

Microclimate and fluxes of water vapour, sensible heat and carbon dioxide in structurally differing subalpine plant communities in the Central Caucasus

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ABSTRACT

Effects of canopy structure on microclimate, energy budget and CO₂ exchange were analysed in a pasture, two hay meadows, a tall herb community and a dwarf shrub community in the subalpine belt of the Central Caucasus. The results show that canopy structure exerts a marked influence on the distribution of photon flux density, temperature and canopy photosynthesis (A_c). Three canopy types were distinguished. Type 1 (pasture) has a small LAI (leaf area index) and more than two-thirds of the phytomass is concentrated in the lowest few cm of the canopy, mainly as planophile leaves. This results in (1) a low degree of utilization of photosynthetic photon flux density (PPFD) by assimilatory plant components, (2) high leaf temperatures and a high soil heat flux during the phase of incoming radiation, and (3) a relatively low A_c / LAI ratio. Type 2 (meadows), in spite of its erect leaves, which at high solar elevations permit light to penetrate to the lower canopy layers, is characterized by (1) marked effects of mutual shading in the lower canopy layers for most of the day, and thus (2) only slight variations in air and leaf temperatures and (3) a comparatively low A_c / LAI ratio. In canopies of type 3 (tall herb and dwarf shrub communities), there is a concentration of flat leaves in the upper layers. This results in (1) very good utilization of PPFD; (2) no strong fluctuations in canopy temperature as the flat leaves act as a buffer, reducing the amounts of incoming and outgoing radiation in lower canopy layers, and (3) high values of the A_c / LAI ratio. The energy budgets of the canopies investigated are governed not so much by their spatial structure, but rather indirectly by LAI and the degree of coupling of the canopy with the atmosphere.

Key-words: canopy photosynthesis; canopy resistance; canopy structure; dwarf shrub; energy balance; hay meadow; omega factor; pasture; tall herb.

INTRODUCTION

Measurements of exchange processes between the biosphere and the atmosphere by means of micrometeoro-

logical techniques are the subject of renewed and increasing interest in the context of global environmental change (Baldochi, Hicks & Meyers 1988). The complex interrelations and feedbacks between the planetary boundary layer and ecosystems under different land use are generally not sufficiently understood. Therefore, integrated investigations of the CO₂ and energy exchange of ecosystems are needed to provide information for studies of global climate, carbon balance modelling, dry deposition of atmospheric pollutants and ecophysiology (Verma *et al.* 1986).

Although many micrometeorological investigations of CO₂ and energy exchange have been made over agricultural crops (e.g. Biscoe, Scott & Monteith 1975; Denmead 1976; Baldochi, Verma & Rosenberg 1981; Anderson, Verma & Rosenberg 1984; Held *et al.* 1990; Baldochi 1994a,b) and forests (e.g. Baumgartner 1969; Jarvis, James & Landsberg 1976; Leuning & Attiwil 1978; Verma *et al.* 1986; Valentini *et al.* 1991), there have been few studies on grasslands (e.g. Kim & Verma 1990; Gale *et al.* 1990; Kim, Verma & Clement 1992). Energy balance measurements on ecosystems in mountainous regions are rare (e.g. Cernusca 1976, 1991a; Rott 1979; Cernusca & Seeber 1980; Staudinger & Rott 1981), and no measurements of CO₂ exchange and canopy photosynthesis have been reported for these ecosystems.

In this paper we examine, using a comparative approach, structural and microclimatic characteristics as well as essential parameters of the energy balance and CO₂ exchange of structurally different grasslands and tall herb and dwarf shrub communities in the subalpine belt of the Central Caucasus. Fluxes of CO₂, water vapour and sensible heat were measured using a micrometeorological method (Bowen ratio) combined with measurements of canopy structure and microclimate. It was a primary aim of this study not only to quantify the differences between the canopies studied, but also, in particular, to analyse the effects of the spatial structure of the canopies on the processes investigated.

