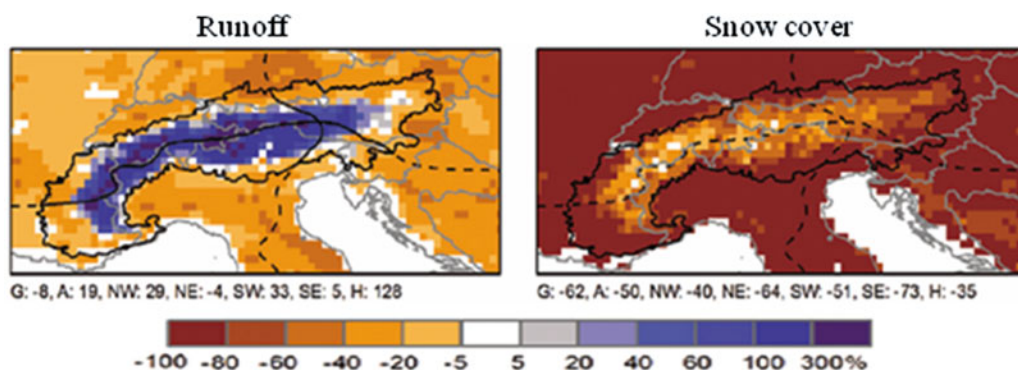


Fig. 9.3 Run-off and snow cover change up until the end of the twenty-first century in the winter, according to the CLM A1B scenario. Figure adapted from European Environment Agency, Regional Climate Change and adaptation (2009)

Choler (2008) demonstrated that the snow-induced changes in the length of the growing season might have a great impact on the seasonal gross primary productivity of alpine plant communities.

However, in real field conditions, one might predict a small impact on carbon uptake if plant communities are dominated by periodic species, i.e. species with a fixed, genetically controlled growing period (Sørensen 1941). Conversely, the short-term consequences for ecosystem productivity would be stronger if aperiodic species, i.e. species able to extend their vegetative growth, were dominant. Besides, there is a realistic

possibility of an increased frequency of freezing events during periods when plants are active in mountain environments, because a warmer climate might advance phenology in many alpine plants with a current risk of freezing temperatures (Inouye 2000, 2008). Indeed, during winter, plants are usually protected from low temperature by snow cover or by specific features (e.g. higher concentration of sugars or supercooling, see previous section). The situation is different once snow disappears because plants generally display rapid dehardening. Hence, if snowmelt is advanced, the plants will be exposed to freezing

temperatures making them much more sensitive to frosts (Körner 1999; Baptist et al. 2009b; Sierra-Almeida and Cavieres 2010).

Besides, since microbiota-derived N represents an important source of N for alpine plants (Schmidt et al. 2007), the temperature effect on bacterial activity will strongly condition plant growth. Studies on plant-microbe interactions in the alpine N cycle have revealed a seasonal separation of N use, with plants absorbing N primarily during the summer months and microbes immobilizing N primarily during the autumn months (Jaeger et al. 1999; Lipson et al. 1999; Schmidt et al. 2007). The peak of nutrients at snowmelt, coupled with the mineral release from snowmelt water, is crucial as it partly supports seasonal plant growth, representing up to 7–12% of total N uptake during the growing season (Bilbrough et al. 2000). Unlike early snowmelt species, late snowmelt alpine species strongly rely on this flush of mineral nitrogen (e.g. Kleijn et al. 2005; Monson et al. 2006), which allows rapid expansion of photosynthetic tissues and ensures efficient light capture and carbon fixation (Bryant et al. 1998; Baptist et al. 2010). In the context of global climate change we can expect that, despite a potential plant growth-stimulating increase in temperature, reduced snow cover and advanced snowmelt might dramatically impact the growth of species from late snowmelt locations (Björk and Molau 2007). This might occur due to (1) the growth period not matching the period with large soil N availability and (2) because the soil may dry out to a great degree during summer. Further studies addressing climate change effects and the overlap between environmental conditions advantageous for plant growth and N release from microorganism collapse will be crucial in order to understand the response of alpine plants to future climate conditions and their redistribution within alpine environments.

