A geochemical study of lacustrine sediments: towards palaeo-climatic reconstructions of high Andean biomes in Colombia

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Citation for published version (APA):
CHAPTER 2

High altitude \( \text{C}_4 \) grasslands in the northern Andes: relics from glacial conditions?


The altitudinal vegetation distribution in the northern Andes during glacial time differed from the present-day conditions as a result of temperature and precipitation change. New evidence indicates that as a response to a reduced atmospheric partial CO\(_2\) pressure (\(p\text{CO}_2\)), the competitive balance between \(\text{C}_3\) and \(\text{C}_4\) plants have changed. Effects may have remained virtually undetected in pollen records, but can be observed using a stable carbon isotope analysis. Vegetation dominated by \(\text{C}_4\) taxa, belonging to the families Cyperaceae (e.g. *Bulbostylis* and *Cyperus*) and Poaceae (e.g. *Muhlenbergia*, *Paspalum* and *Sporobolus*), may have been able to replace for a significant part the modern type \(\text{C}_3\) taxa (e.g. species belonging to *Carex*, *Rhynchospora*, *Aciachne*, *Agrostis*, *Calamagrostis*, and *Chusquea*). Impact of reduced glacial atmospheric \(p\text{CO}_2\) levels and lower glacial temperatures on the composition and the elevational distribution of the vegetation types is discussed. The present high Andean vegetation communities may differ from the glacial equivalents (non-modern analogue situation). We identified dry *Sporobolus lasiophyllus* tussock grassland and *Arcytophyllum nitidum* dwarfsrub paramo as the possible relict communities from glacial time. The effect on previous estimates of palaeo-temperatures is estimated to be small.
2.1. Introduction

Reconstructions of climate change during the Quaternary of tropical South America are mainly based on vegetation change documented in pollen records. Records from tropical mountains are of particular interest for palaeo-climate reconstructions as vegetation belts migrate along altitudinal gradients during glacial, interglacial cycles. Stable carbon isotopic analyses of sedimentary organic matter have been applied to cores from tropical mountain ecosystems. These studies have provided a new proxy of environmental change, which gives a special role to $\text{C}_4$ plants and partial atmospheric CO$_2$ pressure ($p\text{CO}_2$) (Street-Perrott 1994; Street-Perrott et al. 1997; Ficken et al. 1998; Boom et al. 2002). Earlier papers dealing with $\delta^{13}\text{C}$ of tropical records use aridity to explain expansion of $\text{C}_4$ grasslands (Quade et al. 1989; Talbot and Johannessen 1992; Sukumar et al. 1993; Aucour et al. 1994; Giresse et al. 1994).

Among vascular plants, three different major photosynthetic routes can be distinguished: $\text{C}_3$, $\text{C}_4$ and CAM photosynthesis. The most common among present-day plants is the $\text{C}_3$ pathway. The $\text{C}_4$ pathway enables plants a higher water use efficiency (WUE) and a more effective CO$_2$ uptake, because they use a CO$_2$ concentrating mechanism (Leegood 1999). At present, many $\text{C}_4$ plants can be found among the monocot families Cyperaceae (sedges) and Poaceae (grasses). According to Watson and Dallwitz (1994), 407 out of 799 Poaceae genera contain $\text{C}_4$ species, most of them are characteristic elements of tropical to temperate areas with abundant warm-season precipitation. WUE of CAM plants is even better than that of $\text{C}_4$ plants, and thus many of them can be found in hot and arid environments, where other plants cannot grow. Some CAM plants are important components of the high Andean vegetation, such as Bromeliaceae (e.g. $\text{Puya}$ sp.). However, CAM photosynthesis can also be found in aquatic plants and epiphytes. The occurrence of CAM in $\text{Isoëtes}$, an important plant from Andean lakes, may even point to a very remote origin in the evolution of CAM (Keeley 1998), while the $\text{C}_4$ pathway is believed to have evolved during the mid-Cretaceous (Grasses in specific: Brown and Smith 1992; Bocherens et al. 1993). However, little is known about their behaviour in response to Quaternary climate change, neither do they make a significant contribution to the pollen based vegetation reconstructions for tropical South America.

