Inter-specific variation of the biochemical limitation to photosynthesis and related leaf traits of 30 species from mountain grassland ecosystems under different land use

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ABSTRACT

The maximum rate of carboxylation (V_{cmax}) and the potential rate of RuBP regeneration (P_{ml}, which equals $J_{max}/4$), as well as leaf nitrogen content (N_L) and specific leaf area (SLA), were studied in sun leaves of 30 species from differently managed mountain grassland ecosystems (abandoned areas, pastures and meadows) at three study areas in the Eastern Alps. A significant correlation between V_{cmax} and P_{ml} across the investigated species was observed. In comparison to a previous survey on the relationship between P_{ml} and V_{cmax}, the investigated species were found to invest a proportionally smaller amount of available resources into P_{ml}. Despite this close correlation between V_{cmax} and P_{ml}, variation in the V_{cmax}–N_L and P_{ml}–N_L relationships was large, indicating that the investigated species differed widely in their respective nitrogen use efficiencies. Among the investigated species, dwarf shrubs were characterized by significantly lower values of V_{cmax}, P_{ml} and N_L compared to graminoids and forbs, which did not differ significantly from each other. Species from abandoned areas were found to be lower with respect to V_{cmax}, P_{ml}, N_L and SLA than species from pastures and meadows, which were not significantly different from each other.

Key-words: leaf nitrogen; life form; P_{ml}; specific leaf area; V_{cmax}

INTRODUCTION

Among the papers published during recent years, there is one which, especially in the gas exchange modelling community, has received special attention, since it seems to imply a promising approach which could greatly simplify the parameterization of models of C_3 assimilation. In this article, Wullschleger (1993) presents data of the two component processes of photosynthesis, the maximum rate of carboxylation (V_{cmax}) and the potential rate of electron transport (J_{max}), of 109 different species, calculated from previously published A/Ci curves. Despite multi-fold differences in the absolute values of V_{cmax} and J_{max}, when plotting them against each other they surprisingly gather together around a single straight line, indicating a close correlation between these two processes. Later, Leuning (1997) further improved this correlation, accounting for the temperature dependency of V_{cmax} and J_{max}, by scaling the results obtained by Wullschleger (1993) to a common temperature of 20 °C. It was this relationship which attracted the modellers' attention (e.g. Farquhar, Von Caemmerer & Berry 1980; Leuning *et al.* 1995; Baldocchi & Meyers 1998), because it reduces by one the number of parameters to be specified, since once V_{cmax} has been determined, J_{max} may be calculated easily just by multiplication.

Not really surprisingly, however, this approach has also caused criticism (Niinemets & Tenhunen 1997; Wohlfahrt *et al.* 1998) due to the fact that, despite the close correlation between J_{max} and V_{cmax}, there still remains a considerable amount of variation, even after having been scaled to a common temperature (Leuning 1997). It is not clear whether the variation is due to species-specific differences in the proportional allocation between J_{max} and V_{cmax} or whether it is caused by the environmental conditions (day length, length of the growing season, light and nutrient availability, temperature and other micro-climatic factors) encountered by the plants during their development. Among the species analysed by Wullschleger (1993), almost 50% are agricultural or horticultural crops, which gives rise to the question of whether a relationship based largely on these will be successful in predicting assimilation of wild species (Baldocchi & Meyers 1998). Wild herbaceous species are considerably under-represented in the dataset of Wullschleger (1993), comprising less than 10%. Moreover most of the species analysed by Wullschleger (1993) were grown in controlled environments, which potentially may lead to biased results if this relationship derived mainly from plants grown under controlled conditions is used for scaling up gas exchange in the field (Leuning *et al.* 1995; De Pury & Farquhar 1997; Baldocchi & Meyers 1998), since adaptation of the photosynthetic apparatus to growth conditions, such as light, temperature and nutrients, has been documented for a large number of species (e.g.

Björkman 1980; Björkman, Badger & Armond 1980; Evans 1989; Hikosaka & Terashima 1995, 1996).

In order to test whether the relationship between J_{max} and V_{cmax} as set up by Wullschleger (1993) and Leuning (1997) also holds for wild species from natural ecosystems not covered in Wullschleger's (1993) survey, we conducted a field study on 30 species from differently managed semi-natural mountain grasslands at three study areas in the Eastern Alps. The type and intensity of management (e.g. timing and time intervals between mowing and fertilization, grazing frequency, type and number of grazers, time since and history before abandonment) strongly influences the ratio between the major plant resources (e.g. the ratio between light and nutrient availability; Tilman 1988, 1994; Tappeiner & Cernusca 1994). Depending upon species plasticity, these alterations either lead to adaptations in plant form and function or to replacement by other species (Tilman 1988, 1994). Among the aims of the present study is quantification of the differences in J_{max}, V_{cmax} and related leaf traits between different functional groups of species and between species characteristic of different types of land use. In order to provide a physiological basis for future simulation studies in context with land-use changes in mountain grasslands (Cernusca et al. 1998; Tenhunen 1999), we additionally present our results in terms of the parameters of a mechanistic model of C_3 assimilation (Harley & Tenhunen 1991). This may be advantageous especially for use in models at larger spatial scales (Alsheimer et al. 1998; Tenhunen et al. 1998), because appropriate model parameters at these scales are usually hard to find (Running et al. 1989) and much additional effort is required during parameterization (Falge et al. 1996), since most of these data are being expressed in terms of the resulting processes and not in terms of the corresponding model parameters.

In order to exclude variation of nitrogen partitioning within the photosynthetic components caused by different light regimes during plant growth (Evans 1989; Pons & Pearcy 1994; Hikosaka & Terashima 1995, 1996; Niinemets & Tenhunen 1997), we restricted our investigations to sun leaves. J_{max} and V_{cmax} were calculated from photosynthesis measured on attached leaves in the field, which were also analysed with respect to leaf nitrogen content (N_L) and specific leaf area (SLA). Nitrogen is a major component of the enzymes associated with photosynthesis (Evans 1989) and

is well correlated with both V_{cmax} and J_{max} (Field 1983; Harley et al. 1992b; Anten, Hernandez & Medina 1996; Wohlfahrt et al. 1998). SLA is a key measure of leaf morphology/structure (Reich, Ellsworth & Walters 1998a) and may be used to convert rates and fluxes from a leaf mass to a leaf area basis (Niinemets 1997), which is important when comparing species of different life form (Reich et al. 1995, 1998a,b; Poorter & Evans 1998).

Since in the present paper the model of leaf photosynthesis of C_3 plants as presented by Harley & Tenhunen (1991) is applied, P_{ml}, the potential rate of ribulose-1, 5-bisphosphate (RuBP) regeneration, will be used in the following instead of J_{max}, as introduced by Farquhar et al. (1980), to which it is related by $J_{max}/4$.

METHODS

Sites and investigated plant species

Three study areas, situated along a north–south transect across the Eastern Alps, were selected to provide a representative range of mountain grassland ecosystems from the Eastern Alps (Cernusca et al. 1996). Field investigations were carried out during the summers of 1993 and 1996 at the Monte Bondone study area and Passeier Valley and in 1997 in Stubai Valley. The three study areas are situated along an altitudinal gradient, the southern-most study area having the lowest elevation and the northern-most having the highest (Table 1). This altitudinal gradient is reflected in the average air temperatures at the study sites, which continuously decrease along the north–south transect as indicated in Table 1. Average annual precipitation (Table 1) is similar in Stubai and Passeier Valley, whereas the higher precipitation at the Monte Bondone study area reflects its location at the southern border of the Alps, being influenced by both the Mediterranean and the continental climate (Gandolfo & Sulli 1993).

An abandoned area and a hay meadow were investigated in each study area, and at Monte Bondone and Stubai Valley a pasture was also investigated (Cescatti et al. 1999; Bitterlich & Cernusca 1999; Tasser & Tappeiner 1999). These grasslands were created centuries ago by cutting the predominating mixed evergreen/deciduous forests and have been kept in an ecological balance by human man-

	Stubai Valley	Passeier Valley	Monte Bondone
Latitude	47°07′	46°50′	46°01′
Longitude	11°17′	11°17′	11°01′
Altitude (m above sea level)	1900 (1750*)	1770 (1618*)	1540
Average annual rainfall (mm)	1097	1041	1189
Average annual air temperature (°C)	3·0	3·6	5·5
Average air temperature May–October (°C)	8·5	9·7	10·9

Table 1 General geographic and climatic characterization of the three study areas

*Altitude of meteorological station, if different from that of the study area.

agement practices, i.e. hay making and grazing by domestic ungulates (Spatz, Weiss & Dolar 1978). During the last decades however, due to far-reaching socio-economic changes, a rapidly increasing part of this formerly intensively managed grassland has been abandoned, opening these areas to secondary succession by re-colonizing shrub and tree species (Paldele 1994; Schwackhöfer 1977). The abandoned areas in the present study had been abandoned for 35, 10 and 5 years (Monte Bondone, Stubai Valley and Passeier Valley study areas, respectively). The investigated hay meadows are mowed once a year at the end of July/beginning of August, and the pastures are grazed solely by cattle at the Stubai Valley study area, and by cattle and horses at Monte Bondone.