MATERIALS AND METHODS

Studies were carried out during late July and early August 1987 and 1988 near the mountain research station Kasbegi (Lat 42° 48'N, Long 44° 39'E, altitude 1850 m a.s.l.) in the subalpine belt of the northern slope of the Great

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Caucasus. Five different plant communities were investigated: three grassland ecosystems, a tall herbaceous community and a dwarf shrub community. Some relevant site characteristics are summarized in Table 1. The experimental site 'Pasture' is an area grazed by sheep. The dominant species are *Festuca rupicola*, *Pulsatilla violacea* and *Carex buschiorum*. The swampy meadow 'Deschampsietum' is mowed every 2 years. The dominant species are *Deschampsia cespitosa* and *Equisetum palustre*, and the stand is interspersed with *Phragmites australis*. In the hay meadow 'Hordetum', besides grasses such as *Hordeum violaceum* and *Poa pratensis*, there are a considerable number of tall herbaceous species, such as *Anthriscus nemorosa*, *Seseli transcaucasica* and *Heracleum asperum*. The experimental site 'Heracleum' is a tall herbaceous stand triangular in shape situated on a gentle north-exposed slope, bordered on two sides by small streams, so that there is a relatively high air humidity at this site. The community is dominated by *Heracleum sosnowskyi*, which is harvested for silage. The dwarf shrub community 'Rhododendretum' is dominated by *Rhododendron caucasicum*. A very sparse undergrowth of mainly *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Empetrum hermaphroditum* is also present. This community is found exclusively on steeper north- and northwest-exposed slopes.

In all of the plant communities investigated, detailed measurements were made of canopy structure, microclimate, energy fluxes and CO₂ exchange during the main flowering period, when the vegetation was at its maximum. During the experimental periods the stands investigated were not short of water since precipitation prior to and during the investigation period was appreciable. Soil water potentials were between -60 and -290 hPa in the main rooting horizon.

The canopy structure of each community was analysed by the stratified clipping method (Monsi & Saeki 1953) which consisted of harvesting layer by layer the above-ground vegetation, and measuring separately the dry mass of stems, leaves, inflorescences or fruits and dead plant material for each species in each layer. A representative plot of 1 × 1 m was harvested in each stand. Leaf area index (LAI) and total plant area index (PAI) were calculated from measurements of the area of the leaves and the other plant parts, for each species and layer, using a leaf area meter (LI-3100, LI-COR Corp., Lincoln, NE, USA). Field measurements of the leaf and stem inclinations of the dominant species in each layer were made with a hand inclinometer. The mean leaf inclination angle in each canopy layer was calculated on the basis of the proportional contribution of the constituent species to PAI. The inclination index x_L was calculated according to Ross (1975).

Measurements of microclimate, energy fluxes, CO₂ exchange and soil respiration were made using a portable battery-powered data acquisition system (MIKROMET, Cernusca 1987). On each experimental site, data were recorded continuously for 14 to 30 consecutive days.

Measurements of profiles of soil, air and leaf temperature, photosynthetic photon flux density (PPFD), air humidity, wind speed and CO₂ concentration, within and above the canopies, and of soil water potential, incoming global radiation and net radiation (R_n) were made at intervals ranging from 1 min for rapidly changing variables, such as radiation and temperature, to 6 min for soil temperature and soil water potential, and were averaged over 60 min periods. Soil temperature and R_n sensors were mounted parallel to the soil surface. The following sensors were used: star pyranometer and net radiometer (Schenk, Vienna, Austria), quantum sensors (LI-1905, LiCor Inc., Lincoln, NE, USA), small thermocouples for soil, leaf and

Table 1. Relevant characteristics of the sites investigated

	Pasture	Deschampsietum	Hordetum	Heracleum	Rhododendretum
Altitude (m)	2050	1750	1850	2200	2200
Inclination of slope (°)	3	0	0	3	40
Exposure	SW	—	—	N	NNW
Field length/width (m)	350 / 220	300 / 200	150 / 100	350 / 250	450 / 200
Difference between apparent and astronomical horizon (°)	19	17	15	20	21
Soil type	Mountain meadow soil	Mountain brown soil	Mountain meadow soil	Andosol	Andosol
Soil depth (cm)	41	90	45	41	43
Vegetation type	Pasture	Hay meadow	Hay meadow	Tall herb	Dwarf shrub
Number of plant species	25	21	68	8	17
Canopy height (cm) (maximum/mean)	25 / 13	70 / 50	120 / 80	240 / 220	55 / 47
Degree of cover (%)	80	100	100	100	100