Most of the modern $\text{C}_4$ Poaceae are found at places where, during the growing season, average monthly temperature exceed 22°C and rainfall is more than 25 mm/month (Ehleringer et al. 1997; Collatz et al. 1998). By using established models for $\text{C}_3$ and $\text{C}_4$ photosynthesis, a relationship that describes the competitive balance between the two was proposed (Ehleringer et al. 1997; Collatz et al. 1998). The authors defined the point where both types of photosynthesis are equally effective in assimilating carbon, in terms of a crossover point (or crossover temperature), which is a function of $p\text{CO}_2$. Whenever one type is more effective than the other, that type wins the competition (Figure 2.1). Thus under low $p\text{CO}_2$, $\text{C}_4$ grasses will be able to dominate over the $\text{C}_3$ species; even in colder areas where, under current $p\text{CO}_2$ conditions, $\text{C}_4$ grasses are only of minor importance compared to $\text{C}_3$ species. Lowered atmospheric
$pCO_2$ levels in the Miocene are believed to have resulted in the appearance of $C_4$ dominated grasslands (Quade et al. 1989; Cerling et al. 1993; Quade et al. 1995; Cerling et al. 1997; Latorre et al. 1997; Ehleringer et al. 1997).

**Figure 2.1** Model showing that the glacial turnover point of grasses lies at significantly lower temperatures than at present. After Collatz (1998) and Ehleringer (1997).

Independent from the previous model, the $C_4$ plants will also have an advantage over the $C_3$ plants under low atmospheric $CO_2$ concentrations. To maintain a constant influx of $CO_2$, plants will produce more stomata per surface unit (Beerling and Chaloner 1992; Beerling and Chaloner 1994; Beerling et al. 1995; Wagner 1998; Wagner et al. 1999). This will cause increased water loss through evaporation and resulting in water stress. Altered atmospheric $pCO_2$ even influences pure $C_3$ plant communities. Jolly and Haxeltine (1997) used a BIOME-3 modelling experiment (Haxeltine and Prentice 1996) at the site of Kashiru bog in tropical East Africa to show that the montane forest at 2240 m elevation can be completely replaced by ericaceous scrub vegetation by lowering only the $pCO_2$ to last glacial maximum (LGM) values while maintaining a constant temperature. Gas analysis of air bubbles from the Vostok ice core, covering the last 420,000 years, shows that $CO_2$ levels have varied significantly during the late Quaternary (Barnola et al. 1987; Petit et al. 1999b), showing a significant drop of atmospheric $CO_2$ concentrations from 280 ppmV during interglacial time (modern pre-industrial value) to 180 ppmV during the LGM. This pattern is consistent with at least three older glaciations recorded in the Vostok ice core.

Until recently, lower temperatures during the glaciations have been taken as the main cause for the lower altitudinal position of the upper forest line in the northern Andes (van der Hammen and González 1960; e.g. Hooghiemstra 1984; van der
The objective of this paper is to identify the impact of a significant drop in the concentration of atmospheric carbon dioxide on the altitudinal vegetation distribution in the Colombian Andes, the $C_4 - C_3$ grass crossover in particular. With stable carbon isotopic analysis, a Colombian high-altitude record is investigated on the presence of $C_4$ plants in the past. We aim to provide a sketch of potential plant communities that could have occurred under glacial low atmospheric $pCO_2$ and which do not occur under Holocene conditions and finally we suggest the presence of a possible relict of these vegetation types.

2.2. Study area

2.2.1. Location and current altitudinal vegetation zonation

![Altitudinal distribution of vegetation belts in the Eastern Cordillera of Colombia at present. Vertical shifts of the vegetation belts, including the upper forest line, are traditionally related to temperature and precipitation change. The impact of low atmospheric $pCO_2$ on the altitudinal distribution of $C_3$ and $C_4$ plants during glacial conditions is assessed in this study. The map shows the location of the high plain of Bogotá in north-western South America. (after: van der Hammen and González 1960).](image)