Criteria for the selection of the investigated species in the different study areas were high abundance and/or major contribution to stand biomass on any one of the differently managed sites (species typical for a certain type of land use) or on all of the sites (species of overall importance for the study area). According to these criteria, 30 different species, of which four occurred at two study areas, were selected. Eleven species originated from abandoned areas, 17 from meadows and six from pastures, among them 10 graminoids, 21 forbs and three dwarf shrubs, as shown in Table 2.

Experimental methods

Response curves of net photosynthesis and stomatal conductance versus photosynthetic photon flux density (PPFD, light response curves) and ambient CO_2 partial pressure (*A*/*Ci* curves) were calculated using a fully climatized CO_2/H_2O porometer (CIRAS-1, PP-Systems, Hitchin, UK). In addition, at the Monte Bondone study area two CO_2/H_2O porometers (Heinz Walz GmbH, Effeltrich, Germany), together with cuvettes PMK-10 and GK-0235P of the same origin, were used. Light response curves were conducted at average ambient CO_2 partial pressure, average ambient humidity (approximately 1 kPa) and leaf temperatures between 5 and 30 °C, decreasing PPFD stepwise from > 1200–0 μmol m^{-2} s^{-1}. CO_2 response curves were conducted at saturating light intensity (> 1200 μmol m^{-2} s^{-1}), average ambient humidity and leaf temperatures between 5 and 30 °C, increasing CO_2 partial pressure from 7 to 100 Pa. Typically 15–20 healthy looking sun leaves from

Table 2. General characterization of the investigated species

Species	Abbreviation	Family	Study area	Land use	Life form	N value[1]	L value[1]
Achillea millefolium	Acmi	Asteraceae	PV	M	F	–	≥7
Agrostis tenuis	Agte	Poaceae	PV	M	G	4	7
Alchemilla vulgaris	Alvu	Rosaceae	PV, SV	M	F	–	≥6
Arnica montana	Armo	Asteraceae	PV	A	F	2	9
Avenella flexuosa	Avfl	Poaceae	PV	M	G	3	6
Briza media	Brme	Poaceae	SV	A	G	2	8
Campanula scheuchzeri	Casc	Campanulaceae	PV	M	F	3	8
Calluna vulgaris	Cavu	Ericaceae	PV	A	D	1	8
Dactylis glomerata	Dagl	Poaceae	MB	M	G	6	7
Festuca rubra	Feru	Poaceae	PV	M	G	–	≥7
Geranium sylvaticum	Gesy	Geraniaceae	SV	M	F	7	6
Koeleria pyramidata	Kopy	Poaceae	MB	P	G	2	7
Nardus stricta	Nast	Poaceae	MB, PV	A	G	2	8
Plantago atrata	Plat	Plantaginaceae	MB	A	F	5	8
Plantago media	Plme	Plantaginaceae	MB, SV	P	F	3	7
Potentilla aurea	Poau	Rosaceae	MB	P	F	2	8
Polygonum viviparum	Povi	Polygonaceae	MB, PV	M, A	F	2	7
Pulsatilla sulphurea	Pusu	Ranunculaceae	PV	A	F	3	8
Ranunculus acris	Raac	Ranunculaceae	PV	M	F	x	7
Rhinanthus alectorolophus	Rhal	Scrophulariaceae	MB	M	F	3	8
Rumex alpestris	Rual	Polygonaceae	PV	M	F	6	7
Sesleria varia	Seva	Poaceae	SV	P	G	3	7
Trifolium alpinum	Tral	Fabaceae	PV	A	F	2	8
Trollius europaeus	Treu	Ranunculaceae	MB	M	F	5	9
Trisetum flavescens	Trfl	Poaceae	MB	M	G	5	7
Trifolium montanum	Trmo	Fabaceae	MB	P	F	2	8
Trifolium pratense	Trpr	Fabaceae	MB	M	F	x	7
Trifolium repens	Trre	Fabaceae	PV	M	F	6	8
Vaccinium myrtillus	Vamy	Ericaceae	MB	A	D	3	5
Vaccinium uliginosum	Vaul	Ericaceae	SV	A	D	3	≥6

[1]Nitrogen and light values according to Ellenberg *et al.* (1991); MB, Monte Bondone; PV, Passeier Valley; SV, Stubai Valley; A, abandoned area; M, meadow; P, pasture; D, dwarf shrub; G, graminoid; F, forb. x, no difference.

the upper, well-illuminated canopy layers were investigated per species. Measurements were made on fully developed plants (most at the onset of flowering) during the main growing period at these elevations (June, July) on days without rain, starting in the late morning, when the dew on the vegetation had evaporated, until approximately 2 h before sunset. Measurements were interrupted for a few days after periods of cool weather. Soil water availability was high during the entire period of measurements due to frequent precipitation during these months. For further details on the gas exchange measurements, refer to Wohlfahrt *et al.* (1998) and Bahn & Cernusca (1999).

Calculations of net photosynthetic rate, stomatal conductance, transpiration rate and internal CO_2 partial pressure were made using the equations of Von Caemmerer & Farquhar (1981). All gas exchange rates are expressed on the basis of the projected leaf area, except for *N. stricta*, *F. rubra* and *A. tenuis*, whose gas exchange rates are expressed on a surface area basis, because of the uniform circular shape and orientation of their leaves, which is more or less perpendicular to the ground (see Körner, Scheel & Bauer 1979).

The leaf area was measured using a leaf area meter (CI-203, CID Inc., Vancouver, USA). All measured leaves were collected, oven-dried at 70 °C for at least 72 h and weighed (AE-260, Mettler Instrumente AG, Greifensee-Zürich, Switzerland). Total leaf nitrogen was measured using an elemental analyser (CHNS-932, LECO Instruments, St Joseph, Michigan, USA).

Biochemical model of CO_2 assimilation

Following the theory developed by Farquhar and co-workers (Farquhar 1979; Farquhar *et al.* 1980; Farquhar & Von Caemmerer 1982), later modified by Harley & Tenhunen (1991), CO_2 assimilation is either entirely limited by the kinetic properties of Rubisco and the respective partial pressures of the competing gases CO_2 and O_2 at the sites of carboxylation (W_C) or by electron transport (W_J), which limits the rate at which RuBP is regenerated. Limitations of RuBP regeneration arising from the availability of inorganic phosphate (P_i) for photophosphorylation (W_P; Sharkey 1985) are not considered in the present approach. Net photosynthesis A may then be expressed as

$$A = \left(1 - \frac{0 \cdot 5 O}{\tau Ci}\right) \cdot \min\{W_c, \ W_J\} - R_{day} \quad (1)$$

where O and Ci are the partial pressures of O_2 and CO_2 in the intercellular space, respectively. τ is the specificity factor for Rubisco (Jordan & Ogren 1984), R_{day} is the rate of CO_2 evolution from processes other than photo-respiration and min{} denotes 'the minimum of'.

The carboxylation rate limited solely by the amount, activation state and kinetic properties of Rubisco and the respective partial pressures of the competing gases CO_2 and O_2 at the sites of carboxylation is assumed to obey competitive Michaelis–Menten kinetics and is given by

$$W_c = \frac{V_{cmax}Ci}{Ci + K_c\left(1 + \dfrac{O}{K_o}\right)} \quad (2)$$

where V_{cmax} is the maximum rate of carboxylation and K_C and K_O are the Michaelis–Menten constants for carboxylation and oxygenation, respectively.

The rate of carboxylation limited solely by the rate of RuBP regeneration due to electron transport, W_J, is given by

$$W_J = \frac{P_m}{1 + \dfrac{O}{\tau Ci}} \quad (3)$$

where P_m is the CO_2-saturated rate of photosynthesis at any given irradiance and temperature. This expression of W_J is equivalent to that used by Farquhar & Von Caemmerer (1982), if their parameter J is equal to $4 P_m$ (for a detailed discussion of P_m see Harley & Tenhunen 1991).