air temperature (made by the authors: copper/constantan, 0.08 mm diameter), thermocouple psychrometers (Cernusca 1991b), heat flux plates (20452-3, RdF corp., Hudson, NH, USA), three-cup anemometers (Type AMI, Rimco, Australia), tensiometers (2630ALK Soilmoisture equipment corp., Santa Barbara, USA) equipped with an electronic pressure sensor (136 PC 15 G1 Micro Switch, Honeywell, UK), and infrared gas analysers (IRGA; LCA-2, ADC, Hoddesdon, UK and BINOS, Leybold-Heraeus, Hanau, Germany) for measuring CO₂ concentrations. To correct for the zero shift of the IRGA, before each measuring cycle reference and sample cells were flushed with the same air by means of solenoid valves (LFAA1200118H, Lee Co., Westbrook, CT). The span was controlled at regular intervals with a CO₂ standard of known concentration.

Soil heat flux (S) was estimated by a combination of the temperature integral method for the upper 20 cm of the soil and the temperature gradient method for the lower layers of the soil (Gilman 1977). S was considered positive when directed downwards into the soil, whereas latent heat (LE), sensible heat (H) and carbon dioxide (F_c) fluxes were considered positive when directed upwards and negative when directed towards the soil surface. LE , H and F_c were calculated by the Bowen ratio energy balance method (BREB), which is considered to be one of the best methods in sloping landscapes (Fritchen & Qian 1990) and has been used successfully in complex sloping terrain by us and other investigators (Cernusca 1976, 1991a; Cernusca & Seeber 1989; Rott 1979; Staudinger & Rott 1981; Halbsguth *et al.* 1984; Whitmann *et al.* 1989; Nie, Demetriades-Shah & Kanemasu 1992). The theory and operation of our BREB system were described in detail by Cernusca (1982). Briefly, dry and wet-bulb temperature and CO₂ concentration were measured at two heights (0.1 m and 1.2 m in the Hordetum, 0.1 m and 1.5 m in the other sites) above the canopy. The heights were chosen as a compromise between sufficient fetch and greatest possible gradients (fetch-to-height ratios 45:1 to 150:1 in the prevailing wind direction). Fritschen, Gay & Simpson (1983) and Heilmann, Brittin & Neale (1989) suggest that a fetch-to-height ratio as low as 20:1 is sufficient when the Bowen ratio ($\beta = H/LE$) is small. In the Rhododendretum it was further considered that the mean wind streamlines must adjust to the slope of the underlying terrain, so that the assumption of one-dimensional transport is fulfilled and horizontal gradients are zero. The BREB method provides reasonable estimates of LE and H and a uniform β even on a steep slope as long as the measuring system is within a certain distance of the slope (Nie, Flitcroft & Kanemasu 1992). Measurements were carried out in the upper third of the 450 × 200 m homogenous slope. On the selected days, only slight up-slope wind or even air flow at right angles to the direction of the slope occurred. It can therefore be assumed that the boundary layer was fully adjusted to the surface conditions of the slope. Cernusca & Seeber (1989), who used the same measuring system and arrangement as we did, proved the validity of BREB measurements on a 35° slope in the Alps by means of weighing lysimeters.

The arrangement of the gradient system close to the top of the canopies results in the lower sensor being in the so-called 'roughness sublayer', in which the Moni-Obkuhov scaling theory breaks down and eddy exchange coefficients are enhanced. However, as Raupach & Legg (1984) and Cellier & Brunet (1992) showed, the BREB method can still be applied down to the canopy top, because the basic assumption, i.e. the similarity of transfer processes for heat and water vapour, still holds in the roughness sublayer. In order to test the validity of the BREB, a third psychrometer was mounted at a height of 0.7 m above the canopy, and β was calculated both for the gradients between 0.1 and 1.5 m and between 0.1 and 0.7 m. On all experimental sites, β estimates for the selected clear days were independent of height. A t -test showed that the mean $\Delta\beta$ did not differ significantly from 0. This proves that no horizontal gradients occurred and that fetch and placement of the gradient system were sufficient on all experimental sites. The BREB results for the pasture and the Deschampsietum were further tested directly with weighing mini-lysimeters (for details of the method, see Körner, Hoflacher & Wieser 1978) on selected days. The daily totals of lysimeter LE and BREB LE differed by no more than 5%.

