CHAPTER 2

SPECIES-RICH SWARDS OF THE ALPS

Constraints and opportunities for dairy production

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Abstract. The swards of the alpine grasslands represent a unique feed resource that sustains animal agriculture to the present. The complex animal–plant interactions during cattle grazing influence grassland dynamics, which under proper grazing management maintain the sustainability of these alpine swards and thereby the persistence of alpine dairy production systems. However, dairy production on alpine swards is limited by the herbage quality and the physiological impact of alpine summer grazing on dairy cattle. Abandonment of the alpine regions and shifts from milk production towards more extensive livestock systems are trends increasingly seen during recent decades. Current interest in the positive health aspects of animal products, especially in beneficial functional fatty acids in milk, may revive the interest in alpine dairy farming, because high concentrations of beneficial functional fatty acids in the lipid fraction of the milk are found in dairy products of alpine origin
Keywords: mountain; grazing; herbage quality; fatty acids

INTRODUCTION

Among the mountainous regions in Europe, the Alps are one of the richest plant species areas in Europe. Up to the present, their grasslands have remained a unique feed resource that sustains alpine animal agriculture during the European summer months. Hence, alpine animal agriculture evolved around these unique multi-species swards and subsequently sustains their existence. However, animal agriculture in the Alps has declined in the past decades, both in number of animals and in intensity of grassland utilization, by a shift towards more extensive livestock production systems. This leaves several alpine regions progressively abandoned, facilitating an intrusion of shrubs and other plant species, which gradually reduces large proportions of open grassland (Laiolo et al. 2004). The renewed interest in alpine farming in recent years may slow down, or even reverse this development. The problems with food supply due to incidences of mad-cow disease (or rather BSE) and foot-and-mouth disease, for example, and an increasing rejection of intensive

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farming practices, have stimulated the market for high-quality animal products produced from extensive farming systems as found under the unique environmental conditions of the Alps (Jewell 2002). Additionally, more recently the scientific interest in positive health aspects of animal products has grown, especially with regard to beneficial functional fatty acids in animal products. Milk produced on alpine pastures has been shown by several studies to cause considerable increases in beneficial functional fatty acids, such as the so-called omega-3 fatty acids and conjugated linoleic acids (CLA) in the lipid fraction of the milk (Collomb et al. 2004; Hauswirth et al. 2004; Leiber et al. 2005a), compared to milk produced on lowland pastures. A better understanding of alpine dairy production systems and resulting dairy products is needed to explain these observations. This review will focus on the main issues around milk production on swards of the Alps by highlighting vulnerabilities and new opportunities.

GRAZING AS BENEFIT?

The species-rich swards of the Alps

The Alps reach a length of roughly 1200 km and have a maximum width of 240 km. They are politically shared by six countries and the greatest portions are in France, Italy, Switzerland and Austria. The alpine zone, with its distinct alpine grasslands, is located above the timberline (the upper limit of the forest is around 1800 m in the north and climbs to 2300 m in the centre, Mosimann 1986). Compared to swards in the lowlands, alpine swards are heterogeneous and consist of grasses, legumes, herbs and shrubs. In total, 750 to 800 plant species can be found in the alpine zone, which as an area represents 7.5 % of the total area the Alps (Nagy et al. 2003). Furthermore, alpine swards have a high presence of plant secondary metabolites as a result of a higher occurrence of dicotyledons (Mariaca et al. 1997; Jeangros et al. 1999).

The growing season for the alpine vegetation is short; it starts roughly around May/June and continues through September. Due to this short season, alpine pastures are characterized by a rapid growth of biomass at the beginning of summer, followed by a progressive decline of the growth rate of herbage. Brühlmann and Thomet (1991) found, by studying fertile alpine cow pastures in the Bernese Alps from 1984 to 1988, that over 80 % of the forage biomass grew during June and July. The short growing season is related with rapid plant development, whereby relatively high levels of lignification, high fibre proportions and poor digestibility are reached early (Brühlmann and Thomet 1991; Bovolenta et al. 2002; Mayer et al. 2003).

Sustainability of heterogeneous swards, such as the alpine swards, depends on well-managed grazing activities (Bailey et al. 1998; Bullock and Armstrong 2000). Grazing activities of livestock affect individual plants, plant species and plant communities. In general, grassland dynamics are influenced by grazing activities in three ways: herbage removal, dung deposition and trampling (Bullock and Marriott 2000; Kohler et al. 2004), which are discussed further in the following paragraphs.