P_m is expressed as a light dependency using the equation by Tenhunen *et al.* (1976), which was derived from Smith (1937),

$$P_m = \frac{\alpha \text{PPFD}}{\left(1 + \dfrac{\alpha^2 \text{PPFD}^2}{P_{ml}^2}\right)^{0 \cdot 5}} \quad (4)$$

where α is the initial slope of the curve relating CO_2-saturated net photosynthesis to irradiance (on an incident light basis) and P_{ml} is the potential rate of RuBP regeneration, which is related to J_{max} as used by Farquhar *et al.* (1980) by $J_{max}/4$.

V_{cmax} and P_{ml} depend upon temperature and, given their optimum response to temperature (Harley & Tenhunen 1991; Leuning 1997), each is described using an equation based on absolute reaction theory by Johnson, Eyring & Williams (1942) and Sharpe & DeMichele (1977), normalized to a reference temperature (293·16 K) as in Leuning (1997)

$$\text{parameter} = \frac{\text{parameter}(T_{ref}) \exp\left[\dfrac{\Delta H_a}{R T_{ref}}\left(1 - \dfrac{T_{ref}}{T_K}\right)\right]}{1 + \exp\left[\dfrac{\Delta S T_K - \Delta H_d}{R T_K}\right]} \quad (5)$$

where 'parameter' is either V_{cmax} or P_{ml}, and 'parameter(T_{ref})' is the potential value that this parameter would have at the reference temperature of 293·16 K, in the absence of any deactivation due to high temperature (Schoolfield, Sharpe & Magnuson 1981). ΔH_a is the energy of activation, ΔH_d is the energy of deactivation, ΔS is an entropy term, T_K is the absolute leaf temperature and R is the gas constant.

The temperature optimum (T_{opt}) of V_{cmax} and P_{ml} is described by the following expression, which was derived by differentiation of eqn 5 with respect to T_K.

$$T_{opt} = \frac{-\Delta H_d}{R \ln\left(\dfrac{-\Delta H_a}{\Delta H_a - \Delta H_d}\right) - \Delta S} \quad (6)$$

Model parameterization

Temperature-dependent parameters for τ were taken from Jordan & Ogren (1984), those for K_C and K_O from Badger & Collatz (1977). Model parameters, describing the temperature dependencies of V_{cmax} and P_{ml}, are shown in Table 3 and were estimated from measured A/C_i and/or light response curves using non-linear regression techniques as described by Wohlfahrt *et al.* (1998). We thereby assumed an infinite CO_2 transfer conductance from the intercellular air spaces to the chloroplasts (g_{ic}), i.e. the CO_2 partial pressure in the chloroplasts (C_c) to be equal to C_i, as have numerous other researchers (Farquhar *et al.* 1980; Harley & Tenhunen 1991; Harley & Baldocchi 1995; Niinemets & Tenhunen 1997). However, recent evidence suggests that g_{ic} may represent an appreciable limitation to net photosynthesis (Harley *et al.* 1992a; Evans *et al.* 1994; Epron *et al.* 1995; Evans & Von Caemmerer 1996). Estimation of g_{ic} requires a considerable experimental effort using a combination of gas exchange measurements together with either carbon isotope fractionation or fluorescence techniques (Von Caemmerer & Evans 1991; Loreto *et al.* 1992), which were not available in the present study. Therefore, we have assessed the error introduced in the estimation of V_{cmax} by re-calculating several of our V_{cmax} values using parameters for K_C and K_O derived under the assumption of an infinite g_{ic} (Von Caemmerer *et al.* 1994). It showed that using the parameters from Badger & Collatz (1977) over-estimated V_{cmax} by less than 5% as compared to the values obtained using the parameters by Von Caemmerer *et al.* (1994). The parameter estimation of P_{ml} is relatively insensitive to the CO_2 partial pressure, leading likewise to an over-estimation of not more than 5%, which implies that the ratio between P_{ml} and V_{cmax} is little affected by the assumption of an infinite g_{ic}.

For five species from Passeier Valley (*A. tenuis*, *A. flexuosa*, *C. scheuchzeri*, *P. viviparum* and *P. sulphurea*), response curves were available only at a leaf temperature of 20 °C.

Table 3. Parameters describing the temperature dependencies of the maximum rate of carboxylation (V_{cmax}) and the potential rate of RuBP regeneration (P_{ml})

	$V_{cmax}(T_{ref})$ ($\mu mol\ m^{-2}\ s^{-1}$)	$\Delta H_a(V_{cmax})$ ($J\ mol^{-1}$)	$\Delta H_d(V_{cmax})$ ($J\ mol^{-1}$)	$P_{ml}(T_{ref})$ ($\mu mol\ m^{-2}\ s^{-1}$)	$\Delta H_a(P_{ml})$ ($J\ mol^{-1}$)	$\Delta H_d(P_{ml})$ ($J\ mol^{-1}$)
Monte Bondone						
Dagl	45·58	88 434	199 390	28·57	65 649	195 860
Kopy	28·88	149 061	198 000	17·51	78 754	200 000
Nast	37·93	61 304	202 583	25·29	44 386	196 168
Plat	52·88	64 490	200 000	31·18	51 014	197 551
Plme	47·05	79 294	200 415	25·61	56 292	198 050
Povi	37·16	60 940	199 571	27·85	61 521	192 521
Poau	30·03	57 098	204 000	17·48	57 101	199 247
Rhal	53·24	60 600	202 000	26·71	37 407	201 000
Trmo	56·67	118 599	197 500	35·38	115 191	191 300
Trpr	48·79	53 017	202 000	27·03	68 707	199 000
Trfl	24·85	54 051	201 186	15·36	67 161	194 000
Treu	35·07	68 000	201 000	22·93	55 465	199 521
Vamy	13·30	102 568	201 194	5·57	57 329	198 922
Passeier Valley						
Acmi	63·67	109 740	199 500	29·93	41 052	199 400
Alvu	64·17	105 945	197 250	28·50	56 324	198 582
Armo	28·96	54 726	201 500	18·62	55 973	197 000
Cavu	16·39	102 570	200 000	10·67	57 330	197 100
Feru	65·50	130 500	194 800	27·05	112 049	190 676
Nast	12·25	61 304	202 583	5·93	44 386	196 168
Raac	80·79	98 400	196 900	49·81	66 000	194 000
Rual	47·32	83 300	200 000	26·12	89 742	196 268
Tral	26·56	103 100	198 800	14·13	54 452	195 872
Trre	71·25	56 796	202 000	43·10	44 281	196 000
Stubai Valley						
Aluv	47·08	59 316	202 000	23·56	55 034	197 263
Brme	61·91	56 700	199 500	39·77	47 790	195 900
Gesy	55·10	56 935	199 500	29·90	49 995	195 337
Plme	57·53	51 300	200 000	35·71	43 594	196 200
Seva	32·58	106 500	199 666	20·12	52 739	195 575
Vaul	40·02	57 154	200 645	21·51	52 576	196 000

The first two letters of the generic and species name are used as abbreviations, for full names refer to Table 2, for symbols and other abbreviations to Appendix A. $\Delta S(V_{cmax})$ and $\Delta S(P_{ml})$ were fixed for all species at 656 and 643 $J\ K^{-1}\ mol^{-1}$, respectively (cf. Wohlfahrt *et al.* 1998).

V_{cmax} and P_{ml} of these species were therefore calculated solely for this temperature. This implies that the parameters describing the temperature dependencies of these five species and the respective temperature optima are missing (Tables 3 and 4).