All BREB data were filtered according to criteria of Ohmura (1982) with a slight modification to eliminate measurements of β between -0.75 and -1.25, in which cases LE was averaged from the preceding and succeeding readings to replace the unreasonable value. H and F_c were then computed for that period using the interpolated LE . CO₂ flux was corrected according to Webb, Pearman & Leuning (1980) in order to take into account variations in air density resulting from the simultaneous occurrence of the fluxes of heat and water vapour. These corrections amounted to a maximum of 25% of the total CO₂ flux. Release of CO₂ from the soil was measured *in situ* by IRGA techniques. For these measurements, opaque cuvettes (diameter 19 cm, depth 16 cm) were installed at the soil surface, and continuously flushed with air from a height of 2 m at a rate of 50 dm³ h⁻¹. This flow rate allowed CO₂ enrichment in the cuvette to be maintained below 30 $\mu\text{mol mol}^{-1}$, thus avoiding changes of diffusion gradients from the soil. Reference and cuvette air were drawn into the gas analyser at a rate of 10 dm³ h⁻¹ at 12 min intervals, and the rate of soil respiration was calculated from the difference between the concentrations of CO₂ entering and leaving the cuvette and averaged over 60 min periods. Since even small pressure differences can enhance or suppress soil-atmosphere gas exchange (Kanemasu, Powers & Sij 1974), the cuvette was equipped with an exhaust tube (length 5 cm, diameter 0.5 cm), allowing excess air to leave the cuvette and thus avoiding over- and underpressures in the cuvette (Cernusca & Decker 1989).

Apparent canopy photosynthesis (A_c) was calculated by adding the CO₂ flux from the atmosphere (F_c) and the CO₂ output of the soil (R).

Total canopy resistance (R_c) (aerodynamic + canopy leaf resistance) and the aerodynamic resistance (R_a) to water

vapour transfer were calculated according to Cernusca & Seeber (1980):

$$R_c = \frac{\rho c_p [e - e_s(T_\phi)]}{\gamma LE} \frac{V_0(T + 273 / T_0)}{P_0 / P} \quad (1)$$

$$R_a = \frac{\rho c_p [T - T_\phi]}{H} \frac{V_0(T + 273 / T_0)}{P_0 / P} \quad (2)$$

by employing the measured values of air temperature above the canopy (T), the mean leaf temperature in the canopy layer with the highest energy turnover (T_ϕ), the computed values of H , LE , water vapour pressure above the canopy (e) and saturation vapour pressure at the mean leaf temperature [$e_s(T_\phi)$], and the psychrometric constant (γ). For the conversion from velocity to mol units the molar volume of air (V_0) at T_0 (273 K) and P_0 (1000 hPa), the ambient air pressure (P) and the air temperature were used. Canopy leaf resistance (R_l) was obtained from the difference $R_c - R_a$. The resistances related to the whole plant canopy, R_a and R_l , were combined with the measured values of LAI (L) to calculate approximately the resistances relevant to the single leaf, i.e. stomatal resistance r_l and boundary layer resistance r_a :

$$r_l \approx 2L R_l, r_a \approx 2L R_a. \quad (3)$$

The factor of 2 appears because r_a and r_l are related to the total leaf surface while LAI is based on the projected leaf area per soil area. The calculation of r_l on the basis of canopy resistance in Eqn 3 is only valid as an approximation, since the leaf resistances take into account only leaf transpiration, while calculation of the canopy resistances includes evaporation from the soil surface.

The decoupling coefficient Ω , which describes the extent to which vegetation is coupled to the atmosphere, was calculated according to McNaughton & Jarvis (1983).

Water use efficiency is described in terms of the index WUE ($=A_c / E$, where E is the flux of water vapour in $\text{mol m}^{-2} \text{s}^{-1}$) and the CO_2 -water vapour flux ratio (CWR = F_c / E) according to Baldocchi *et al.* (1981).

Zero-plane displacement (d) and roughness length (z_0) for wind were calculated according to Robinson (1962). Normalized displacement height and normalized roughness length were obtained by dividing by the mean canopy height (h).