Grazing effects by herbage removal

As mentioned above, alpine swards with their large botanical biodiversity are optimally maintained by managed grazing. The reason for that is that they are vulnerable to overgrazing as well as undergrazing, because both can adversely affect plant species diversity and composition. Overgrazing of swards leads to sward degeneration, reduction of soil cover by the canopy and a reduction in plant diversity and abundance (e.g. Oztas et al. 2003). Accordingly, overgrazing on steep slopes, especially by heavier animals, could quickly lead to patches of bare soil that easily erode. Swards that are not grazed tend to be invaded by intrusive species (herbs, shrubs and tall grasses) and therefore show a reduction in the number of species, i.e. of plant diversity, and a progressive decrease in the forage value of the sward (Laiolo et al. 2004). In winter, frozen vegetation in ungrazed swards can be uprooted by the weight of snow clinging to it, which can lead to soil erosion (Larcher 1985, from Jewell 2002, p. 17).

In general, grazing livestock affect the sward composition through selective defoliation and creating gaps in the sward that can be colonized by neighbouring plants (Bullock et al. 1995). Grazing thereby affects the plant-competitive environment by favouring plants with competitive abilities (e.g. fast growing plants and good dispersers) best suited for the situation (Bullock and Marriott 2000). Preference by grazers may also play a role in grazing effects on sward composition. Augustine and McNaughton (1998) concluded from their review that plant species that are less preferred by grazers increase under a grazing situation. This suggestion can be well demonstrated by *Nardus stricta* (matgrass), a well-known species in the Alps that is largely avoided by domestic grazers, and therefore promoted by grazing (Fischer and Wipf 2002). For this reason, *Nardus stricta* is referred to as an important grazing indicator. However, Augustine and McNaughton (1998) also concluded that intensive long-term grazing does not lead to the invasion of unpalatable species into the community and can even increase the dominance of highly palatable species. As demonstrated in the above example, effects of grazing may not be identical in each situation. Variation in key factors such as type of grazing animal species, type and abundance of plant species, or soil type, may provoke different responses to grazing pressure (Proulx and Mazumder 1998). Accordingly, Guardiola et al. (2004) reported that grazing by sheep on subalpine grasslands was found to reduce species richness and increase the dominance of a few low-palatable plants, compared to cattle grazing. Proulx and Mazumder (1998) concluded, from analysing data from 30 studies, that in general, plant species richness decreases with grazing in nutrient-poor ecosystems, while it increases with grazing in nutrient-rich ecosystems. These findings were confirmed by a study from Fischer and Wipf (2002), who found that grazing on nutrient-poor grasslands in the upper subalpine zone near Davos (Switzerland) negatively affected both botanical richness and forage quality as compared to mown grasslands in that area.

Nutrient enrichment through faeces and urine

Grazing cattle may facilitate or reduce plant diversity of the sward through excreta (Dai 2000; Kohler et al. 2004). The often non-uniform activity of cattle in a given pasture area (Bailey et al. 1998; Parsons and Dumont 2003), along with their disproportional faeces and urine excretion, facilitates a heterogeneous distribution of nutrients in the soil (Augustine and Frank 2001). Subsequently, the heterogeneity in soil nutrients causes variation in productivity and in plant species composition of the overall vegetation (Dai 2000; Augustine and Frank 2001). Because of a local enrichment of nutrients by excreta and because there is a general rejection of herbage by cattle around dung pats, species richness may slightly increase on these small deposition areas in the short term, favouring weak competitors and short-lived species. Kohler et al. (2004) found in their study in the Jura mountains in Switzerland that nutrients added through the application of a liquid manure consisting of dung and urine favour tall plant species with a poor capacity for lateral spread. Furthermore, they found that grasses respond positively, and forbs negatively to manure treatment.

A concentration in the amount of dung deposition can be found in places where cattle congregate, such as water sources and resting places, the latter often being flat in otherwise steep alpine pasture areas. Heavily dunged sites like these form an environmental concern, because they are prone to nitrate leaching and ammonia volatilization. In the long term, competitive species may tend to form mono- or oligo-dominant stands on such nutrient-rich sites (Erschbamer et al. 2003).

With respect to soil enrichment with nitrogen from cattle excreta, Berry et al. (2002) found that dairy cows are a better system choice than beef cows in terms of efficient nitrogen (N) utilization. Namely, N intake rates to satisfy requirements of beef cows are easily reached and the excess is excreted in urine at a higher proportion than in dairy cows (see also Figure 1). Estermann et al. (2001) compared Angus suckler beef with Simmental dairy cows in later stages of lactation, grazing in the same alpine pasture, and also found higher urinary N return rates in beef cattle compared with dairy cattle.

Treading, scratching or kicking on swards by cattle

The last of the three grazing effects that can influence sward diversity is cattle treading, scratching or kicking the ground. Similar to grazing and nutrient enrichment through faeces and urine, these activities cause heterogeneity within the sward, which may result in a higher proportion of bare ground on swards being grazed compared to non-grazed swards (Fischer and Wipf 2002). As a result, microsites are created with different conditions for germination, which allow certain plant species to be recruited into the grazed landscape (Harper et al. 1965). Treading, scratching or kicking the ground may therefore also affect sward diversity and composition. In this respect, the original environment determines the pattern of change in diversity in plant communities. Kobayashi et al. (1997) found that at sunny sites trampling depressed species richness due to the reduced soil water potential, whereas the opposite effect was found on shady sites.