RESULTS

V_{cmax} and P_{ml}: the potentially rate-limiting processes of carboxylation

V_{cmax} and P_{ml} (at 20 °C) of the investigated species (Table 4) ranged from 12·1 (*N. stricta*/Passeier Valley) and 5·5 μmol m^{-2} s^{-1} (*V. myrtillus*) to 90·1 and 50·5 μmol m^{-2} s^{-1} (*A. tenuis*), on a leaf area basis (V_{cmax}^{a}, P_{ml}^{a}), and from 10·0 and 4·2 mg kg^{-1} s^{-1} (*V. myrtillus*) to 79·5 and 46·8 mg kg^{-1} s^{-1} (*T. repens*) on a leaf mass basis (V_{cmax}^{m},

P_{ml}^{m}). V_{cmax}^{a} and P_{ml}^{a} of the dwarf shrubs were about 50% smaller than those of graminoids and forbs ($P < 0.05$ for forbs), which were not significantly different from each other (Table 5). Differences in V_{cmax} and P_{ml} between dwarf shrubs and both graminoids and forbs were more pronounced on a mass basis ($P < 0.05$), due to the fact that the SLA of the dwarf shrubs was somewhat lower than that of graminoids and forbs ($P < 0.05$ for forbs). Again, graminoids and forbs did not differ significantly from each other with respect to V_{cmax}^{m} and P_{ml}^{m} (Table 5). The species from the meadows were characterized by a higher V_{cmax}^{a} and P_{ml}^{a} than the species from pastures and abandoned areas ($P < 0.01$ for meadows versus abandoned areas; Table 5). On a mass basis, differences between the three land-use types were even more pronounced (Table 5), since the species from the meadows also exhibited the highest SLA ($P < 0.01$, as compared to species from the

Table 4. Species-specific values of the investigated parameters

| Abbreviation | Area basis | | | Dry weight basis | | | | | T_{opt} | |
	V_{cmax}^{a}	P_{ml}^{a}	N_L^{a}	V_{cmax}^{m}	P_{ml}^{m}	N_L^{m}	P_{ml}/V_{cmax}	SLA	V_{cmax}	P_{ml}
Acmi	60·50	29·59	136·03	43·62	21·34	31·14	0·489	16·37	31·7	31·6
Agte	90·07	50·53	172·13	68·07	38·19	41·30	0·561	17·16	–	–
Alvu-PV	56·69	28·06	115·51	50·81	25·14	32·87	0·495	20·34	28·1	32·0
Alvu-SV	46·21	22·93	109·51	37·90	18·80	28·31	0·496	18·62	31·4	29·9
Armo	28·31	18·07	91·31	17·23	10·99	17·64	0·638	13·82	30·2	29·6
Avfl	47·31	25·53	165·81	48·61	26·23	54·09	0·540	23·32	–	–
Brme	58·83	37·95	107·89	40·79	26·31	23·19	0·645	15·74	27·4	27·1
Casc	81·68	46·82	196·70	48·78	27·96	37·29	0·573	13·56	–	–
Cavu	15·72	10·36	75·63	10·67	7·03	16·29	0·659	15·40	31·9	29·9
Dagl	43·21	27·24	85·80	44·39	27·99	27·99	0·630	23·32	29·9	28·8
Feru	48·15	21·37	–	29·01	12·87	–	0·444	13·67	26·5	26·2
Gesy	52·36	28·20	99·20	45·18	24·33	26·63	0·539	19·59	27·5	26·5
Kopy	26·33	17·36	119·00	16·82	11·09	24·13	0·659	14·50	33·0	36·2
Nast-MB	37·38	24·25	124·30	19·34	12·54	20·41	0·649	11·74	32·4	27·2
Nast-PV	12·08	5·69	63·08	10·24	4·82	16·98	0·471	19·25	32·4	27·2
Plat	50·72	30·43	103·32	32·20	19·32	20·82	0·600	14·41	28·9	29·9
Plme-MB	45·42	25·12	91·39	32·36	17·90	20·67	0·553	16·18	30·7	31·2
Plme-SV	55·18	34·26	110·79	39·26	24·37	24·69	0·621	16·15	27·7	27·1
Poau	29·79	17·27	80·27	33·22	19·26	28·42	0·580	25·32	34·1	33·1
Povi-MB	35·36	23·36	138·08	28·28	18·68	35·06	0·661	18·15	27·9	23·4
Povi-PV	50·86	24·46	164·34	29·40	14·14	30·16	0·481	13·12	–	–
Pusu	24·20	9·91	146·75	12·32	5·05	23·72	0·410	11·56	–	–
Raac	78·80	45·09	145·92	55·50	31·76	32·63	0·572	15·99	27·0	26·0
Rhal	52·26	26·55	109·78	44·16	22·43	29·45	0·508	19·18	31·5	33·6
Rual	45·38	25·08	116·15	54·45	30·09	44·24	0·553	27·23	30·4	31·4
Seva	31·06	19·07	99·23	21·60	13·26	21·23	0·614	15·78	31·7	27·1
Tral	24·83	13·48	124·00	19·23	10·44	30·49	0·543	17·58	30·2	27·8
Treu	34·10	22·69	110·84	22·84	15·20	23·57	0·665	15·20	30·7	33·4
Trfl	24·22	13·90	79·62	28·82	16·54	30·08	0·574	27·01	29·7	26·1
Trmo	50·65	26·86	149·75	38·05	20·18	35·72	0·530	17·05	29·5	26·0
Trpr	47·89	26·67	123·49	47·26	26·32	38·69	0·557	22·40	30·8	33·8
Trre	69·94	41·20	151·59	79·50	46·83	54·70	0·589	25·80	31·2	26·9
Vamy	12·96	5·49	92·01	9·99	4·23	22·52	0·424	17·50	33·7	32·6
Vaul	38·75	20·56	125·53	22·84	12·12	23·25	0·531	13·38	29·2	27·8

MB, Monte Bondone; PV, Passeier Valley; SV, Stubai Valley. For species abbreviations, see Table 2. For abbreviations of parameters and their units refer to Appendix A.

Table 5. Mean values (± standard error) of the maximum rate of carboxylation (V_{cmax}^a (μmol m^{-2} s^{-1}) and V_{cmax}^m (mg kg^{-1} s^{-1})), the potential rate of RuBP regeneration (P_{ml}^a (μmol m^{-2} s^{-1}) and P_{ml}^m (mg kg^{-1} s^{-1})), both at 20 °C, leaf nitrogen content (N_L^a (mmol m^{-2}) and N_L^m (mg g^{-1})), the ratio between P_{ml} and V_{cmax}, specific leaf area (SLA (m^2 kg^{-1})) and the temperature optima of V_{cmax} and P_{ml} (T_{opt} (°C))

	n	Area basis			Dry weight basis			P_{ml}/V_{cmax}	SLA	T_{opt}	
		V_{cmax}^a	P_{ml}^a	N_L^a	V_{cmax}^m	P_{ml}^m	N_L^m			V_{cmax}	P_{ml}
(a) Land use											
Abandoned areas	11	32·2 ± 4·9	18·2 ± 3·2	110·7 ± 9·1	20·4 ± 3·1	11·5 ± 2·0	22·3 ± 1·4	0·550 ± 0·028	14·9 ± 0·8	30·7 ± 0·7 (9)	28·8 ± 0·6 (9)
Meadows	17	53·8 ± 4·3	29·7 ± 2·4	128·5 ± 8·0 (16)	45·7 ± 3·5	25·3 ± 2·1	35·5 ± 2·3 (16)	0·556 ± 0·015	19·8 ± 1·1	30·1 ± 0·6 (14)	29·4 ± 0·8 (14)
Pastures	6	39·7 ± 5·0	23·3 ± 2·7	108·4 ± 10·0	30·2 ± 3·7	17·7 ± 2·0	25·8 ± 2·3	0·593 ± 0·019	17·5 ± 1·6	30·3 ± 0·9	29·7 ± 1·9
		A**	A**	n.s.	A***, C*	a***, C*	A***, C*	n.s.	A**	n.s.	n.s.
(b) Life form											
Graminoids	10	41·9 ± 6·9	24·3 ± 4·0	113·0 ± 12·4 (9)	32·8 ± 5·6	19·0 ± 3·2	28·8 ± 3·9 (9)	0·579 ± 0·024	18·2 ± 1·6	30·4 ± 0·9 (8)	28·2 ± 1·2 (8)
Forbs	21	48·6 ± 3·5	27·0 ± 2·0	124·5 ± 6·1	38·7 ± 3·4	21·5 ± 1·9	30·8 ± 1·9	0·555 ± 0·014	18·0 ± 0·9	30·1 ± 0·5 (18)	29·6 ± 0·7 (18)
Dwarf shrubs	3	22·5 ± 8·2	12·1 ± 4·4	97·7 ± 14·7	14·5 ± 4·2	7·8 ± 2·3	20·7 ± 2·2	0·538 ± 0·068	15·4 ± 1·2	31·6 ± 1·3	30·1 ± 1·4
		C*	C*	n.s.	C*	B*, C*	C*	n.s.	n.s.	n.s.	n.s.
(c) Graminoids											
Abandoned areas	3	36·1 ± 13·5	22·6 ± 9·4	98·4 ± 18·3	23·5 ± 9·1	14·6 ± 6·3	20·2 ± 1·8	0·588 ± 0·059	15·6 ± 2·2	30·8 ± 1·7	27·1 ± 0·0
Meadows	5	50·6 ± 10·8	27·7 ± 6·2	125·8 ± 25·0 (4)	43·8 ± 7·3	24·4 ± 4·5	38·4 ± 6·0 (4)	0·550 ± 0·030	20·9 ± 2·4	28·7 ± 1·1 (3)	27·0 ± 0·9 (3)
Pastures	2	28·7 ± 2·4	18·2 ± 0·9	109·1 ± 9·9	19·2 ± 2·4	12·2 ± 1·1	22·7 ± 1·5	0·637 ± 0·023	15·1 ± 0·6	32·4 ± 0·6	31·7 ± 4·5
		n.s.	n.s.	n.s.	n.s.	n.s.	A*	n.s.	n.s.	n.s.	n.s.
(d) Forbs											
Abandoned areas	5	35·8 ± 6·2	19·3 ± 3·7	125·9 ± 13·5	22·1 ± 3·8	12·0 ± 2·3	24·6 ± 2·5	0·534 ± 0·041	14·1 ± 1·0	29·8 ± 0·4 (3)	29·1 ± 0·7(3)
Meadows	12	55·1 ± 4·4	30·5 ± 2·5	129·4 ± 7·7	46·5 ± 4·1	25·7 ± 2·4	34·6 ± 2·5	0·558 ± 0·017	19·4 ± 1·2	30·4 ± 0·7 (11)	30·0 ± 0·9 (11)
Pastures	4	45·3 ± 5·5	25·9 ± 3·5	108·1 ± 15·3	35·7 ± 1·7	20·4 ± 1·4	27·4 ± 3·2	0·571 ± 0·019	18·7 ± 2·2	29·2 ± 0·8	28·8 ± 2·2
		A*	n.s.	n.s.	A**, B*	A**, B*	A*	n.s.	A*	n.s.	n.s.