9.4.3 Elevated CO₂ Effect on C and N Interactions in Alpine Plants

Changes in C and N metabolism, implying changes to overall plant growth, cannot be dissociated from the ‘fertilization effect’ of increasing atmospheric CO₂. Understanding how plants will respond to the rapid CO₂ increase and developing knowledge about their capacity to adapt is an essential initial step in

understanding the full impact that global climate change will have on terrestrial ecosystems (Leakey et al. 2009). During recent decades, several CO₂ enrichment experiments have been conducted in plants, and the results have shown that elevated CO₂ can have significant effects on the growth and physiology of plants (Saxe et al. 1998; Ainsworth and Long 2005; Körner et al. 2005; Hovenden et al. 2008; Aranjuelo et al. 2008). Primary effects of CO₂ enhancement on plants are well documented (Nowak et al. 2004; Long et al. 2004; Aranjuelo et al. 2009) and include increased plant biomass and leaf net photosynthetic rates (Long et al. 2004; Nowak et al. 2004; Ainsworth and Long 2005). However, photosynthetic and growth responses will depend on their genetically determined potential (Long et al. 2004; Nowak et al. 2004; Aranjuelo et al. 2009). Although most of the research on climate change effects in plants has been conducted in fast-growing plants, it should be considered that slow-growing plants account for a large proportion of species. Because these plants usually grow in extreme environmental conditions, such as alpine environments, it is not clear to what extent their growth rate and, consequently, their responsiveness to elevated CO₂ is going to be conditioned by their own metabolic limitations. In this context, Poorter and Pérez-Soba (2001) stated that slow-growing plants would be less responsive to elevated CO₂ as a consequence of their metabolism and the construction costs. However, based on photosynthetic models, Lloyd and Farquhar (2000) suggested that slow-growing plants would be more responsive to enhanced CO₂ than fast-growing plants. In a first report, Körner and Diemer (1987) compared the CO₂ response curves of 12 plants, later extended to 20 species (Körner and Pelaez Menendez-Riedl 1989) grown at different altitudes and CO₂ levels and observed that high altitude plants with lower ambient CO₂ increased their efficiency of CO₂ utilization. In a later study conducted by Körner et al. (1997), where alpine plants were exposed to elevated CO₂ conditions (355 versus 680 μmol mol⁻¹) in open top chambers (OTC), the authors observed that plant biomass was not affected by the CO₂ level. The study also indicated that ecosystem gas exchange was increased in plants grown under elevated CO₂ conditions. This increase in CO₂ concentration may enhance the potential net photosynthesis for C₃ plants, because ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) is not CO₂ saturated

at the current concentration (Drake et al., 1997). This enzyme catalyses the photosynthesis and photorespiration reactions, but the current atmospheric CO₂ concentration is insufficient to saturate Rubisco in C₃ plants. Thus, an increase in ambient CO₂ increases the leaf internal CO₂ concentration and the CO₂/O₂ ratio at the Rubisco site, which favours carboxylation rather than oxygenation of ribulose-1,5-bisphosphate (RuBP) (Andrews and Lorimer 1987). In this context, a study conducted in alpine plants exposed to CO₂ conditions by Körner et al. (1997) revealed that although photosynthetic activity increased under elevated CO₂ conditions, no statistical differences were observed in biomass production. The excess C associated with the enhanced CO₂ fixation in these plants was accumulated in the leaves (Körner et al. 1997). This study suggested that with some exceptions, total non-structural carbohydrates (TNC) increased (mainly due to sucrose, glucose and fructose enhancement) under elevated CO₂ conditions. As observed by the authors, these results are in agreement with previous studies (Sakai and Larcher 1987; Guy 1990) which support the idea that plants from cold habitats accumulate soluble sugars so as to maintain a high degree of frost resistance throughout the vegetation period (see above).

Many studies have shown that photosynthesis acclimates to elevated CO₂ over long-term experiments, a process often referred to as 'down-regulation' (Long et al. 2004). A study conducted on alpine plants described that although exposure to elevated CO₂ conditions increased CO₂ utilization efficiency, depending upon the extent and duration of CO₂ enhancement, a tendency to downward adjustment of photosynthesis was observed (Körner and Diemer 1994; Körner et al. 1997). Reduced or acclimated stimulation of photosynthesis is attributed to stomatal (Naumburg et al. 2004) and non-stomatal limitations (Aranjuelo et al. 2009). Non-stomatal limitations reduce photosynthesis due to reduced light capture (Aranjuelo et al. 2008) or decreased Rubisco carboxylation of RuBP (Stitt and Krapp 1999; Long et al. 2004; Aranjuelo et al. 2005). There are two basic mechanisms by which Rubisco down-regulation occurs. The first mechanism hypothesizes that the reduction in Rubisco content occurs as a consequence of the leaf C build-up (Moore et al. 1999; Aranjuelo et al. 2009). According to the second mechanism, decreases in Rubisco content may reflect a general decrease in leaf N availability (Ainsworth and Rogers 2007).