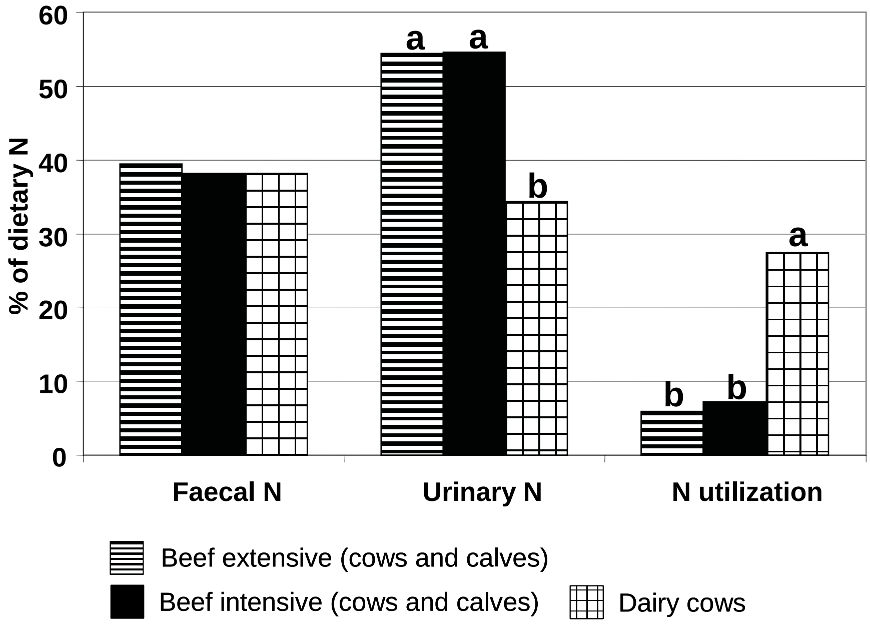

Figure 1. *Nitrogen loss and utilization (% of dietary N) of beef and dairy cattle in extensive and intensive alpine grazing systems (Sutter et al. 2000). Bars carrying no common superscript are significantly different, P<0.05*

INTAKE BEHAVIOUR, HERBAGE QUALITY AND SUPPLEMENTATION

Selection, intake and nutritive value of alpine herbage

Since the herbage of high-altitude pastures is very heterogeneous (Schubiger et al. 1998), selective grazing is probably essential for animals to meet their nutritional requirements (Prache et al. 1998). Under these conditions, the choices available to the grazing animal are complex. In a heterogeneous sward, cattle generally avoid feeding areas with lower forage quality and alternate among feeding areas with higher forage quality (Bailey et al. 1998; Prache et al. 1998; Jewell 2002). As a result, selection in these heterogeneous swards could occur on the basis of a range of factors such as visual and olfactory, as well as physical and structural characteristics of the vegetation, influencing ease of intake and intake rate. Additionally, biochemical and nutritional characteristics of plants, and by-products of microbial fermentation such as volatile fatty acids and ammonia, can influence food preferences. Berry et al. (2002) concluded from their studies in the Swiss Alps that cattle tend to select an NDF-rich diet on improved pasture, whereas on a poor-quality pasture the selection to maintain N content seems to be overriding. Mayer et al. (2003) found on sub-alpine wood pastures that cattle selected herbage of relatively constant digestibility, on both the short and the long term.

In general, cattle that graze heterogeneous alpine swards are observed to prefer feeding on grasses rather than forbs (Estermann et al. 2001; Erschbamer et al. 2003; Mayer et al. 2003). The preference for grass species could be related to their abundance (e.g. Fischer and Wipf 2002) or to the size or shape of forbs' leaves, which make them more difficult for cattle to find and ingest (Mayer et al. 2003). Furthermore, foraging costs and social characteristics of the animals also play important roles in diet selection on heterogeneous grasslands (Dumont et al. 2002). Despite the ability of dairy cattle to select for herbage with higher quality, alpine herbage may not be sufficient to meet the nutritional requirements of dairy cows with medium to high milk yield (Zemp et al. 1989b; Christen et al. 1996; Bovolenta et al. 1998; Berry et al. 2001). This could, firstly, be related to the sub-maximal intake of alpine herbage. In the beginning of the alpine summer grazing (Berry et al. 2001; Leiber et al. 2004), intake may be relatively low, because of metabolic stress due to adaptation to the hypoxic environment (Bianca and Puhan 1974). Later during alpine summering, low digestibility and large fractions of fibre of the alpine herbage (Mertens 1994) and limited palatability of the food, which may be affected by secondary plant ingredients (Mariaca et al. 1997; Jeangros et al. 1999), may cause sub-maximal intake. However, higher intakes during alpine summer grazing compared to intake in the lowland have also been observed (Christen et al. 1996) and could be explained by the fact that cows increase their intake in order to compensate for the extra energy requirements during alpine summer grazing.