V_{cmax}, P_{ml} and their respective temperature optima were calculated with the corresponding leaf model parameters (Table 3) of each species using eqns 5 and 6. The investigated species (n = 34) are grouped according to land use (a) and life form (b). Additionally, graminoids and forbs are grouped according to land use in (c) and (d), respectively. Numbers in parentheses indicate a number of species (n) different from the one given in the second column of the table. Mean values are compared using a Student's t test (n.s., not significant at $P < 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; A, differences between the lst and 2nd group, B, differences between the 1st and 3rd group, C, differences between the 2nd and 3rd group)

abandoned areas). Differences in V_{cmax} and P_{ml} between species from meadows and pastures occurred mostly in the graminoids, which on pastures reached only 65% of the values observed for graminoids on meadows (Table 5). The low V_{cmax} and P_{ml} values of the species from abandoned areas (Table 5) were not only caused by the dwarf shrubs (Table 5), but also resulted from the comparatively lower V_{cmax} and P_{ml} values of the forbs occurring on these sites (on a mass basis $P < 0.01$ and $P < 0.05$, respectively; Table 5).

The ratio between P_{ml} and V_{cmax}

The ratio between P_{ml} and V_{cmax} at 20 °C ranged from 0·410 (*P. sulphurea*) to 0·665 (*T. europaeus*) as shown in Table 4. Linear regressions, forced through the origin, relating P_{ml} to V_{cmax} for all species pooled, resulted in no differences between area- (Fig. 1a) and mass-based (Fig. 1b) estimates. No significant differences with respect to the ratio between P_{ml} and V_{cmax} were found when pooling the investigated species according to land use and life form (Table 5). The ratio between P_{ml} and V_{cmax} varied with temperature, decreasing with increasing temperature until the temperature optimum is reached, followed by a subsequent increase (Fig. 2).

The temperature response of V_{cmax} and P_{ml}

The temperature optima of V_{cmax} and P_{ml} covered a range from 26·5 °C (*F. rubra*) and 23·4 °C (*P. viviparum*/Monte Bondone) to 34·1 °C (*P. aurea*) and 36·2 °C (*K. pyramidata*), respectively, as shown in Table 4. Grouping species according to land use and life form did not yield significant results for any of these combinations (Table 5). With respect to the shape of the temperature response of V_{cmax} and P_{ml}, slight differences were found between the three life form groups separated according to land use (Fig. 2). The difference in

V_{cmax} and P_{ml} at 20 °C between forbs and graminoids on the meadows, with forbs attaining higher rates of V_{cmax} and P_{ml} than graminoids (Table 5), increased at higher temperatures, since on meadows the temperature optimum of both V_{cmax} and P_{ml} for forbs was higher than for graminoids (Table 5, Fig. 2). The contrary could be observed on the pastures, where at higher temperatures the rates for graminoids exceeded those of forbs, due to the fact that on pastures the temperature optima for graminoids was higher than for forbs (Table 5, Fig. 2).

Leaf nitrogen content and its correlation with V_{cmax} and P_{ml}

Area-based estimates of leaf nitrogen content ($N_L{}^a$) covered a range from 63·1 mmol m^{-2} (*N. stricta*/Passeier Valley) to 196·7 mmol m^{-2} (*C. scheuchzeri*). Mass-based estimates of leaf nitrogen content ($N_L{}^m$) ranged from 16·3 mg g^{-1} (*C. vulgaris*) to 54·7 mg g^{-1} (*T. repens*). Dwarf shrubs were characterized by a lower $N_L{}^m$ than graminoids and forbs ($P < 0.05$ for forbs). Due to a lower SLA of the dwarf shrubs, these differences became less evident, when N_L was based on leaf area (Table 5). $N_L{}^m$ of the species from the meadows was significantly higher compared to the species from the pastures ($P < 0.05$) and abandoned areas ($P < 0.001$) (Table 5). These differences were largely the result of the graminoids occurring on the meadows (Table 5), since they reached considerably higher values of $N_L{}^m$ than graminoids from both abandoned areas ($P < 0.05$) and pastures ($P < 0.1$), but differences in $N_L{}^m$ were also significant for forbs between meadows and abandoned areas (Table 5). Differences in $N_L{}^a$ were not as pronounced as in $N_L{}^m$, due to the fact that species from the meadows also had the highest SLA (Table 5).