Based on the C build-up theory, enhancement of leaf carbon content caused by the greater photosynthetic rates of plants exposed to elevated CO₂ induces suppression of gene encoding for proteins belonging to the photosynthetic apparatus, resulting in decreased photosynthetic capacity (Moore et al. 1999; Jifon and Wolfe 2002). When plants exposed to elevated CO₂ are limited in their ability to increase C sink strength, they decrease their photosynthetic activity to balance C source activity and sink capacity (Thomas and Strain 1991). Although the C source capacity increases as a consequence of photosynthesis and carbohydrate synthesis during the early stages of elevated CO₂ exposure (Drake et al. 1997), the capacity to make use of such an increased C supply will condition responsiveness of the photosynthetic apparatus in the long term (Aranjuelo et al. 2009). The ability to "use" such an increase in C depends on the capacity of the actual sinks or development of new sinks (Stitt and Krapp 1999; Lewis et al. 2002; Aranjuelo et al. 2009). As explained by Körner et al. (1997), there are four pathways through which excess C could be diverted: (1) respiratory losses during the dormant season, (2) C accumulation in soil microorganisms, (3) accretion of soil organic matter, and (4) export from the system in the form of dissolved organic matter. In the case of alpine plants, the previously mentioned study conducted by Körner et al. (1997) did not detect significant differences in respiratory losses. Likewise, elevated CO₂ had no effect on soil respiration, microbial biomass or on soil C and N. These results suggest that the inability of such plants to "use" the extra C caused the carbohydrate build-up that led to adjustments in photosynthetic activity in alpine plants exposed to elevated CO₂ conditions. Furthermore, it should be considered that, since N availability is a key factor conditioning responsiveness of the photosynthetic apparatus, there is evidence that the carbohydrate-mediated repression of photosynthetic genes is more severe in nitrogen-deficient plants than in nitrogen-depleted plants (Stitt and Krapp 1999).

The second hypothesis states that Rubisco activity decreases due to the relocation of N within the plant. Recent studies indicated that, under elevated CO₂ conditions, plants increased their N use efficiency (NUE) through the redistribution of the excess N invested in Rubisco (Ainsworth and Rogers 2007). Low leaf N could lead to either a proportional (Geiger et al. 1999) or a selective (Reviere-Rolland et al. 1996)

reduction in Rubisco. This hypothesis suggests that there is N limitation where N uptake from soils fails to keep pace with photosynthesis and C acquisition. According to the description of Körner et al. (1997), in alpine plants, the exposure to elevated CO₂ has no measurable effect on sugar and amino acids exuded by the roots into the soil. This study also showed that, at elevated CO₂ concentration, a low soil N supply could limit photosynthesis, leading to diminished plant N availability in the long term. Limited C supply to soil microbiota together with the low soil N availability of those plants might have limited N availability. N availability is a critical factor, limiting plant growth and increasing the response to elevated CO₂ conditions. Since low N availability often strongly limits biomass production in alpine plants (Bowman et al. 1993; Haselwandter et al. 1983), changes in plant N availability induced by exposure to elevated CO₂ could modify rates of N cycling and cause shifts in plant species dominance. However, according to the observations of Arnone (1997, 1999) on different high-elevation native Swiss alpine plants, elevated CO₂ does not modify soil N content.

These studies highlighted the fact that the CO₂ effect on photosynthetic activity and consequently on plant growth will be strongly mediated by N availability. Although little is known about the CO₂ × N effect in alpine plants, studies conducted on other plants suggest that the role of N availability will be a key factor conditioning the capacity of such plants to develop or increase C sink strength. More research is therefore needed on this topic.