Error analysis for calculations in the BREB method followed Fuchs & Tanner (1970) and Sinclair, Allen & Lemon (1975) and was performed in the same manner for the calculations of F_c , A_c , R , WUE, R_a , R_l and Ω . Taking account of the accuracy of the sensors and the resolution of the datalogger (± 0.03 K for dry- and wet-bulb temperature, $\pm 6\%$ for net radiation, $\pm 0.5 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ air}$) the mean probable relative errors for the selected days were 0.09 for $\delta\beta/\beta$, 0.06 for $\delta H/H$, 0.04 for $\delta LE/LE$, 0.06 for $\delta F_c/F_c$, 0.02 for $\delta R/R$, 0.07 for $\delta A_c/A_c$, 0.10 for $\delta WUE/WUE$, 0.10 for $\delta R_a/R_a$, 0.04 for $\delta R_l/R_l$ and 0.05 for $\delta\Omega/\Omega$. These errors are very similar to those reported by Spittlehouse & Black (1980) for relatively small β (< 1).

RESULTS

Canopy structure

During the main flowering period, the above-ground phytomass of the stands differed considerably in total amount (Table 2) as well as in vertical distribution (Fig. 1). In the pasture, two-thirds of the phytomass was contained in the lowest 3 cm of the canopy, while in the upper layers the phytomass decreased sharply. The Deschampsietum showed a gradual decrease in phytomass with increasing height above the ground. In the Hordetum more than 80% of the phytomass was distributed quite evenly in the lowest 40 cm of the canopy. In the Heracleetum and the Rhododendretum, leaf mass was concentrated in the upper half of the canopy and photosynthetically inactive phytomass in the lower half of the canopy. These striking differences in the vertical distribution of phytomass imply a totally different dry matter investment in the various plant organs (Table 2).

Table 2 shows the mean leaf inclination angles (α) of the stands. In Fig. 1, α is shown for the individual layers. The inclination index x_L given in Table 2 is used to compare the canopies with respect to the leaf inclination angle distribution function: x_L ranges from +0.6 (purely horizontal leaves) to -0.4 (purely vertical leaves). Because of the erect leaves of the grasses and of *Equisetum*, the Deschampsietum was a typical erectophile canopy ($x_L = -0.26$), while the Heracleetum, with almost horizontal leaves, showed strong planophile tendencies ($x_L = 0.54$). The other canopies investigated displayed strong variation of α with canopy height.

Microclimate

In Fig. 1a & b, mean profiles of photosynthetic photon flux density (1100–1400 h) on a clear day are shown. In the Deschampsietum PPFD absorption decreased steadily down to the soil surface. In the pasture, however, 60% of the incoming PPFD was absorbed in the lowest 6 cm of the canopy, a thin layer in which a major part of the phytomass was concentrated. Of the incoming PPFD, 26% was not absorbed in the canopy, but reached the soil surface. In the Hordetum, Heracleetum and Rhododendretum, the major part of the PPFD was absorbed in a narrow layer of dense foliage in the upper part of the canopies. The dense foliage of *Seseli transcaucasica* and *Anthriscus nemorosa* in the Hordetum was responsible for absorption of 80% of PPFD in the layer between 25 and 40 cm. In the Heracleetum and the Rhododendretum, 90% of the incoming PPFD was absorbed in the uppermost 20 cm of the foliage layer. Light attenuation depends on the leaf area and density distribution, and in particular on the leaf inclination angle. This can be clearly seen from the calculated extinction coefficient (k) (Table 2). According to Monsi & Saeki (1953), the values of k given in Table 2 characterize two canopy types: the erectophile type with a low k value at maximum solar elevation for the Deschampsietum ($k_{\text{noon}} = 0.21$) and the planophile type with

Table 2. Characteristics of canopy structure, microclimate, energy balance and CO₂ exchange of the sites investigated in the Central Caucasus. Measurements were taken in the main flowering period on clear days in 1987 and 1988. For some parameters the standard deviation is given