V_{cmax} and P_{ml} were positively correlated with N_L when all investigated species were pooled (Fig. 3), coefficients of
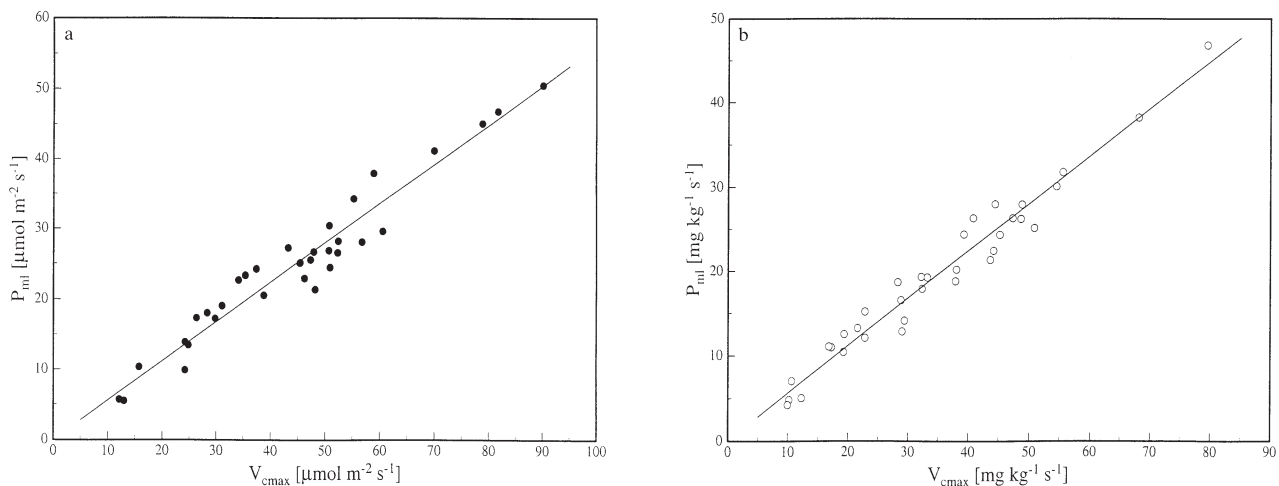
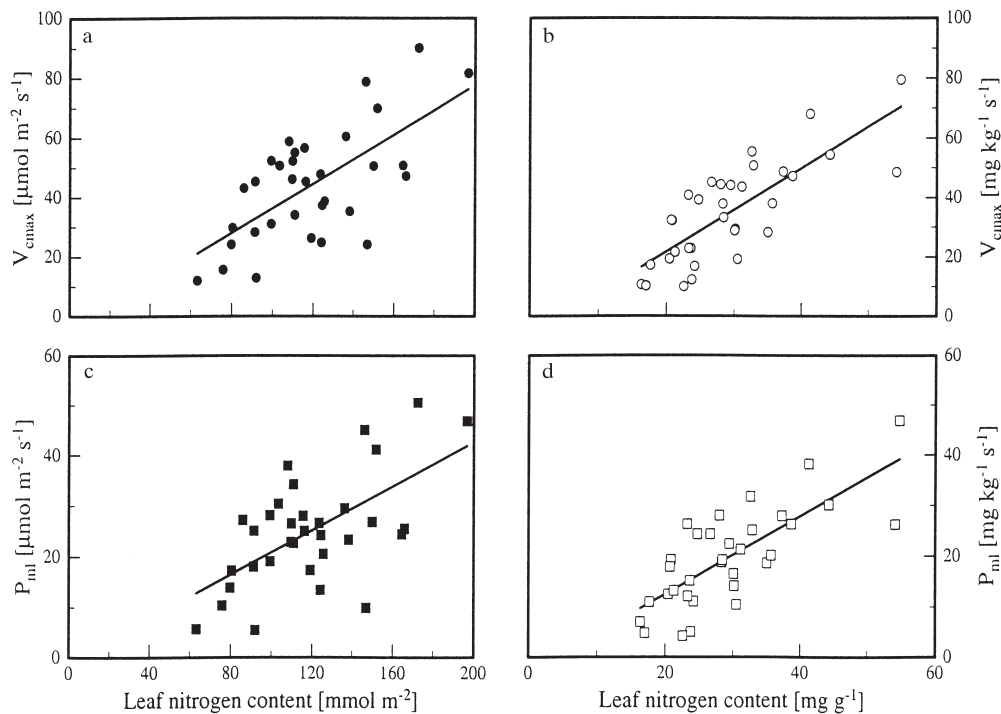
Figure 1. Relationship between the maximum rate of carboxylation, V_{cmax}, and the potential rate of RuBP regeneration, P_{ml}, on a leaf area (a) and leaf mass (b) basis. Solid lines represent linear regressions forced through the origin ($P_{ml} = 0.560 \cdot V_{cmax}$, $R^2 = 0.94$, $P < 0.000$; $P_{ml} = 0.561 \cdot V_{cmax}$, $R^2 = 0.96$, $P < 0.000$, respectively). All data refer to a reference temperature of 20 °C.
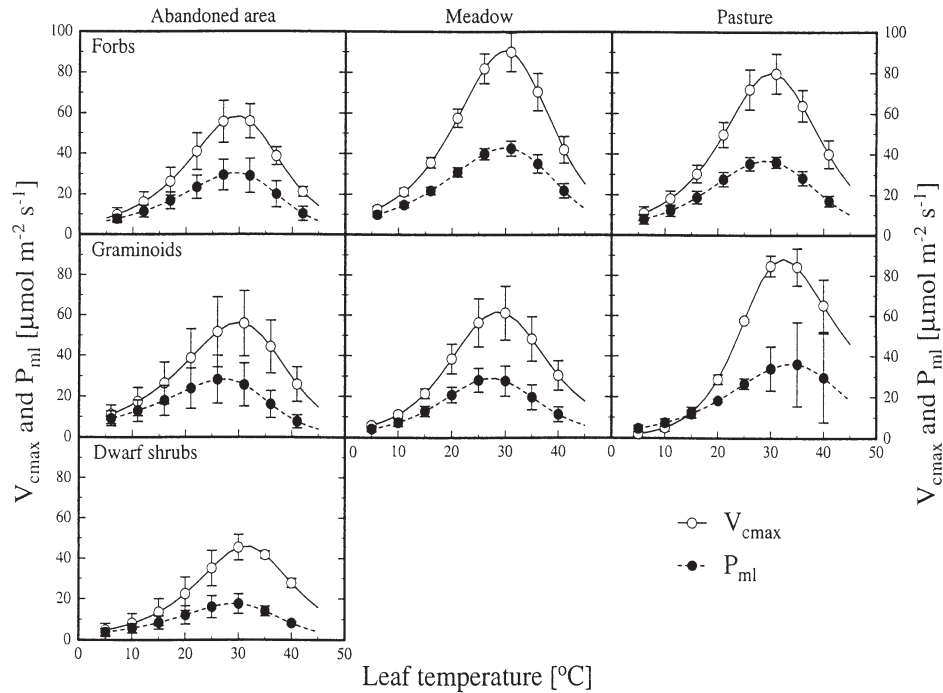
Figure 2. Temperature response of the maximum rate of carboxylation (V_{cmax}, open symbols and solid lines), and the potential rate of RuBP regeneration (P_{ml}, closed symbols and dashed lines) separated according to land use and life form (error bars represent 1 standard error).

Figure 3. Relationship between the maximum rate of carboxylation (V_{cmax}) and the potential rate of RuBP regeneration (P_{ml}) versus leaf nitrogen content on a leaf area (a,c, respectively) and a leaf mass (b,d, respectively) basis. V_{cmax} and P_{ml} refer to a reference temperature of 20 °C ($V_{cmax}^a = -4·93 + 0·41·N_a$, $R^2 = 0·45$, $P < 1·0$; $V_{cmax}^m = -6·25 + 1·41·N_m$, $R^2 = 0·62$, $P < 1·0$; $P_{ml}^a = -0·87 + 0·22·N_a$, $R^2 = 0·37$, $P < 1·0$; $P_{ml}^m = -2·76 + 0·77·N_m$, $R^2 = 0·57$, $P < 1·0$).

determination being higher when values were expressed on a mass basis (Fig. 3b,d).

DISCUSSION

Carbon assimilation is potentially limited by two processes, the maximum rate of carboxylation (V_{cmax}) and the potential rate of RuBP regeneration (P_{ml}), with the penalty of excess investment of expensive resources (e.g. nitrogen) in the non-limiting process, which has led Farquhar *et al.* (1980) to suggest that plants should allocate their resources in a manner to achieve co-limitation between the two processes. Clearly, environmental conditions vary at time scales much smaller than adaptation among the components of the photosynthetic apparatus may occur; the ratio between V_{cmax} and P_{ml} thus represents a medium to long-term measure for adaptive trade-offs among the main photosynthetic components, governed by the environmental conditions during leaf development (Wullschleger 1993; Hikosaka 1997). The present study attempts to explore

whether the relationship between V_{cmax} and P_{ml} as set up by Wullschleger (1993) and Leuning (1997) for species grown mainly under controlled conditions, half of them being either agricultural or horticultural crops, also holds for 30 wild species from semi-natural mountain grasslands.