9.5 Conclusions and Perspectives

In alpine areas, the productivity of most communities and species is constrained by the supply of N, but also by the length of the growing season and water availability. These constraints are distributed along topographical gradients and vary from energy-limited species to nutrient- and water-limited plants from late to early snowmelt locations. As a result the acquisitive nutrient strategies of alpine plants shift towards conservative nutrient strategies. Little information is

available concerning the coupling between C and N fluxes within the alpine plants as well as the residence time of C and N in different organs. In fertile habitats, species experienced high C fixation coupled with higher root N uptake, although most species reduce nitrogen in the leaves rather than in the roots. By contrast, alpine species do not display a correlation between nutrient acquisition strategies and preferential N-form uptake. This process appears to be highly idiosyncratic and can be interpreted as an adaptation to seasonal variations in N-form and a way to maintain plant coexistence in the ecosystem. Alpine plants store large amounts of C and N in the different storage organs (roots, bulb etc.). However, even though C stores appear to be crucial for the start of growth at the beginning of the growing season, N reserves seem to support the high demand for resources during the growing season when soil uptake alone cannot provide adequate supplies for whole plant demand.

As discussed above, although very few studies have considered the predicted climate change effect on the performance of alpine plants, it is crucial to improve our knowledge of this topic, because plant growth and species distribution will be strongly affected in the near future. Lengthened growing seasons might lead to an increase in net primary productivity depending on the phenological and frost tolerance features of alpine plants. Also, for the correct performance of alpine plants it will be crucial that the growth period matches the period of large soil N availability, namely at snowmelt. Accordingly, the species growing in late snowmelt locations might be the most sensitive to climatic change, as they generally display a low capacity to recover from frost events and depend greatly on the pulse of nitrogen at snowmelt.

Furthermore, due to synergistic and antagonistic phenomena, future studies should consider the interaction of the elevated CO₂ effect and other predicted growth-limiting conditions, such as temperature, and N and water availability. The very few studies conducted up to this point on this topic show that the CO₂ effect will be mediated by N and temperature. However, very little is known about the key processes involved in these responses. Knowledge of these topics is imperative to further understand how alpine plants (at the individual and community level) will cope with climatic change in the following decades.