	Pasture	Deschampsietum	Hordetum	Heracleum	Rhododendretum
Canopy structure					
Phytomass (g DM m ⁻²)	219	427	658	768	1893
Biomass (%)	75	86	88	88	96
Leaves (%)	67	60	34	34	27
Stems (%)	5	25	31	47	65
Litter (g DM m ⁻²)	92	44	132	70	1066
LAI (m ² m ⁻²)	2.4	5.8	5.4	6.2	3.8
PAI (m ² m ⁻²)	3.1	6.7	8.4	8.1	4.7
Mean inclination angle (°)	47 ± 28	66 ± 26	41 ± 20	29 ± 24	36 ± 20
Inclination index α_L	0.19	-0.26	0.37	0.54	0.39
Microclimate					
PPFD utilization by assimilatory plant components (%)	53	84	84	88	92
Extinction coefficient (noon/ evening)	0.25/0.66	0.21/0.56	0.52/0.55	0.95/1.14	1.10/1.34
Active layer (cm)	0-2	6-12	25-35	100-130	30-40
Temperature difference between active layer and 1.5 m above canopy at noon (K)	17.2	7.6	4.0	3.1	5.3
Mean soil temperature ² at 0 cm	22.2 ± 9.7	17.9 ± 2.5	17.0 ± 5.4	13.9 ± 2.0	12.7 ± 1.6
Mean soil temperature ² at 5 cm	17.4 ± 5.5	16.1 ± 0.8	13.8 ± 2.1	12.4 ± 0.9	10.8 ± 0.4
d^1 (cm)	6 ± 2.6	29 ± 3.3	54 ± 5.6	112 ± 5.2	39 ± 4.3
z_0^1 (cm)	0.7 ± 0.3	2.9 ± 0.8	3.7 ± 1.3	12.9 ± 3.9	2.8 ± 0.7
Energy balance					
LE/R_n	0.58	0.70	0.77	0.81	0.73
H/R_n	0.30	0.27	0.17	0.16	0.23
S/R_n	0.12	0.03	0.06	0.03	0.03
Bowen ratio (H/LE)	0.52	0.38	0.22	0.19	0.32
Median value of Omega factor	0.70	0.49	0.68	0.86	0.52
CO₂ exchange					
F_{c3} (mmol m ⁻² d ⁻¹)	-177.5	-444.9	-491.9	-708.5	-386.2
A_{c3} (mmol m ⁻² d ⁻¹)	210.3	494.6	584.1	756.4	428.8
daytime R^3 (mmol m ⁻² d ⁻¹)	32.8	49.7	92.2	47.9	42.8
nighttime R (mmol m ⁻² 12 h ⁻¹)	62.8	28.4	77.0	49.0	57.4
WUE ² (mmol CO ₂ mol ⁻¹ H ₂ O)	1.1	2.3	1.9	2.2	1.6
CWFR ² (mmol CO ₂ mol ⁻¹ H ₂ O)	0.9	2.1	1.6	2.1	1.4

¹Wind speed at 1.5 m above canopy surface was 2-3 m s⁻¹.

²Mean between sunrise and sunset.

³Total between sunrise and sunset.

more horizontal leaves and a higher k value for the Heracleum ($k_{\text{noon}}=0.95$) and the Rhododendretum ($k_{\text{noon}}=1.10$). Furthermore, the erect leaves of the graminaceous type cause a strong diurnal change in the extinction coefficient, while in the other canopies investigated only slight diurnal changes of k were observed (Table 2).

Air temperature profiles in the vegetation canopies on a clear day (Fig. 1a,b) showed further that the highest temperatures were observed in those canopy layers where radiation absorption was at its maximum. In the pasture, the so-called 'active layer for energy turnover' was found near the ground, whereas in the other stands the most active layers were higher up in the canopy (Table 2). In the Heracleum, the Hordetum and the Rhododendretum the differences between air temperature 1.5 m above the canopy and the

temperature inside the canopy were much smaller than in the Deschampsietum and the pasture (Table 2). Nocturnal cooling was least in the Rhododendretum and greatest in the pasture. The difference between the minimum and the maximum temperatures on a clear day in the active layer of the pasture was 34.1 K, which was twice the difference observed in the Rhododendretum (17.2 K).

Leaf temperatures during the night were somewhat lower than canopy temperatures at the same height (Fig. 1a,b). However, there were considerable differences between the canopies during the day. In the pasture, leaf temperatures in all parts of the canopy were considerably higher than air temperatures (0.9 to 4.1 K), while in the Deschampsietum they were lower (-0.2 to -1.1 K). In the other three canopies leaf temperatures in the uppermost