The main factor explaining why the alpine herbage is not covering the nutritional requirements of early- and high-lactating cows is the limited quality, or rather the low density, of net energy of alpine herbage (Brühlmann and Thomet 1991; Mayer et al. 2003). Schubiger et al. (1998) found in their study in the Swiss Alps that in the beginning of the growing season (June and July), the alpine pasture provided herbage with good digestibility, a high net energy content and a favourable crude-protein content. The energy content was found to be comparable to that from herbage in the lowland (mid-May). Later during the growing season, the digestibility of alpine herbage dropped, however, which is explained by the climatic factors and botanical composition of pastures. Bovolenta et al. (2002) found in their study that the content of crude protein and neutral detergent fibre in the grazed herbage changed by -36 % and +38 %, respectively, over an eight-week period from the beginning of July to the end of August (see Figure 2). In this respect, Schubiger et al. (1998) reported that the net energy content of the alpine grass species decreases more rapidly than that of legumes and herbs. Additionally, legumes and herbs compared to grass species showed a lower content of cell walls, but a higher content of crude protein. Researchers concluded that the botanical composition of an alpine pasture has a significant influence on the nutritive value of the forage, which next to the general rapid decline in forage value may be the reason for an imbalance of net energy and absorbable protein (Berry et al. 2002).

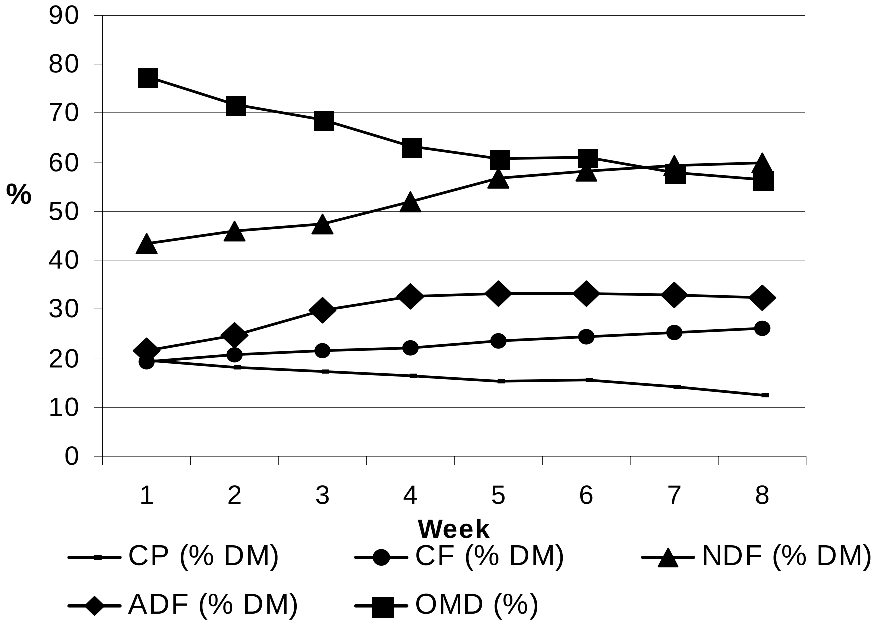

Figure 2. *Chemical composition and digestibility of grazed herbage over an eight-week period in July and August (from Bovolenta et al. 2002). CP, crude protein; CF, crude fibre; NDF, neutral detergent fibre; ADF, acid detergent fibre; OMD, organic-matter digestibility.*