We focus on the northern Andes, more specifically the area around the high plain of Bogotá, which is situated at 2550 m elevation in the Eastern Cordillera, Colombia. The basin, which represents the bottom of a dry palaeo-lake, accumulated an extraordinary sequence of lake sediments during the Quaternary. Core Funza-II was drilled at the site where the basin was expected to have maximum depth. From the tropical lowlands to the temperate high altitudes, six distinct modern vegetation belts
are recognized (Figure 2.2). Vegetation characteristics of these belts can be recognized in the fossil pollen assemblages by indicative taxa (van der Hammen 1974; Hooghiemstra 1984; Van't Veer and Hooghiemstra 2000). The position of the high plain of Bogotá, halfway the maximum (3400 m) and minimum (1800 m) elevation reached by the upper forest line during interglacial and glacial periods, respectively, renders the high plain sediments a sensitive recorder of climatic change. At present, the average monthly temperature varies a little among different localities but at the centre of the high plain it is 12.4°C with small seasonal changes and a rainfall average of 786 mm/yr (Kuhry 1988).

The following vegetation belts can be recognized (Figure 2.2): tropical lowland vegetation (0-1000 m), lower montane forest (=subandean forest; 1000-2300 m), upper montane forest (=Andean forest; 2300-3200 m), subparamo (3200-3500 m), grassparamo (3500-4200 m), and superparamo (4200-4700 m). Modern paramo ecosystems can consist of a large part of *Calamagrostis effusa* bunch grasses, a substantial amount of the bamboo *Chusquea tesselata*, and to some extent also *Cortaderia* and *Festuca* species (Cleef 1978; Cleef 1981), all C₃ grasses. On estimation, these grasses can make up to 95% of the total vegetation cover and thus must be considered as important elements of biomass production. A synthesis of the composition of the present-day forest and paramo communities in the study area was published by (Hooghiemstra 1984). The paramo communities for almost the entire Eastern Cordillera of Colombia were treated in more detail by (Cleef 1981).

### 2.3. Methods

Aliquots of about 0.5 g of sediment from Funza-II were decalcified for isotopic determinations of organic matter by overnight reaction with 5N HCl at room temperature. The acidic solution was removed by centrifugation and aspiration. The insoluble residue was neutralized using repeated suspension in distilled/de-ionized water followed by centrifugation and vacuum aspiration. Neutralized residues were dried overnight at 60°C, mixed with about 1.5 g of CuO, and put into 9 mm quartz tubes. The tubes were sealed under vacuum and combusted overnight at 850°C. Evolved CO₂ was trapped in 6 mm Pyrex tubes using a cryogenic vacuum-distillation line and the isotopic composition of the trapped CO₂ was determined using a Finnigan Mat-252 mass spectrometer. Isotopic compositions are reported in per mil units (‰) relative to the Peedee belemnite (PDB) standard.

\[
\delta^{13}C(\text{‰}) = 1000 \left[ \frac{R_{\text{sample}}}{R_{\text{PDB}}} - 1 \right], \quad \text{where} \quad R = ^{13}C/^{12}C.
\]

Duplicate analyses of selected samples were performed and yielded a reproducibility ranging from ±0.05 to ±0.41‰. Triphenylamide (TPA) standards were repeatedly analyzed and indicted an instrumental precision of 0.012‰. Several dried grass and sedge samples collected in the field were analyzed for δ¹³C using the same equipment.

To assess the contribution of C₃ and C₄ grasses to the present-day vegetation cover in Andes of Ecuador and the Eastern Cordillera of Colombia, 220 grass species
published by (Jørgensen and Ulloa 1994), and 187 grass species published by Pinto-Escobar and Mora-Osejo (1966), were categorized into a C\textsubscript{3} or a C\textsubscript{4} component, using data from (Watson and Dallwitz 1994) in conjunction with our own data. The published data on Ecuador give a much larger data set covering a wider area; since this vegetation has many features in common with that of the Colombian Eastern Cordillera, it is valuable. At intervals of 100 m of altitude, the percentage C\textsubscript{3} species on the total number of grass species was calculated. Vegetation relevées were sampled by A.M. Cleef using methods described by (Cleef 1981).