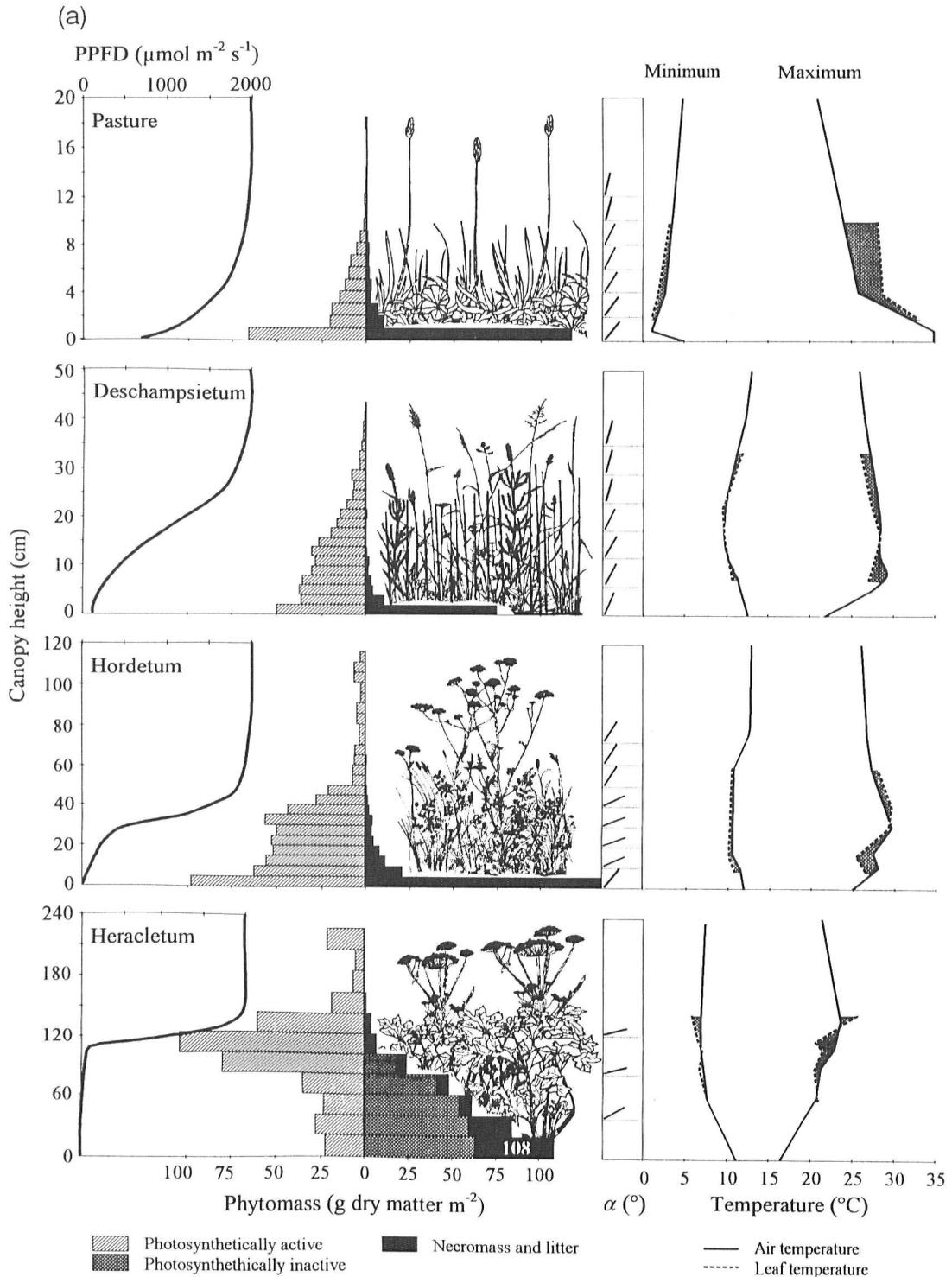


Figure 1

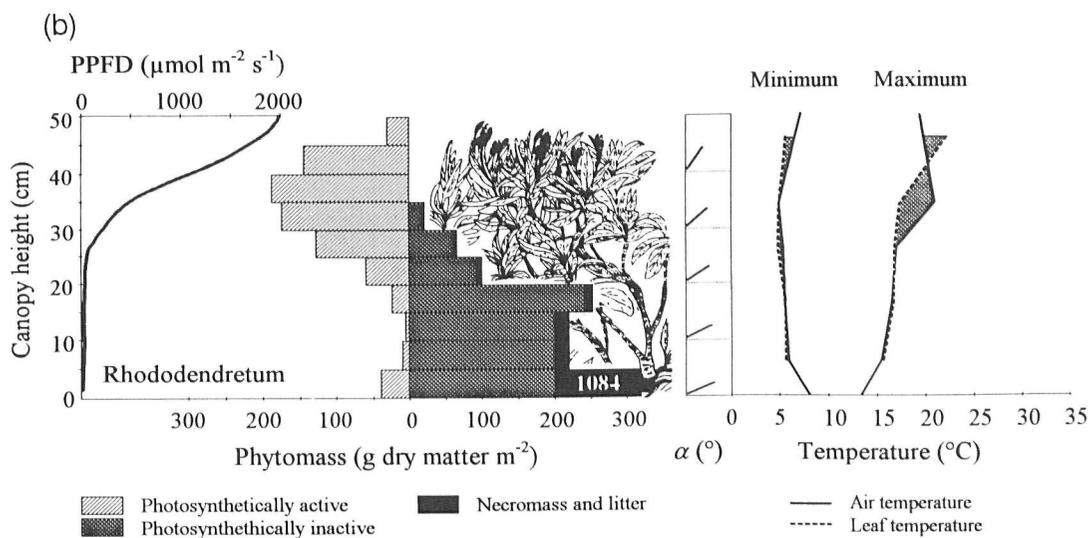


Figure 1. Profiles of the attenuation of photosynthetically active radiation (PPFD) at midday (1100–1400 h) (left), the stratification of phytomass and the mean leaf inclination angle (middle), and profiles of air temperature and leaf temperature (right) for the plant communities investigated in the Central Caucasus. Values for comparable clear days were chosen for the figure.

layer were higher than air temperatures (0.7 to 2.1 K), while in the lower layers the differences between leaf and air temperatures were clearly negative (–2.2 to –3.9 K).

The values of d and z_0 presented in Table 2 are means of all wind profiles with near-neutral stability, for which the wind speed at 1.5 m above the canopy surface was in the range 2–3 m s⁻¹. The normalized displacement height (d/h) was very high in the Rhododendretum (0.83), and less in the Hordetum (0.68), the Deschampsietum (0.58), the Heracleum (0.51) and the pasture (0.46), whereas the normalized roughness length (z_0/h) was nearly the same in all stands.

Components of energy balance and Bowen ratio

Figure 2 shows typical diurnal patterns of the energy balance components and of the Bowen ratio on selected fairly clear days. In all canopies investigated, the major part of the absorbed energy was used for evapotranspiration, but there were considerable differences in the amount of energy consumed by the canopies (Table 2). Further characteristic differences are discernible in the diurnal courses of LE , H and S in relation to R_n . Only in the Heracleum did diurnal patterns of LE , H and S follow R_n quite closely, with the result that β changed very little throughout the day. In the Hordetum, too, the Bowen ratio remained relatively constant over the course of the day, with somewhat higher values