Supplementation of dairy cows during alpine summer grazing

To meet the dairy cows' requirements for maintenance and milk production, additional nutrients for the specific conditions at high altitudes are required (Christen et al. 1996). Hence, increased milk production due to the continuous increase in genetic merit of the dairy cows even more enlarged the gap between requirements and nutrient availability, calling for supplementation during alpine summer grazing (Christen et al. 1996; Kreuzer et al. 1998). Berry et al. (2001) estimated the maintenance energy requirement for alpine conditions to be 1.72 times greater than that of lowland maintenance requirement, while the estimates of Christen et al. (1996) were even higher with 1.35 to 2.55 times that of lowland requirements. Several studies have been conducted to look for effects of supplements on dairy performance in the Alps (Berry et al. 2001; Bovolenta et al. 2002). In the study of Bovolenta et al. (2002) it was concluded that the best results regarding milk yield were obtained by a constant level of concentrate compared to a concentrate level at a declining rate, according to the decline of lactation. This involved a slightly higher concentrate supply with a little lower herbage intake, but it mainly allowed a balance of the rapid and progressive decline in feeding value of the herbage. Berry et al. (2001) illustrated in their study that cows grazing swards at a high altitude show a response to supplementation differing from that of cows in a lowland area. In general, the substitution rate of herbage by concentrate is low with poor-quality herbage (low digestibility) compared to good-quality herbage (high digestibility), since voluntary intake of poor-quality forages is lower in comparison to forages with high digestibility (Dixon and Stockdale 1999). The difference between voluntary forage intake and maximum dry-matter intake is therefore higher for poor-quality forage, which allows more concentrate to be given before a significant substitution takes place. However, Berry et al. (2001) presumed that herbage intake levels of cows grazing on alpine pastures were reduced in order to limit energy expenditure required to graze in an unfavourable environment. This presumption is confirmed by Bailey et al. (1998), who concluded that livestock have accurate spatial memories and sufficient cognitive abilities to select patches and feeding sites based on travel costs and the quality and quantity of forage expected to be present. Supplementation can also have ecological effects. Providing supplementation could lead to the possible substitution of forage by concentrate, which leads to either underutilization of the swards (Bailey et al. 1998) or increased cattle densities on the sward. Thus, supplementation could also lead to increased excretions per unit forage area and thereby nutrients, which again could have implications for sward composition and plant diversity. On the other hand, Berry et al. (2001) found that a high-energy–low-protein concentrate offered at a level of 4 kg/day can limit potential ammonia-N losses from alpine pastures by corresponding reductions in urine-N proportion of manure N. Another way of meeting the dairy cows' nutrient requirements is to improve the forage value of the alpine swards with inclusion of clover (Leiber et al. 2004). Introducing clover would directly affect the plant composition of the sward and may not be acceptable from an ecological point of view.

MILK PRODUCTION DURING ALPINE SUMMER GRAZING

Adaptation to alpine conditions

Not only do cows need to adapt to the lower quality of available feed from the alpine swards, but the alpine summer grazing of dairy cows as a whole represents a stress to the animals, which affects their production. Animals exposed to alpine conditions undergo a period of adaptation, which requires additional energy (Christen et al. 1996; Kreuzer et al. 1998). Firstly, transportation to the Alps imposes a stress resulting in metabolic disturbances (elevated cortisol, lactate and non-esterified fatty-acid levels) and an immediate weight loss through excreta (Zemp et al. 1989b; Kreuzer et al. 1998). Upon arrival, dairy cows show elevated levels of thyroid hormones and β-hydroxybutyrate (Zemp et al. 1989a; Kreuzer et al. 1998; Leiber et al. 2004, see Figure 3). Elevated thyroid hormones indicated a higher metabolic turn-over possibly due to cold stress, whereas the elevated β-hydroxybutyrate could indicate a shortage of energy. Zemp et al. (1989a) and Leiber et al. (2004) also found decreased plasma insulin and glucose levels, which they related to a metabolic shortage of energy intake. Transportation stress is followed by a hypoxic environment at high altitude, which has physiological consequences for the animals.

Ruminants exposed to hypoxia respond metabolically by increased levels of erythrocytes, haemoglobin and leucocytes, increased respiratory and heart rates and increased blood pH in order to improve oxygen uptake capacity (Bianca and Puhan 1974; Bianca and Naf 1979; Zemp et al. 1989a). Leiber et al. (2004) suggested that the metabolic changes of cows during transport and upon arrival could explain the suppressed intakes at the start of exposure to high altitude, occurring already at 2000 m a.s.l.

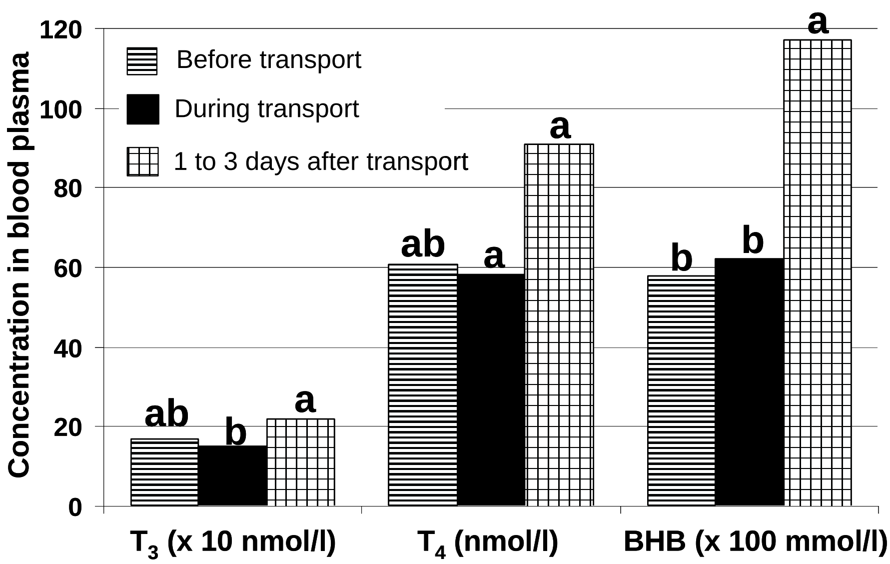

Figure 3. *Short-term response of cows in thyroid hormones (T_3 and T_4) and β-hydroxybutyrate (BHB) to 4.5 h vehicle transport and to high-altitude pasture (from Kreuzer et al. 1998). Bars carrying no common superscript are significantly different, $P<0.05$.*