The ratio between P_{ml} and V_{cmax}: a measure for resource allocation

The slope of the relationship between P_{ml} and V_{cmax} of the investigated species is significantly less steep ($P < 0.001$) than the one reported by Wullschleger (1993) if only the data points measured at 20 °C are used (cf. Wohlfahrt, Bahn & Cernusca 1999), as shown in Fig. 4. This means that the species investigated in this study reach comparably lower values of P_{ml} for any given value of V_{cmax}, or, in other words, invest a smaller proportion of available resources into electron transport. The discrepancy between the two datasets may be attributed to differences in species composition, species from semi-natural mountain grassland typ-
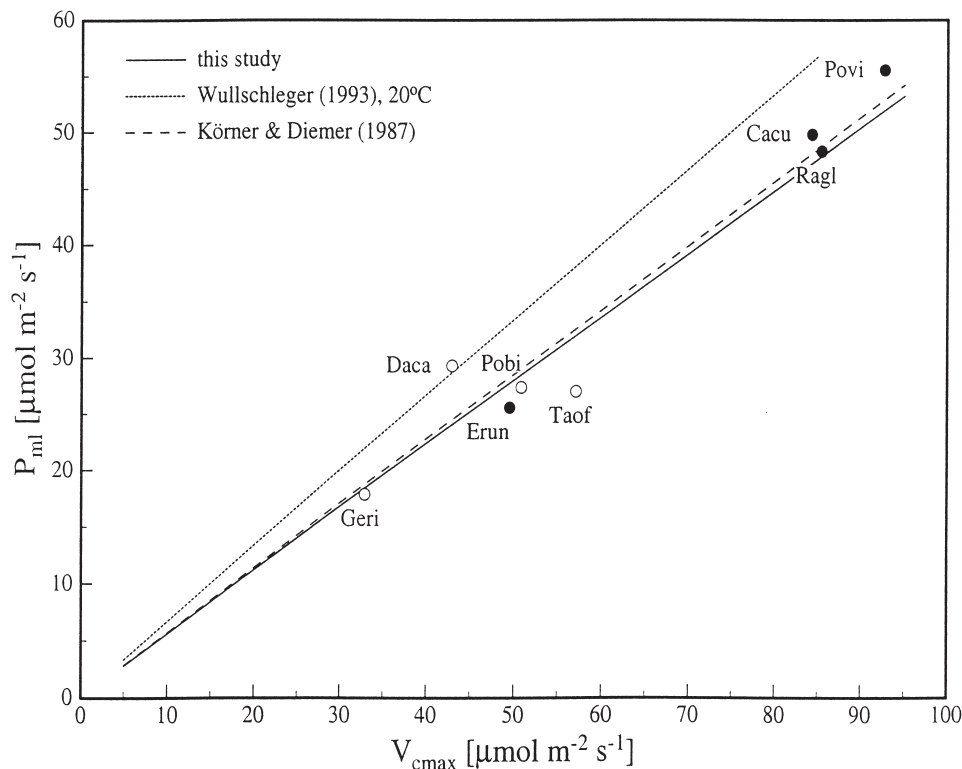
Figure 4. Relationship between the maximum rate of carboxylation (V_{cmax}) and the potential rate of RuBP regeneration (P_{ml}) at a reference temperature of 20 °C. Lines represent linear regressions forced through the origin. The solid line ($P_{ml} = 0.560 \cdot V_{cmax}$, $R^2 = 0.94$, $P < 0.000$) refers to this study (see also Figure 1a), the dashed line ($P_{ml} = 0.578 \cdot V_{cmax}$, $R^2 = 0.95$, $P < 0.068$) refers to data from four low- and high-elevation species re-calculated from Körner & Diemer (1987) as described in the text, using the parameters given in Table 6 for forbs and graminoids from meadows. For the high-altitude species, the slope of the relationship between P_{ml} and V_{cmax} ranges from 0.582 to 0.587, depending on whether the parameters for meadows, pastures or abandoned areas are used, and from 0.572 to 0.578 when the low-elevation species are included. The dotted line ($P_{ml} = 0.668 \cdot V_{cmax}$, $R^2 = 0.92$, $P < 0.151$) represents results re-calculated from Wullschleger (1993; restricted to those measured at 20 °C; cf. Wohlfahrt *et al.* 1999), assuming that four electrons are sufficient to regenerate one molecule of RuBP (Farquhar & Von Caemmerer 1982). Filled symbols represent high-elevation species (Povi, *Polygonum viviparum*, Cacu, *Carex curvula*, Ragl, *Ranunculus glacialis*, Erun, *Erigeron uniflorum*), open symbols low-elevation species (Daca, *Daucus carota*, Pobi, *Polygonum bistorta*, Taof, *Taraxacum officinalis*, Geri, *Geum rivale*) from Körner & Diemer (1987).

ically investing a smaller proportion of available resources into electron transport than the species examined by Wullschleger (1993), of which more than 90% were either agricultural/horticultural crops or woody species. Additionally, besides species composition, the observed differences could also result from the growth conditions (day length, length of the growing season, light and nutrient availability, temperature and other micro-climatic factors) experienced by the plants, or from a combination of both. Most of the species investigated by Wullschleger (1993) were grown in controlled environments and none may be considered typical for the investigated mountain grasslands or similar ecosystems (e.g. arctic tundra), which are characterized by a short growing season, comparably low air temperatures and abundant precipitation. Another explanation for the proportionally smaller investment of available resources into electron transport in the present study could be that our investigations were restricted to sun leaves, which typically invest proportionally less resources into electron transport (Evans 1989; Evans & Seemann 1989; Pons & Pearcy 1994; Hikosaka & Terashima 1995, 1996).

Testing for these hypotheses proves difficult, since neither species nor growth conditions overlap between the two datasets. However, further evidence confirming the validity of our relationship for mountain grassland species may be derived from Körner & Diemer (1987), who compared several herbaceous species from low- (600 m above sea level) and high-altitude (2600 m above sea level) sites in the Eastern Alps with respect to a number of gas exchange parameters and related leaf traits. The species investigated by Körner & Diemer (1987) are typical for grassland ecosystems, although only one species, *P. viviparum*, is covered by both surveys. Parameterizing the *A*/*Ci* curves of all species from Körner & Diemer (1987) for which sufficient data were available (as described by Wohlfahrt *et al.* 1998), and scaling them to a reference temperature of 20 °C using the parameters for forbs and graminoids from Table 6, shows that the slope of the relationship between P_{ml} and V_{cmax} of the high- and low-altitude species matches our data very closely (Fig. 4).

Clearly there is a a need for further investigations on a larger variety of species from natural environments to elucidate the underlying mechanisms which cause the observed differences between our data and the dataset as presented by Wullschleger (1993). Promising approaches for this purpose include investigating the biochemical limitations to photosynthesis together with related leaf traits across a number of different biomes and functional groups, as presented recently by Reich *et al.* (1998a,b).

The temperature response of V_{cmax} and P_{ml}

The ratio between P_{ml} and V_{cmax} is not constant with temperature (Fig. 2), as noted already by Von Caemmerer & Farquhar (1981), in Leuning's (1997) re-analysis of the data compiled by Wullschleger (1993), and for *Pinus radiata* by Walcroft *et al.* (1997). The reason for this is that P_{ml} increases less with temperature and reaches the optimum at lower temperatures compared to V_{cmax} (Fig. 2, Table 5), resulting in a decrease of the ratio between P_{ml} and V_{cmax} with temperature. Contrary to the reports by Leuning (1997) and Walcroft *et al.* (1997), our study suggests that the ratio between P_{ml} and V_{cmax} increases again at high temperatures due to V_{cmax} exhibiting a pronounced temperature optimum, which is not observed within the temperature range reported by the papers cited above. This clearly indicates the necessity to derive the temperature dependency of P_{ml} and V_{cmax} for species in different environments. On the canopy level, however, neglecting the temperature dependency of the ratio between P_{ml} and V_{cmax} has minor implications for model predictions of canopy carbon gain (Wohlfahrt *et al.* 1999).

V_{cmax}–N_L and P_{ml}–N_L relationships

Several studies have dealt with the intra-specific correlation between V_{cmax}, P_{ml}, and N_L (Field 1983; Harley *et al.* 1992b; Anten *et al.* 1996; Walcroft *et al.* 1997; Wohlfahrt *et al.* 1998), reporting a positive relationship, but we do not know of any other study which established an inter-specific relationship between N_L and V_{cmax}, respectively, P_{ml}. However, a large number of studies exist on the inter-specific correlation between photosynthetic capacity (A_{max}) and N_L (Evans 1989; Mooney *et al.* 1981; Field & Mooney 1986; Körner

Table 6. Model parameters describing the temperature dependencies of the maximum rate of carboxylation (V_{cmax}) and the potential rate of RuBP regeneration (P_{ml}) of dwarf shrubs, graminoids and forbs, separated according to land use. $\Delta S(V_{cmax})$ and $\Delta S(P_{ml})$ were fixed at 656 and 643 J K^{-1} mol^{-1}, respectively (cf. Wohlfahrt *et al.* 1998)

Parameter	Units	Abandoned area			Meadow		Pasture	
		Dwarf shrubs	Graminoids	Forbs	Graminoids	Forbs	Graminoids	Forbs
$V_{cmax}(T_{ref})$	µmol m^{-2} s^{-1}	23·02	36·24	35·86	39·41	53·52	30·21	45·78
$\Delta H_a(V_{cmax})$	J mol^{-1}	73 366	55 125	69 022	87 624	69 752	131 966	70 296
$\Delta H_d(V_{cmax})$	J mol^{-1}	201 388	201 578	200 336	198 801	200 652	198 603	200 870
$P_{ml}(T_{ref})$	µmol m^{-2} s^{-1}	12·39	23·66	21·21	22·21	28·73	17·98	25·52
$\Delta H_a(P_{ml})$	J mol^{-1}	53 016	46 270	52 710	75 926	48 840	55 488	54 135
$\Delta H_d(P_{ml})$	J mol^{-1}	197 057	196 019	197 095	194 482	198 190	200 141	197 265