2.4. Results and discussion

2.4.1. Stable carbon isotopic record of Funza-II

The stable isotopic record of the total organic matter (TOC) is given in Figure 2.3. Since the Funza-II sediments are lacustrine, TOC include both terrestrial and lacustrine components. A detailed analysis of the Funza-II \(\delta^{13}\text{C}_{\text{TOC}}\) (Mora et al., in press) demonstrates that the \(\delta^{13}\text{C}_{\text{TOC}}\) shows mainly changes in terrestrial C\textsubscript{3} and C\textsubscript{4} dominated ecosystems (Figure 2.3). Many of the glacial periods show enrichments in \(\delta^{13}\text{C}_{\text{TOC}}\). C\textsubscript{4} plants have characteristic average \(\delta^{13}\text{C}_{\text{TOC}}\) values of -12\%o (Bender 1971) as opposed to -27\%o of C\textsubscript{3} plants (O'Leary 1981). Thus, it can be explained that increased input of C\textsubscript{4} plant material caused the enrichment in \(\delta^{13}\text{C}_{\text{TOC}}\) during the glacial periods. Moreover, all glacial periods are characterized by an increase of grass pollen (Hooghiemstra and Ran 1994), so it is most likely the C\textsubscript{4} grasses that contribute to the TOC at times of glacial \(\delta^{13}\text{C}\) enrichment. This agrees with the results of the Mt. Kenya records, which only show the period of the Holocene until the LGM; while our Funza-II interval shows the last 10 glacial, interglacial cycles, excluding the transition from the LGM and the Holocene. In this part of the Funza-II record, every glacial is characterized by an enrichment in the \(\delta^{13}\text{C}_{\text{TOC}}\) indicative of C\textsubscript{4} plant biomass.

2.4.2. Prediction of C\textsubscript{4} grasslands in the Andes at low p\textsubscript{CO\textsubscript{2}}

At sea level, \(p\text{CO}_2\) today is around 36 Pa while at the elevation of the high plain of Bogotá \(p\text{CO}_2\) is around 26 Pa as a result of the altitudinal decline of atmospheric pressure, while the CO\textsubscript{2} concentration ([CO\textsubscript{2}]\textsubscript{am})=360 ppmV. During the LGM, global [CO\textsubscript{2}]\textsubscript{am} was as low as 180 ppmV (Petit et al. 1999a). At sea level this would be equivalent to \(p\text{CO}_2=18\text{ Pa}\); but at 2550 m elevation, the \(p\text{CO}_2\) will then have been further reduced to 13 Pa. However, the altitudinal decline of \(p\text{CO}_2\) coincides with a decline in \(p\text{O}_2\), and since the equilibrium between C\textsubscript{4} and C\textsubscript{3} is a function involving the ratio of \(p\text{O}_2\) and \(p\text{CO}_2\), the altitudinal decline of pressure therefore has no impact upon the competition between the C\textsubscript{3} and C\textsubscript{4} plants (Ehleringer et al. 1997). However, the extremely low \(p\text{CO}_2\) of 13 Pa may in itself have an effect upon plant growth at a high elevation.
Thus, since the cross-over temperature is not affected by altitude, we use 18 Pa for the LGM and a drop of around 10°C of the cross-over temperature can be inferred from the model, compared with the present (Figure 2.1 after: Ehleringer (1997) and Collatz (1998)). This potentially allows the presence of C\textsubscript{4} dominated grasslands around the high plain at the present-day high plain temperature. Since \(pCO\textsubscript{2}\) also influences pure C\textsubscript{3} plant communities, the upper forest line is potentially able to descend independently from temperature (Jolly and Haxeltine 1997). Thus, a fixed relationship between the position of the upper forest line and the 9.5°C isotherm, commonly used

\[
\delta^{13}C_{TOC}
\]

Figure 2.3 Down core changes of \(\delta^{13}C_{TOC}\) of the first 156m of the Funza II record. The numbers refer to the marine isotope stages.
in previous studies (e.g. Hooghiemstra 1984), may need revision. Based on our previous considerations, the glacial upper forest limit may relate to a slightly higher average annual isotherm, reducing the glacial, interglacial amplitude of the estimated temperature change.