Other stressors cows are confronted with upon arrival and while grazing in the Alps include changes in housing, climatic conditions, solar radiation, adaptation to alpine forage, and topographic challenges. Adaptation is often achieved within a few weeks by a rapid decline in milk yield (Zemp et al. 1989a; Leiber et al. 2004), normally accompanied by a failure to recover body condition (Zemp et al. 1989b). Kreuzer et al. (1998) concluded from their study that metabolic adaptation to the immediate energy deficit on high-altitude pasture requires at least three weeks, which represent a considerable part of the whole high-alpine season.

Alpine milk production, composition and other properties of milk

High-alpine grazing of dairy cows affects the yield and composition of milk. Due to the lower energy supply under the conditions of the alpine summer grazing, milk production often decreases, as do the concentrations of milk protein and lactose (Zemp et al. 1989b; Christen et al. 1996; Leiber et al. 2004). In contrast, milk fat content increases, especially in the beginning of the alpine period (Zemp et al. 1989b; Christen et al. 1996) (Berry et al. 2001), which may be a response to the sudden lipolysis from body stores due to the lack of energy (Christen et al. 1996), and possibly from the generally higher fibre content of alpine forage (Zemp et al. 1989b). Both milk fat and protein are important for cheese making and cheese yield (Melilli et al. 2002). Reduced levels of milk protein suppress the expected cheese yield and additionally impair rennet coagulation properties of alpine milk (Leiber et al. 2005b). Furthermore, alpine herbage, as lowland fresh herbage, increases the proportion of polyunsaturated fatty acid (PUFA) in milk fat, which reduces the oxidative stability (Al-Mabruk et al. 2004) and affects technological aspects such as the spreading properties of butter (Eyer et al. 2002). Along with changes of milk composition, an elevated milk somatic-cell count (SCC) can be observed by cows grazing alpine pastures (Lamarche et al. 2000). Reasons for this could be the physical strain on cows during foraging under alpine conditions (Coulon and Pradel 1997) and often unfavourable hygienic conditions of milking on the pasture. In the absence of mastitis breed type, lactation stage or parity and age are generally known to impact milk SCC (Lamarche et al. 2000). The latter two factors may play a particular role in this situation. In cases where only a part of the dairy herd is exposed to the Alps, dairy cows in late lactation stages are preferred to cows early in lactation because of their lower requirement for energy and nutrients (Bianca and Puhan 1974). In addition to the alpine summer grazing itself, this may have an impact on the SCC of alpine milk.

ALPINE DAIRY PRODUCTS IN A NEW LIGHT

Revealing the uniqueness of alpine dairy products

Dairy products from the Alps, such as the Protected Designated Origin (PDO) cheeses, are well known for their unique taste, colour, flavour and tradition. Research to the present day is still further revealing these unique aspects by specifically looking at plant and sward compositional influences, and influences of plant secondary metabolites (e.g. Buchin et al. 1999; Mariaca et al. 1997). Namely, herbage from natural highland pastures has a highly diversified botanical composition as well as abundant secondary metabolites (Jeangros et al. 1999), which may influence milk and therefore cheese quality. Terpenoids in plants are products of secondary metabolism and may be considered potential biochemical indicators or markers for characterizing cheeses that originate from the highlands (Bosset and Jeangros 2000). Bosset and Jeangros (2000) show in their study that highland pasture, with a diverse botanical and chemical composition, allows the production of milk and cheese with a chemical composition and flavour intensity (odour and taste) that is clearly different from that of lowland pasture.

Beneficial fatty acids in alpine dairy products

In recent years, n-3-polyunsaturated fatty acids (alternatively called omega-3 PUFA) and conjugated linoleic acids (CLA) in dairy products have received much attention. The benefits of n-3 PUFA to human health have been extensively studied and were acknowledged in many studies (e.g. Simopoulos 2002; Burdge 2004). However, claims on health benefits related to CLA have to be made with care. While most positive effects related to CLA intake mainly resulted from animal studies, findings from short-term human studies are divergent from outcomes of animal studies and include beneficial as well as detrimental effects on health when CLA is administrated at high levels (Tricon et al. 2005).

In general, with 5 % of total milk fat, the proportion of PUFA in milk fat is small in comparison to 68 % for saturated fatty acids and 27 % for monounsaturated fatty acids (Sieber 2003). This small proportion of PUFA in milk fat is found to be elevated in dairy products derived from cows grazing/feeding on fresh herbage compared to dairy products derived from production systems based on Total Mixed Ration feeding (e.g. Kelly et al. 1998). The increase in unsaturated fatty acids is due to an increase of the total PUFA, the n-3 PUFA and the CLA content.