References

- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytol* 165:351–372
- Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO₂]: mechanisms and environmental interactions. *Plant Cell Environ* 30:258–270
- Alley R, Berntsen T, Bindoff NL et al (2007) Climate change 2007: the physical 613 science basis. In: Summary of policy-makers fourth assessment report of working group I, Intergovernmental panel on climate change, Geneva, Switzerland
- Andrews M (1986) The partitioning of nitrate assimilation between root and shoot of higher plants. *Plant Cell Environ* 9:511–519
- Andrews JT, Lorimer GH (1987) Rubisco: structure, mechanisms and prospects for improvement. In: Hatch MD, Broadman NK (eds) *Biochemistry of plants*, vol 10. Academic, New York, pp 132–207
- Aranjuelo I, Irigoyen JJ, Pérez P, Martínez-Carrasco R, Sánchez-Díaz M (2005) The use of temperature gradient tunnels for studying the combined effect of CO₂, temperature and water availability in N₂ fixing alfalfa plants. *Ann Appl Biol* 146:51–60
- Aranjuelo I, Irigoyen JJ, Sánchez-Díaz M, Nogués S (2008) Carbon partitioning in N₂ fixing *Medicago sativa* plants exposed to different CO₂ and temperature conditions. *Funct Plant Biol* 35:306–317
- Aranjuelo I, Pardo T, Biel C, Savé R, Azcón-Bieto J, Nogués S (2009) Leaf carbon management in slow-growing plants exposed to elevated CO₂. *Glob Chang Biol* 15:97–109
- Arnone JA III (1997) Indices of plant N availability in an alpine grassland under elevated atmospheric CO₂. *Plant Soil* 190: 61–66
- Arnone JA III (1999) Symbiotic N₂ fixation in a high Alpine grassland: effects of four growing seasons of elevated CO₂. *Funct Ecol* 13:383–387
- Auer I, Böhm R, Jurkovic A et al (2007) HISTALP – Historical instrumental climatological surface time series of the Greater Alpine Region 1760–2003. *Int J Climatol* 27:17–46
- Avice JC, Ourry A, Lemaire G, Boucaud J (1996) Nitrogen and carbon flows estimated by ¹⁵N and ¹³C pulse chase labelling during regrowth of alfalfa. *Plant Phys* 112:281–290
- Baptist F, Choler P (2008) A simulation on the importance of growing season length and canopy functional properties on the seasonal gross primary production of temperate alpine meadows. *Ann Bot* 101:549–559
- Baptist F, Tcherkez G, Aubert S, Pontailler JY, Choler P, Nogués S (2009a) ¹³C and ¹⁵N allocations of two alpine species from early and late snowmelt locations reflect their different growth strategies. *J Exp Bot* 60:2725–2735
- Baptist F, Flahaut C, Streb P, Choler P (2009b) No increase in alpine snowbed productivity in response to experimental lengthening of the growing season. *Plant Biol*. doi:10.1111/j.1438-8677.2009.00286.x
- Baptist F, Yoccoz G, Choler P (2010) Direct and indirect control by snow cover over decomposition in alpine tundra along a snowmelt gradient. *Plant soil* 328:397–410
- Beniston M (2003) Climatic change in mountain regions: a review of possible impacts. *Clim Chang* 59:5–31
- Bilbrough CJ, Welker JM, Bowman WD (2000) Early spring nitrogen uptake by snow-covered plants: a comparison of arctic and alpine plant function under the snowpack. *Arct Antarctic Alp Res* 32(2):404–411
- Björk RG, Molau U (2007) Ecology of alpine snowbed and the impact of global change. *Arc Antarctic Alp Res* 39:34–43
- Bliss L (1956) A comparison of plant development in micro-environments of arctic and alpine tundras. *Ecol Monogr* 26: 303–307
- Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants – an economic analogy. *Ann Rev Ecol Syst* 16: 363–392
- Bowman WD, Theodose TA, Schardt JC, Conant RT (1993) Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology* 74:2085–2097
- Bryant DM, Holland EA, Seastedt TR, Walker MD (1998) Analysis of litter decomposition in an alpine tundra. *Can J Bot* 76:1295–1304
- Chapin F (1980) The mineral nutrition of wild plants. *Ann Rev Ecol Systematics* 11:37–52
- Chapin FS, Schulze ED, Mooney HA (1990) The ecology and economics of storage in plants. *Ann Rev Ecol Syst* 21: 423–447
- Chapin F, Moilanen L, Kielland K (1993) Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. *Nature* 361:743–751
- Choler P (2005) Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arct Antarctic Alp Res* 37(4): 444–453
- Craine JM, Tilman D, Wedin D, Reich P, Tjoelker M, Knops J (2002) Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Funct Ecol* 16:563–574
- Craine JM, Lee WG, Bond WJ, Williams RJ, Johnson LC (2005) Environmental constraints on a global relationship among leaf and root traits of grasses. *Ecology* 86:12–19
- Drake BG, González-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO₂? *Ann Rev Plant Phys Mol Biol* 48:609–639
- Dye DG, Tucker CJ (2003) Seasonality and trends of snow-cover, vegetation index, and temperature in northern Eurasia. *Geophys Res Lett* 30:9–12
- European Environment Agency (2009) Regional climate change and adaptation. The Alps facing the challenge of changing water resources 8, ISSN 1725–9177
- Evans JR, Seemann JR (1989) The allocation of protein nitrogen in the photosynthetic apparatus: costs, consequences, and control. In: Briggs WR (ed) *Photosynthesis*. Alan R. Liss Press, New York
- Fisk MC, Schmidt SK, Seastedt TR (1998) Topographic patterns of above- and belowground production and nitrogen cycling in Alpine tundra. *Ecology* 79:2253–2266
- Garnier E (1991) Resource capture, biomass allocation and growth in herbaceous plants. *Trends Ecol Evol* 6:126–131
- Garnier E, Salager JL, Laurent G, Sonie L (1999) Relationships between photosynthesis, nitrogen and leaf structure in 14