Under present conditions (high \( pCO_2 \)), the palaeo-lake would not receive a substantial amount of \( C_4 \) detritus from the Andean forest and paramo (Boom, unpublished data), but mainly \( C_3 \) detritus. A changing competitive balance between \( C_3 \) and \( C_4 \) genera, however, as described by Ehleringer and Collatz, should easily move the ‘crossover point’ to higher elevations. This shift would influence the character of the plant detritus received by the palaeo-lake of Bogotá. To which altitude the ‘crossover point’ will rise is unclear, but at LGM \( pCO_2 \) of 18 Pa, it might occur at an average annual isotherm of around 10°C (Figure 2.1). Even when the shift of the ‘crossover point’ to higher elevations is minimal, the paramo should have still descended during cold and dry climatic conditions as far down as approximately 1900 m and, as a consequence, shall be influenced by any upslope migration of the ‘crossover point’.

2.4.3. Present-day \( C_4 \) grasslands in the Northern Andes

Several grass and sedge species have been analysed for \( \delta^{13}C_{TOC} \) to find potential \( C_4 \) sources. Species from the following important Andean Poaceae genera contained only \( C_3 \) specimens; Aciachne, Agrostis, Calamagrostis, Chusquea, Cortaderia, Denthonia, Festuca and Ortachne (Lorenzochloa). This result was as expected from the literature (Watson and Dallwitz 1994). However, three \( C_4 \) specimens were found: Muhlenbergia cleefit (-16.0‰), Paspalum bonplandianum (-12.2‰) and Sporobolus lasiophyllus (-12.6‰). From the Cyperaceae, two genera contained \( C_4 \) specimens: Bulbostylis junciformis (-12.8‰) and B. tropicalis (-11.7‰), Cyperus brevifolia (-11.9‰) and C. giganteus (-13.5‰). Several other Andean plant genera have been investigated (table 1.1) and no other \( C_4 \) plants have been found. The number of plant taxa that can account for \( ^{13}C \) enrichment are thus restricted mainly to a few genera belonging to the Cyperaceae and Poaceae. As expected, the modern Andean ecosystem is \( C_3 \) dominated.

Other \( C_4 \) grass taxa occurring in the Andes belong to the genera Aegopogon, Andropogon, Axonopus, Bothriochloa and Bouteloua. In terms of species numbers, as well as percentage of vegetation cover, the \( C_4 \) grasses and the \( C_4 \) sedge species belonging to terrestrial Bulbostylis and aquatic Cyperus represent only a minor fraction of the modern vegetation communities in the paramo. However, with regard to Cyperus, which can contain both \( C_3 \) or \( C_4 \) species, it is not clear yet, whether or not high altitude species can be ranked as \( C_3 \) or \( C_4 \) plants. The Cyperus dominated swamp communities have not been documented yet from the high plain of Bogotá, nor from the nearby Fúquene and Tota lakes. A Cyperus rivularis association (correct name probably C. aggregatus) has been reported from wet valley floors between 3300 and 3500 m
north of the high plain of Bogotá (Cleef 1981). However, it is likely that they are all $C_3$
species.

A tiny still, unidentified *Cyperus* species is also very common in open degraded
vegetation on dry semi-arid hills near the La Herrera lake bordering the western edge
of the high plain of Bogotá (Vink and Wijninga 1988). In this vegetation, a number of
$C_4$ grass species were reported, e.g. *Andropogon barbinoides*, *A. hirtiflora*, *A.
saccaroides*, *Bouteloua simplex*, *Chloris submitica*, *Eragrostis palula*, *Eragrostis* sp.,
*Microchloa kunthi*, *Muhlenbergia* sp. and *Setaria geniculata*. In this area also, the
proportion of CAM species, both in number and cover, is elevated as compared to the
natural paramo and Andean forest. This is to be expected since the CAM species are
extremely well adapted to aridity. Representatives are Agavaceae: 2 spp.; Aizoaceae:
1 sp.; Bromeliaceae: 4 spp.; Cactaceae: 4 spp.; Crassulaceae: 1 sp. and Orchidaceae:
4 spp.

![Diagram](image)

**Figure 2.4A** Schematic diagram of *Arcytophyllum nitidum* with *Sporobolus lasiophyllus* and
*Achyrocline lehmannii* vegetation. Dry, stony, subparamo with *Espeletiopsis corymbosa* and
*Gaultheria rigida* at 3610 m elevation, near Bogotá. (after: Cleef 1981: fig. 15).