1989; Reich & Walters 1994; Reich *et al*. 1994, 1995; Bahn *et al*. 1999), also reporting a positive relationship between the two parameters. Since A_{max} is determined at saturating light intensity, it may be assumed to be limited mainly by Rubisco activity and thus by V_{cmax} (Woodrow & Berry 1988), which allows us to place trends, observed in the present study in terms of V_{cmax}, in context with regard to studies on A_{max}. The V_{cmax}–N_L and P_{ml}–N_L relationships in the present study are positive, but characterized by a considerably large scatter (Fig. 3). Some of this scatter is removed when expressing V_{cmax}, P_{ml} and N_L on a mass basis (Fig. 3b,d), thereby eliminating variation caused by differences in leaf morphology (SLA), an observation shared by a number of other studies in terms of A_{max} (Field & Mooney 1986; Reich *et al*. 1994, 1995; Bahn *et al*. 1999). From the variation in the V_{cmax}–N_L and P_{ml}–N_L relationships, it is inferred that the investigated species, despite investing similar proportions of available resources into V_{cmax} and P_{ml}, as discussed in the previous section, strongly differ in the respective nitrogen use efficiencies. This corresponds with the findings of Wohlfahrt *et al*. (1998), who studied a subsample of the Monte Bondone species and found the slopes of linear relationships between V_{cmax}[a] and N_L[a] within the investigated species to vary by a factor of 7·5. Similar reasoning was put forward by Wullschleger (1993) and in terms of the A_{max}–N_L relationship by Reich *et al*. (1994, 1995) and Bahn *et al*. (1999). Other causes affecting the A_{max}–N_L relationship among different species may be nutrient availability (Reich & Schoettle 1988; Reich *et al*. 1994) and leaf longevity (Reich *et al*. 1991, 1995).

Differences between the functional groups

The present study reveals that minor differences exist between graminoids and forbs, whereas dwarf shrubs are lower in N_L, SLA, V_{cmax} and P_{ml} (both on a leaf area and a leaf mass basis). This corresponds well with the results obtained by Wullschleger (1993), who found no significant differences in J_{max} and V_{cmax} between monocot and dicot agricultural crops, whereas sclerophyllous shrubs reached 60–70% of the capacities of dicots. This ranking has also been confirmed in terms of A_{max} by several studies (Körner *et al*. 1979; Schulze 1982; Schulze & Chapin 1987; Cernusca *et al*. 1992; Larcher 1995; Tappeiner & Cernusca 1998; Bahn *et al*. 1999). Since the observed differences become much more evident when rates are expressed per unit leaf mass, it is clear that the observed differences between dwarf shrubs and graminoids/forbs are not just a result of differences in morphology (SLA), but result from *de facto* lower capacities for the biochemical reactions of photosynthesis of the dwarf shrubs (Poorter & Evans 1998; Reich *et al*. 1998a).

Effects of land use

According to Schulze & Chapin (1987), plants have to keep resource use (carbon assimilation, translocation and allocation) in balance with resource acquisition (water and nutrient uptake/transport). This results in a superior competitive ability of graminoids/forbs in habitats which are characterized by a high nutrient availability, since these habitats meet the potential for carbon assimilation of graminoids/forbs more than those of dwarf shrubs. The present study confirms these considerations: The abandoned areas are to a large extent composed of dwarf shrubs and species such as *N. stricta, A. montana, T. alpinum, P. sulphurea*, all characterized by low capacities for the biochemical reactions. On the other hand, the meadows are characterized by graminoids (*A. tenuis, F. rubra, D. glomerata*) and forbs (*R. acris, T. repens, A. millefolium*) with high capacities for the biochemical reactions. In a previous study at Monte Bondone, Cernusca *et al*. (1992) found A_{max} of the species from the abandoned area to be approximately 25% lower than A_{max} of the species from the meadow. Bahn *et al*. (1999), using the same sample of species as in this study, also found species from meadows to exhibit a higher A_{max} as compared to species from pastures and abandoned areas. Considerably lower values of A_{max} for unmanaged dwarf shrub communities in comparison to intensively used hay meadows and pastures have likewise been reported by Tappeiner & Cernusca (1998) for the Central Caucasus.

Implications of the present study for up-scaling studies

The success of scaling-up gas exchange depends on a number of factors, including an adequate description of the gas exchange behaviour of the vegetation elements (Baldocchi 1993; Norman 1993; Baldocchi *et al*. 1996). The larger the spatial scale, the smaller the influence of leaf level gas exchange characteristics (Baldocchi 1993; Field & Ehleringer 1993; Williams *et al*. 1997), but also the more difficult it becomes to find appropriate model parameters (Running *et al*. 1989; Tenhunen 1999). Especially in the absence of their own measurements, modellers often have to refer to the literature to derive parameters corresponding to their needs (Falge *et al*. 1996). However, most of these data cannot be implemented directly, as they are often expressed in terms of the resulting processes, and not in terms of the corresponding model parameters.

Being aware of these problems, we have decided to present the temperature dependencies of V_{cmax} and P_{ml}, separated according to life form and land use, in a form which allows easy implementation into the model by Harley & Tenhunen (1991). The data from Fig. 2 have thus been expressed in terms of the corresponding model parameters as shown in Table 6, and are meant to serve modellers dealing with CO_2 assimilation in semi-natural mountain grassland ecosystems at least as a starting point for their up-scaling studies.

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APPENDIX A. SYMBOLS AND ABBREVIATIONS

A	net photosynthesis (μmol m^{-2} s^{-1})
A_{max}	photosynthetic capacity (μmol m^{-2} s^{-1})
Cc	CO_2 partial pressure in the chloroplasts (Pa)
Ci	CO_2 partial pressure in the leaf intercellular space (Pa)
g_{ic}	internal conductance for CO_2 (mmol m^{-2} s^{-1} bar^{-1})
J_{max}	maximum electron transport capacity (μmol electrons m^{-2} s^{-1})
K_C	Michaelis–Menten constant for carboxylation (Pa)
K_O	Michaelis–Menten constant for oxygenation (Pa)
N_L	leaf nitrogen content, not specified whether area- or mass-based
$N_l{}^a$	area-based leaf nitrogen content (mmol m^{-2})
$N_L{}^m$	mass-based leaf nitrogen content (mg g^{-1})
O	internal O_2 partial pressure (Pa)
P_i	inorganic phosphate
P_m	CO_2-saturated photosynthesis rate at any given irradiance and temperature (μmol m^{-2} s^{-1})
P_{ml}	potential rate of RuBP regeneration, not specified whether area- or mass-based
$P_{ml}{}^a$	area-based potential rate of RuBP regeneration (μmol m^{-2} s^{-1})
$P_{ml}{}^m$	mass-based potential rate of RuBP regeneration (mg kg^{-1} s^{-1})
$P_{ml}(T_{ref})$	potential rate of RuBP regeneration at the reference temperature of 293·16 K in the absence of any deactivation due to high temperature (μmol m^{-2} s^{-1})
PPFD	photosynthetic photon flux density (μmol m^{-2} s^{-1})
R	gas constant (8·314 m^3 Pa mol^{-1} K^{-1})
R_{day}	respiration rate from processes other than photorespiration (μmol m^{-2} s^{-1})
Rubisco	ribulose-1,5-bisphosphate carboxylase/oxygenase
RuBP	ribulose-1,5-bisphosphate
SLA	specific leaf area (m^2 kg^{-1})
T_K	leaf temperature (K)
T_{opt}	temperature optimum (°C)
V_{cmax}	maximum rate of carboxylation, not specified whether area- or mass-based
$V_{cmax}{}^a$	area-based maximum rate of carboxylation (μmol m^{-2} s^{-1})
$V_{cmax}{}^m$	mass-based maximum rate of carboxylation (mg kg^{-1} s^{-1})
$V_{cmax}(T_{ref})$	maximum rate of carboxylation at the reference temperature of 293·16 K in the absence of any deactivation due to high temperature (μmol m^{-2} s^{-1})
W_C	Rubisco limited rate of carboxylation (μmol m^{-2} s^{-1})
W_J	RuBP limited rate of carboxylation, when RuBP regeneration is limited by electron transport (μmol m^{-2} s^{-1})
W_P	RuBP limited rate of carboxylation, when RuBP regeneration is limited by inorganic phosphate (μmol m^{-2} s^{-1})
α	apparent quantum yield of net photosynthesis at saturating CO_2 (mol CO_2 mol photons^{-1})
ΔH_a	energy of activation (J mol^{-1})
ΔH_d	energy of deactivation (J mol^{-1})
ΔS	entropy term (J K^{-1} mol^{-1})
τ	Rubisco specificity factor