- grass species and their dependence on the basis of expression. *New Phytol* 143:119–129
- Geiger M, Haake V, Ludewig F, Sonnwald U, Stitt M (1999) The nitrate and ammonium nitrate supply have a major influence on the response of photosynthesis, carbon metabolism and growth to elevated carbon dioxide in tobacco. *Plant Cell Env* 22:1177–1199
- Germino MJ, Smith WK (2000) High resistance to low temperature photoinhibition in two alpine, snowbank species. *Physiol Plant* 110:89–95
- Grime J (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194
- Grime J (1997) Biodiversity and ecosystem function: the debate deepens. *Science* 277:1260–1261
- Guy CL (1990) Cold acclimation and freezing stress tolerance: role of protein metabolism. *Ann Rev Plant Phys Plant Mol Biol* 41:187–223
- Haselwandter K, Hofmann A, Holzmann HP, Read DJ (1983) Availability of nitrogen and phosphorus in the nival zone of the Alps. *Oecologia* 57:266–269
- Hendry G (1987) The ecological significance of fructan in a contemporary flora. *New Phytol* 106:201–216
- Hovenden MJ, Karen EW, Vander Schoor JK, Williams AL, Newton PCD (2008) Flowering phenology in a species-rich temperate grassland is sensitive to warming but not to elevated CO₂. *New Phytol* 178(4):815–822
- Inouye DW (2000) The ecological and evolutionary significance of frost in the context of climate change. *Ecol Lett* 3: 457–463
- Inouye D (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecol* 89:353–362
- IPCC (Intergovernmental Panel on Climate Change) (2007) Climatic change 2007: the physical science basis. In: Proceedings of the 10th session of working group I of the IPCC, Paris, February 2007
- Jaeger C, Monson R (1992) Adaptive significance of nitrogen storage in *Bistorta bistortoides*, an alpine herb. *Oecologia* 92:121–131
- Jaeger C, Monson RK, Fisk MC, Schmidt S (1999) Seasonal partitioning of nitrogen by plants and soil microorganisms in an alpine ecosystem. *Ecol* 80:1883–1891
- Jifon JL, Wolfe DW (2002) Photosynthetic acclimation to elevated CO₂ in *Phaseolus vulgaris* L. is altered by growth response to nitrogen supply. *Glob Chang Biol* 8:1018–1027
- Jones H, Pomeroy J, Walker DA, Hoham R (2000) Snow ecology: an interdisciplinary examination of snow-covered ecosystems. Cambridge University Press, Cambridge
- Justes E, Thiébeau P, Avice JC, Lemaire G, Volenec JJ, Ourry A (2002) Influence of sowing dates, N fertilization and irrigation on autumn VSP accumulation and dynamics of spring regrowth in alfalfa (*Medicago sativa* L.). *J Exp Bot* 53: 111–121
- Kielland K (1994) Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. *Ecol* 75: 155–181
- Kleijn D, Treier UA, Muller Scharer H (2005) The importance of nitrogen and carbohydrate storage for plant growth of the alpine herb *Veratrum album*. *New Phytol* 166:565–575
- Komarkova V, Webber PJ (1978) An alpine vegetation map of Niwot Ridge, Colorado. *Arct Alp Res* 1:1–29
- Körner C (1999) Alpine plant life. Springer Verlag, Berlin/Heidelberg/New York
- Körner C, Diemer M (1987) In situ photosynthetic response to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. *Funct Ecol* 1:179–194
- Körner C, Diemer M (1994) Evidence that plants from high altitudes retain their greater photosynthetic efficiency under elevated CO₂. *Funct Ecol* 8:58–68
- Körner C, Peláez Menéndez-Riedl S (1989) The significance of developmental aspects in plant growth analysis. In: Lambers H, Cambridge ML, Konings H, Pons TL (eds) Causes and consequences of variation in growth rate productivity of higher plants. Springer Verlag Academic Publishing, The Hague, pp 141–157
- Körner C, Diemer M, Scäppi B, Niklaus P, Arnone J III (1997) Response of alpine grassland to four seasons of CO₂ enrichment: a synthesis. *Acta Ecol* 18:165–175
- Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Peláez-Riedl S, Pepin S, Siegwolf RTW, Zotz G (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO₂. *Science* 309:1360–1362
- Kudo G, Ito K (1992) Plant distribution in relation to the length of the growing season in a snow-bed in the Taisetsu Mountains, northern Japan. *Vegetatio* 98:319–328
- Kudo G, Nordenhall U, Molau U (1999) Effects of snowmelt timing on leaf traits, leaf production, and shoot growth of alpine plants: comparisons along a snowmelt gradient in northern Sweden. *Ecoscience* 6:439–450
- Lawlor D (2002) Carbon and nitrogen assimilation in relation to yield: mechanisms are the key to understanding production systems. *J Exp Bot* 53:773–787
- Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A (2009) Elevated CO₂ effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *J Exp Bot* 60: 2859–2876
- Lewis JD, Wang XZ, Griffin KL, Tissue DT (2002) Effects of age and ontogeny on photosynthetic responses of a determinate annual plant to elevated CO₂ concentrations. *Plant Cell Env* 25:359–368
- Liebig J (1840) Die organische chemie in ihrer anwendung auf agrilkultur und physiologie. Friedrich Vieweg, Braunschweig
- Lipson D, Monson R, Bowman W (1996) Luxury uptake and storage of nitrogen in the rhizomatous alpine herb, *Bistorta bistortoides*. *Ecology* 77:569–576
- Lipson DA, Schmidt SK, Monson RK (1999) Links between microbial population dynamics and nitrogen availability in an alpine ecosystem. *Ecology* 80:1623–1631
- Lloyd J, Farquhar GD (2000) Do slow-growing species and nutrient-stressed plants consistently respond less to elevated CO₂? A clarification of some issues raised by Poorter (1998). *Glob Chang Biol* 6:871–876
- Long SP, Ainsworth EA, Rogers A, Ort DR (2004) Rising atmospheric carbon dioxide: plants FACE the future. *Ann Rev Plant Biol* 55:591–628
- May DE, Webber PJ et al (1982) Spatial and temporal variation of vegetation and its productivity on Niwot Ridge, Colorado. In: Ecological studies in the Colorado alpine, a Festschrift for John W. Marr. Occasional Paper Number 37. Institute of