The savanna ($C_4$) grasslands are common at sea level (e.g. savannas of the
Colombian Llanos Orientales). Patches of mountain savannas also locally thrive at
various altitudes, for example, in sub arid Colombian inter-Andean valleys from 1500
to 2500 m, where they occur up to the supposed upper forest line, and even may grade
into lowered subparamo (e.g. in the Chichamocha Valley, some 200 km north of Bogotá).
These $C_4$ grass-dominated communities thrive well under low $pCO_2$ conditions and
must have been able to colonize significant parts of the mountains, including the more
temperate areas at higher altitude. In addition, the dry climatic conditions during the
LGM must have favoured the expansion of $C_4$ dominated ecosystems. At some places,
the montane forest belt may have been reduced to a narrow zone, or virtually
disappeared. Such a disappearance is documented in the late glacial part of the pollen record of Laguna Pedro Palo, located at 2000 m on the outer slope of the high plain of Bogotá, facing the Magdalena Valley. There, subandean semi-open dry vegetation was locally in contact with dry paramo vegetation because a sensu-stricto Andean forest belt was apparently absent during the early late glacial stage (Hooghiemstra and van der Hammen 1993). While the paramo was forced to lower elevations in order to survive the combination of low temperatures and low $pCO_2$ conditions, $C_4$ dominated grasslands extended upslope and may have reached and merged with the paramo belt. Thus grassland communities, significantly different from today, could have occurred. They would perhaps resemble modern most dry grass paramos. Some characteristic paramo species may not have suffered from $C_4$ competition. Consequently this hypothesised $C_4$ dominated vegetation does not necessarily need to have a full modern analogue. However, remnants of such vegetation communities can still be found in the paramos of today (Figure 2.4A and B).

Species richness of $C_3$ and $C_4$ grasses is shown in Figure 2.5 along the altitudinal gradient of the northern Andes. The emergent pattern is in full agreement with similar studies of grass biomass along the slopes of Mt. Kenya (Tieszen et al. 1979; Young and Young 1983), the Argentinean Andes (Cavargano 1988; Cabido et al. 1997), and on Hawaii (Rundel 1980). The trend in $C_3$ grass species richness is apparently equal to a trend in $C_3$ grass biomass. From Figure 2.5, it follows that the present-day ‘cross-over point’ (at 50% $C_3$ species) lies at 1950 m for the data set from the province of Cundinamarca, that includes the high plain of Bogotá. This altitude roughly corresponds to an annual isotherm of 18°C. Applying this to the area of Bogotá, located at 2550 m, this means that the $C_4$ dominated grass ecosystems reach altitudes up to only 600 m below the high plain.

The distribution of $C_3$ and $C_4$ grasses from Ecuador follow a clearer pattern of increasing $C_3$ species richness with higher elevations. Because the data used here cover the whole of Ecuador, distribution is smoothed out. This is in contrast to the Colombian data set, which covers a relative small area resulting in anomalies caused by geographical features. However, the crossover point for the Ecuadorian data set is
easily determined and lies at 2400 m. Due to the scatter in data points of the Colombian dataset, exact determination of the cross-over point is difficult. The Ecuadorian data set is probably also valid for the Eastern Cordillera, because of similarities in vegetation and local climate.

Figure 2.5 $C_3$ versus $C_4$ grass species diversity along an altitudinal gradient, based on (a: open circles) analysis of 180 grass species and their altitudinal distribution in the Colombian province of Cundinamarca, and (b: solid circles) analysis of 220 grass species from Ecuador. The 'crossover point' of $C_4$ to $C_3$ dominance lies at present at 1950 m in Cundinamarca, and at 2400 m in Ecuador. (Data for Colombia after Pinto-Escobar and Mora-Osejo, 1966. For Ecuador after Jørgensen and Ulloa-Ulloa, 1994).