In comparison to lowland grazing, the impact of alpine grazing on the content of these beneficial fatty acids has been reported in several studies to be even more pronounced (Bugaud et al. 2001; Collomb et al. 2002a; Innocente et al. 2002; Leiber et al. 2005a). In milk samples collected from three geographical sites in Switzerland, Collomb et al. (2002a) reported the proportion of PUFA in milk fat to increase with altitude (lowlands (600-650 m): 4.2 %, mountains (900-1210 m): 5.4 %, and highlands (1275-2120 m): 6.9 %. This was mainly due to the increasing concentration of CLA with altitude (0.87 %, 1.61 % and 2.36 % of milk fat, respectively). Similar findings were also made by Mantovani et al. (2003). Collomb et al. (2004) studied CLA isomers in more detail and found that, in addition to the well-known isomer *cis-9, trans-11* (rumenic acid), the CLA isomer *trans-11, cis-13* was formed in large quantity by cows grazing mountain pasture. An elevated content of CLA isomer *trans-11, cis-13* due to alpine grazing and grass feeding was also observed by Leiber et al. (2005a), but these researchers did not find the CLA isomer *cis-9, trans-11* to be elevated during alpine grazing. Ferlay et al. (2002) found a considerable reduction of CLA after three weeks of cattle alpine grazing, which demonstrates that alpine grazing may not result in additional elevations of beneficial fatty acids in milk in all cases.

Then again, a considerable number of studies have found positive effects from alpine grazing on functional fatty acids in alpine cheeses as well (Innocente et al. 2002; Mantovani et al. 2003; Hauswirth et al. 2004). Hauswirth et al. (2004) have demonstrated that alpine cheeses were superior in two n-3 PUFA, α-linolenic acid and eicosapentaenoic acid (EPA), and in CLA, and had more favourable ratios of arachidonic acid (AA) to EPA and n-6/n-3 fatty acids over non-alpine cheeses and alpine cheeses with partial silage feeding. This was even the case when alpine cheeses were compared to cheeses from cows supplemented with linseed, which is an additional source of α-linolenic acid. Mantovani et al. (2003) found a reduction in the percentage of saturated fatty acids and consequently an increase in the percentage of mono-unsaturated fatty acids and PUFA in Fontina cheese produced from alpine pasture compared to lowland cheese. Additionally, they reported that CLA content in cheese increases with altitude as well. Innocente et al. (2002) found unsaturated fatty acids (C18:1; C18:2; C18:3 and C18:2, *cis-9, trans-11*) present in higher quantities in the cheese produced on the mountains. The latter was even found more than doubled in mountain cheese compared to lowland cheese.

The reason for this phenomenon is not straightforward, and it may possibly be an interaction of different factors. A first factor being discussed by researchers as one of the reasons for the elevation of these beneficial fatty acids in dairy products derived from the Alps is altitude. Altitude may be responsible for the elevation of PUFA in dairy products, because often a higher percentage of α-linolenic acid in plant lipids is found in plants growing under low ambient temperatures (Hawke 1973). Namely, at low temperatures, plant membrane lipids become more unsaturated (especially due to an increase of linolenic acid) in order to maintain membrane fluidity (Lag et al. 1991). This is confirmed by Dorne et al. (1986), who found in nine typical alpine plant species in the French Alps (2100 to 2800 m.a.s.l.) the proportion of linolenic acid (C18:3) to be highest compared to the other fatty acids present (see Table 1).

Table 1. *Fatty-acid composition of total lipids(g/100 g) from leaves of nine alpine plant species (from Dorne et al. 1986)*

Species	Altitude (m)	C16:0	C16:1[t]	C16:3	C18:0	C18:1	C18:2	C18:3
Elyna spicata	2100	12.8	2.5		tr*	1.2	7.8	75.7
Salix herbacea	2100	11.5	3.2		tr	1.6	12.0	71.8
Saussurea depressa	2100	13.6	1.8		0.1	1.4	17.0	66.1
Salix retusa	2400	13.8	3.4		0.3	1.3	13.3	67.9
Salix reticulata	2400	14.1	2.8		tr	1.7	16.9	64.4
Alchemilla pentaphyllea	2600	9.5	4.2		1.0	4.2	17.3	63.8
Ranunculus glacialis	2700	12.0	4.8	12.9	tr	0.6	12.3	57.4
Geum reptans	2700	11.0	4.1		1.3	2.6	8.6	72.4
Saussurea depressa	2700	10.0	2.5		tr	1.0	11.2	75.3
Androsace helvetica	2800	13.0	2.4		tr	5.3	29.6	49.7