- Arctic and Alpine Research, University of Colorado, Boulder/Colorado, pp 35–62
- Menke J, Trlica M (1981) Carbohydrate reserve, phenology, and growth cycles of nine Colorado range species. *J Range Management* 34:269–277
- Meuriot F, Simon JC, Decau MP, Prudhomme MP, Morvan-Bertrand A, Gastal F, Volenec JJ, Avise JC (2005) Contribution of initial C and N reserves in *Medicago sativa* L. recovering from defoliation: modulation by the cutting height and the residual leaf area. *Funct Plant Biol* 32:321–334
- Miller AE, Bowman WD (2003) Alpine plants show species-level differences in the uptake of organic and inorganic nitrogen. *Plant Soil* 250:283–292
- Miller A, Schimel J, Sickman J, Skeen K, Meixner T, Melack J (2009) Seasonal variation in nitrogen uptake and turnover in two high-elevation soils: mineralization responses are site-dependent. *Biogeochemistry* 93:253–270
- Monson RK, Rosenstiel TN, Forbis TA, Lipson DA, Jaeger CH (2006) Nitrogen and carbon storage in alpine plants. *Integrative Comparative Biol* 46:35–48
- Moore BD, Cheng SH, Sims D, Seemann JR (1999) The biochemical and molecular basis for photosynthetic acclimation to elevated atmospheric CO₂. *Plant Cell Environ* 22:567–582
- Naumburg E, Loik ME, Smith SD (2004) Photosynthetic responses of *Larrea tridentata* to seasonal extreme temperatures under elevated CO₂. *New Phytol* 162:323–330
- Nogués-Bravo D, Araujo M, Errea M, Martínez-Rica J (2007) Exposure of global mountain systems to climate warming during the 21st century. *Glob Env Chang* 17:420–428
- Nowak RS, Ellsworth DS, Smith S (2004) Functional responses of plants to elevated atmospheric CO₂: do photosynthetic and productivity data from FACE experiments support early prediction? *New Phytol* 162:253–280
- Oaks A, Hirel B (1986) Nitrogen metabolism in roots. *Ann Rev Plant Physiol* 36:345–365
- Öncel I, Yurdakulol E, Keles Y, Kurt L, Yildiz A (2004) Role of antioxidant defense system and biochemical adaptation on stress tolerance of high mountain and steppe plants. *Acta Oecol* 26:211–218
- Osone Y, Ishida A, Tateno M (2008) Correlation between relative growth rate and specific leaf area requires associations of specific leaf area with nitrogen absorption rate of roots. *New Phytol* 179:417–427
- Pate JS (1980) Transport and partitioning of nitrogenous solutes. *Ann Rev Plant Physiol* 31:313–340
- Pate JS (1983) Patterns of nitrogen metabolism in higher plants and their ecological significance. In: Lee JA, McNeill S, Rorison IH (eds) *Nitrogen as an ecological factor*. Blackwell Scientific Publishing, Oxford, pp 225–255
- Pollock CJ, Cairns AJ (1991) Fructan metabolism in grasses and cereals. *Ann Rev Plant Physiol Plant Mol Biol* 42:77–101
- Poorter H, Pérez-Soba M (2001) The growth response of plants to elevated CO₂ under non-optimal environmental conditions. *Oecologia* 129:1–20
- Pornon A, Escavara N, Lamaze T (2007) Complementarity in mineral nitrogen use among dominant plant species in a subalpine community. *Am J Bot* 11:1778–1785
- Raab TK, Lipson DA, Monson RK (1999) Soil amino acid utilization among species of the cyperaceae: plant and soil processes. *Ecol* 80:2408–2419
- Reich P, Walters M, Ellsworth D (1992) Leaf-life span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol Monogr* 62:2142–2147
- Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology* 80:1955–1969