The $C_4$ grass *Sporobolus lasiophyllus*, occurring between about 2000 and 3700 m in the northern Andes, forms true open bunch grassland in the lowermost open paramos of the Colombian Eastern Cordillera (Table 1); occasionally almost pure stands occur. *Paspalum bonplandianum* (2600–4000 m) does not form true communities, but is usually found associated with *Calamagrostis effusa* bunch grassland, where it covers up to 20%. Apparently, this $C_4$ species is favoured by open habitats created by burning and grazing of dense natural bunch grassparamo vegetation. *Muhlenbergia cleefii* is a recently described species (Laegaard 1995) that grows in low dense cushions along sloping lake shores and humid to wet valley floor meadows in the paramos of the Eastern Cordillera of Colombia between 3500 and 4200 m. This species is sub-dominant in the azonal ‘*Muhlenbergia fastagiata*’ association described by Cleef (1981). This $C_4$ grass of azonal humid habitat is not supposed to be favoured for expansion during
Pleniglacial conditions. On the high Mexican volcanoes tussock vegetation of *Muhlenbergia* species is mainly present below the upper forest line (Almeida-Leñero 1997). Under Pleniglacial conditions, these *Muhlenbergia* species could have replaced the modern local tussocks of *Calamagrostis* and *Festuca*.

### 2.4.4. Andean C₄ grassland evolution

C₄ genera, which are elements within the paramo today, with *Sporobolus* as most characteristic example, originated in open savanna and savanna-like lowland habitats (Cleef et al. 1993). These taxa migrated to the level of the modern lower paramo during Neogene-Quaternary times by migrating upslope via open habitats and/or via upslope extensions of this vegetation type during glacials with low pCO₂ and possibly in combination with dry conditions (Hooghiemstra and Cleef 1995). During the Holocene, under increasing atmospheric pCO₂ conditions, most of the C₄ grasses were no longer able to compete with the C₃ grasses, and almost disappeared, but were able to survive in the lower reaches of the driest paramos due to their higher WUE. The C₄ species, that are still present there today, occupy small niches in the high Andean ecosystems that can be considered as relict areas. They are able to survive because of local more arid conditions, and in case of *Muhlenbergia* species, possibly even slightly saline environments (Ruhtsatz 1977). Under increasing arid and saline conditions, C₄ plants are able to out-compete the C₃ elements because of their higher WUE.

As shown above, presently C₄ grasslands exist in the drier hills of the high plain of Bogotá, but significant parts of these modern grasslands are believed to be the result of large-scale deforestation and soil erosion, leading to sub arid conditions. In early Holocene, palaeosols from the Guasca valley, which makes contact with the high plain of Bogotá, stable carbon isotope evidence points to past presence of C₄ grasslands (Guillet et al. 1988). This was not attributed to climate change but to anthropogenic impact on the valley floor.

The previously discussed pollen record of Laguna Pedro Palo (Hooghiemstra and van der Hammen 1993) indeed represents a mid-altitude location on the west slope of the high plain of Bogotá, where the Andean forest belt had virtually disappeared and was largely replaced by grassland during the Pleniglacial to late glacial transition. This grassland was characterised as tropical (sub) Andean semi-open dry vegetation that came in contact with dry paramo during cold and dry climatic conditions. This is an indication that it was physically possible for plant taxa derived from intermontane and other lowland savannas to migrate upslope into the paramo during glacial conditions. The example of Laguna Pedro Palo is the only physical evidence in a pollen record so far of a site where expansion of the Andean C₄ grasslands actually merged with the paramo grassland. Today, this is most visible in the area of Villa de Leiva, some 100 km north of the high plain of Bogotá. At about 2200 m within the arid open vegetation, the C₄ grasses *Andropogon hirtiflorum, Andropogon lehmannii, Andropogon leucostachia, Andropogon tener, Digitaria sp.*, Melinis
Table 2.1 Selected vascular plant species displaying \( \text{C}_3 \) and \( \text{C}_4 \) characteristics of the paramos of the Colombian Eastern Cordillera. Vegetation relevées were sampled by A.M. Cleef. Localities abbreviations: CH=Chia (Cundinamarca); SO=Socha (Boyacá); TO=Torca (Cundinamarca); GU=Guina (Boyacá); RU=Rúdia (Boyacá); SA=Sarna-Tota (Boyacá); CI=Chisacá (Cundinamarca).

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<th>Relevée nr Cleef</th>
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<th>Cover (%)</th>
<th>Inclination in °</th>
<th>Soil depth (cm)</th>
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<td>408</td>
<td>GU</td>
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<td>364</td>
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<td>133</td>
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</tr>
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minutiflora, Paspalum sp., and Sporobolus sp. (Cleef, unpublished data) have been collected which extend locally up to 2500-3000 m.