* tr = trace amount

However, the content of α-linolenic acid in alpine herbage may not necessarily be higher compared to the content of α-linolenic acid in lowland herbage. Accordingly, Dorne et al. (1986), comparing the fatty-acid pattern in the leaves of the nine alpine species with studies on the fatty-acid composition of spinach and barley, originating from habitats with little variation in temperature, did not find large differences in the proportion of α-linolenic acid in the total plant lipids (60.0

and 60.6 % for spinach and barley, respectively). Although spinach and barley are not forage types for ruminants, a similar result was found by Leiber et al. (2005a) in case of lowland and highland pastures. Namely, they found proportions of α-linolenic acid of 56 and 47 g/100g lipids for lowland and alpine pastures, respectively. They observed an almost exclusive alpine summer-grazing effect on α-linolenic acid concentration in milk, which, however, consequently could not have been caused by an elevated intake of α-linolenic acid with the alpine herbage. This confirms conclusions made by Bugaud et al. (2001), who neither found a clear relationship between the fatty acids in the milk and the pasture.

Another explanatory factor being discussed by researchers that might be responsible for an elevated content of beneficial fatty acids in alpine dairy products is abundance of plant species including species with particular lipid composition or specific secondary compounds. In general, lowland leys show smaller botanical diversity compared to permanent pastures of the mountains. Jeangros et al. (1999) observed a decreased proportion of grasses and an increase in dicotyledonous species, such as *Compositae* (*Asteraceae*), *Rosaceae* and *Plantaginaceae*, with increasing altitude. Collomb et al. (2002b) correlated fatty acids of milk fat with botanical families and individual plant species and found that the percentages of several plant species dominant in the Alps correlate negatively with the concentration of saturated fatty acids. They also found that the percentages of certain plant species correlate positively with the concentration of PUFA and CLA in milk fat. The occurrence of certain plant species found in the Alps may be responsible for an elevated activity of the rumen microbial flora. Namely, a higher degree of biohydrogenation in the rumen of the cows was concluded from the increase in trans-vaccenic acid (C18:1 t11) and CLA as a function of the altitude when cows were transferred from the lowlands to the highlands (Collomb et al. 2002b). However, also this finding was not confirmed by Leiber et al. (2005a), who found in their experiment elevated CLA values already in the lowland pasture in comparison to alpine pasture. Leiber et al. (2005a) as well as Bugaud et al. (2001) concluded from their studies that factors other than alpine herbage may cause the increase of beneficial fatty acids in milk fat, and both groups of researchers suggest that the rumen microbial population may even be reduced by lack of dietary energy due to a lower intake. The lower feed intake might be the cause for the decrease in precursors of *de novo* fatty-acid synthesis and therefore for the decrease in secretion of short- and medium-chain fatty acids (Tamminga 2001). Next to a lack of dietary fermentable energy, Leiber et al. (2005a) suggest plant secondary compounds to be possible causes for their results since these compounds, such as tannins, which are especially found in dicotyledonous species (Mariaca et al. 1997; Jeangros et al. 1999), may inhibit the rumen microbial population and, along with that, their biohydrogenating capacity.

A reduced feed intake, which is typical for cows kept in high alpine regions (Kreuzer et al. 1998), also triggers mobilization of fat depots. This occurs by mobilizing long-chain fatty acids from body reserves in adipose tissue, which results in a relatively high proportion of the fatty acids in milk fat being long-chain fatty acids (Bonfoh et al. 2005), and explains the elevated level of PUFA in the milk of cows grazing alpine swards (Bugaud et al. 2001). This has also been demonstrated in the study of Leiber et al. (2005a), who found that α-linolenic acid in milk fat was markedly elevated by the alpine conditions, parallel to the cows having lost weight.

The contradiction between the findings of the different research groups as described above requires follow-up studies in order to confirm the involvement and relative contribution of the discussed factors to an elevated PUFA and CLA content of dairy products originating from the Alps.

CONCLUSIONS

In this review we have described and discussed the uniqueness of the alpine swards in relation to the grazing dairy cow. Furthermore, the cows' physiological adaptation to the alpine environment and herbage was dealt with along with the consequences for milk production and milk constituents. With regard to the latter, the so-called omega-3 fatty acids and conjugated linoleic acids (CLA) received specific attention. In summary, the following main conclusions can be drawn:

1. An understanding of the complex animal–plant interactions on alpine swards can facilitate sustainable grazing management, which should keep alpine grasslands ecologically stable and productive and facilitate sustainable dairy production.
2. Alpine herbage and summer grazing can best sustain extensive and semi-intensive dairy production systems, involving breed types with traits that make them adapt and produce well during alpine summer grazing.
3. Both alpine herbage and summer grazing are factors responsible for the elevated beneficial fatty acids of dairy products originating from the Alps.
4. Due to the heterogeneity of alpine swards and the lack of a greater number of (controlled) experiments conducted in the Alps on beneficial fatty acids in milk fat, more research is required to create a better understanding of the contribution of the major factors to this phenomenon.

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