- Reviere-Rolland H, Contard P, Betsche T (1996) Adaptation of pea to elevated CO₂: rubisco, phosphoenolpyruvate carboxylase and chloroplast phosphate translocator at different levels of nitrogen and phosphorus nutrition. *Plant Cell Env* 19:109–117
- Riedo M, Grub A, Rosset M, Fuhrer J (1997) A pasture simulation model for dry matter production, and fluxes of carbon, nitrogen, and water energy. *Ecol Model* 105:141–183
- Rigollier C, Bauer O, Wald L (1999) On the clear sky model of the 4th European Solar Radiation Atlas with respect to the Heliosat method. *Solar Energy* 68:33–48
- Sakai A, Larcher W (1987) Frost survival of plants. Response and adaptation to freezing stress, *Ecological Studies* 62. Springer, Berlin
- Saxe H, Ellsworth DS, Heath J (1998) Tree and forest functioning in an enriched CO₂ atmosphere. *New Phytol* 139:395–436
- Scheurwater M, Koren M, Lambers H, Atkin OK (2002) The contribution of roots and shoots to whole plant nitrate reduction in fast- and slow-growing grass species. *J Exp Bot* 53:1635–1642
- Schmidt SK, Costello EK, Nemergut DR, Cleveland CC, Reed SC, Weintraub MN, Meyer AF, Martin AM (2007) Biogeochemical consequences of rapid microbial turnover and seasonal succession in soil. *Ecology* 88:1379–1385
- Shaver G, Chapin F, Gartner B (1986) Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. *J Ecol* 74:983–989
- Sierra-Almeida A, Cavieres L (2010) Summer freezing resistance decreased in high-elevation plants exposed to experimental warming in the central Chilean Andes. *Oecologia* 163:267–276
- Sørensen T (1941) Temperature relations and phenology of the northeast Greenland flowering plants. *Meddelelser om Grønland* 125:1–305
- Stewart IT (2009) Changes in snowpack and snowmelt runoff for key mountain regions. *Hydrol Process* 23:78–94
- Stitt M, Krapp A (1999) The interaction between elevated carbon dioxide and nitrogen nutrition: the physiological and molecular background. *Plant Cell Env* 22:583–621
- Theurillat JP, Guisan A (2001) Potential impact of climate change on vegetation in the European Alps: a review. *Clim Chang* 50:77–109
- Theurillat J-P, Aeschmann D, Küpfer P, Spichiger R (1994) The higher vegetation units of the Alps. *Colloq Phytosociol* 23:189–239
- Thomas RB, Strain BR (1991) Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. *Plant Phys* 96:627–634
- Tjoelker MG, Craine JM, Wedin D, Reich PB, Tilman D (2005) Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytol* 167:493–508

- Valladares F, Pearcy RW (1997) Interactions between water stresses, sunshade acclimation, heat tolerance and photoinhibition in the sclerophyll *Heteromeles arbutifoliar*. *Plant Cell Env* 20:25–36
- Valladares F, Pugnaire FI (1999) Tradeoffs between irradiance capture and avoidance in semi-arid environments assessed with a crown architecture model. *Ann Bot* 83:459–469
- Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199:213–227
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. *Nature* 428:821–827
- Wyka T (1999) Carbohydrate storage and use in an alpine population of the perennial herb, *Oxytropis sericea*. *Oecologia* 120(2):198–208
- Xu XL, Ouyang H, Kuzyakov Y, Richter A, Wanek W (2006) Significance of organic nitrogen acquisition for dominant plant species in an alpine meadow on the Tibet plateau, China. *Plant Soil* 285:221–231