CAM plants are another group that may have become more important during glacial times. Although CAM plants are more adapted to survive periods with poor water supply, than to deal with low \( \text{CO}_2 \) availability, we cannot rule out that they may thrive well under glacial conditions that may also be dry. Among the characteristic genera of the paramos are Greigia and Puya (both Bromeliaceae), Echeveria and Crassula (both Crassulaceae). Many Clusia species are able to use the CAM photosynthetic pathway too (Tinoco Ojanguren and Vazquez Yañez 1983; Hooghiemstra and van der Hammen 1993; Lütte 1996; Herzog et al. 1999). Cover of these taxa may have increased significantly under glacial conditions. It should be noted, however, that there is no strong evidence within the pollen records to support this suggestion, since their pollen are never abundant in the records.

The contribution of the \( \text{C}_3 \) and \( \text{C}_4 \) plants to the total vegetation cover cannot be determined from pollen analysis. Therefore additional compound-specific stable carbon isotope data from the high plain of Bogotá is needed to further substantiate that \( \text{C}_3/\text{C}_4 \) changes in vegetation communities did take place. This data will be presented elsewhere dealing with the organic geochemistry of the Funza-II core (Boom et al. 2002).
2.4.5. Effect of upward C₄ grass migration upon palaeo-treeline investigation

Expanding C₄ grasslands from lower elevations upslope dilute the forest signal in pollen spectra and glacial C₄ grassland might be interpreted in the pollen record as ‘descending high-altitude C₃ grasslands’; the position of the upper forest line may be estimated as too low and, as a consequence, the palaeo-temperature may have been estimated too low. The forest line itself is also influenced by pCO₂ and environmental aridity as shown in Central Africa (Jolly and Haxeltine 1997), which potentially may lead to over-estimation of the downslope migration of the upper forest line. At this moment we are unable to quantify this impact. In a palaeo-ecological study of the altitudinal migration of the subandean forest belt Wille et al. (2001) show that the glacial lapse-rate in the Andes was steeper than today (Farrera et al. 1999), which perhaps could counterbalance the error discussed above.

2.5. Conclusions

Based on theoretical considerations and stable carbon isotope data, we propose that C₄ grasslands must have developed during (parts of) glacial periods in the basin of Bogotá. There is sufficient information available to accept that replacement of C₃ grasslands by C₄ grasslands is climatically controlled and thus has implications for climatic reconstruction of the area. Changes in temperature, precipitation, and pCO₂ play an important role in the altitudinal zonation of vegetation belts. Several vegetation types such as the *Arcytophyllum/Sporobolus* vegetation community are recognized as a relict of the C₄ *Sporobolus* grasslands that probably covered large areas in the high Andes during the glacial periods with low pCO₂. Moreover, the modern taxon *Sporobolus lasiophyllus* is the only high altitude C₄ grass in the area capable of forming dense stands of grassland.

Treeline position and its relation to climatic variables is more complex as realised before. Temperature, precipitation, pCO₂, lapse rate, floral composition of the forest communities and physiological balance between C₃ and C₄ plants above and below the upper forest line play a role. Some variables may partly counterbalance and reduce the total effect on current practice of estimating palaeo-temperatures.

2.6. Acknowledgements

The authors thank M. Bush, M. Cabido and H. Visscher for useful comments. We thank J.J. Boon (FOM/ Hugo de Vries Laboratory, Amsterdam), R. Marchant (Hugo de Vries Laboratory, Amsterdam) and J.S. Sinninghe Damsté (NIOZ, Texel) for constructive comments on the manuscript, S. Schouten (NIOZ, Texel) for advise and support, and J.W. de Leeuw (NIOZ, Texel) for making facilities at the NIOZ Institute available. J.C. Berrio (Bogotá/Amsterdam), the family Berrio in Puntalarga (Boyacá), and C. Rodriguez (director of the TROPENBOS Colombia office, Bogotá) are acknowledged for assistance and hospitality during the field work. We thank T. van...
der Hammen (Chia, Colombia) for his advice and encouraging support in Colombia. This study was financially supported by The Netherlands Geosciences Foundation (GOA-NWO), grant 750.196.16 to H. Hooghiemstra and J.J. Boon. This is NIOZ contribution 3391.

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