between 1100 h and 1500 h, caused by the slightly asymmetric courses of LE , H and S . In the other three canopies the energy budget components, and hence β , displayed strongly asymmetric diurnal courses. For the Deschampsietum and the Rhododendretum these asymmetric diurnal courses of LE and H resulted from the dependence of LE on R_n and water vapour pressure deficit

(vpd). In the Deschampsietum on most summer days moist-air advection occurred in the early afternoon, which was caused by air ascending from the gorge of the river Terek. This was the situation on 14 August 1987 (Fig. 3), so that towards 1400 h vpd decreased sharply from 15.5 to 5.5 hPa causing a reduction of LE and an increase of H . On 6 August 1987, however, such moist-air advection did not occur, and evapotranspiration followed the typical course for a meadow with a good water supply. The asymmetry of the diurnal course observed for the Rhododendretum can also be explained by the asymmetric course of vpd which increased very slowly during the morning to higher values in the afternoon. This resulted in a higher LE/R_n ratio in the afternoon than in the morning. It is interesting to note that a similar diurnal course of vpd also occurred in the Heracleum and the pasture with no comparable effects on LE . By contrast the asymmetric diurnal course of H in the pasture was determined by the strongly asymmetric course of S . Soil heat flux in the pasture increased immediately when net radiation became positive, reaching its maximum 1 h later at approximately 1000 h. From 1600 h onwards S was directed upwards (i.e. was negative). The energy not consumed by evapotranspiration was mainly directed towards the soil heat flux in the morning and towards the sensible heat flux in the afternoon.

Aerodynamic and canopy leaf resistances, and the decoupling coefficient Ω

Mean values (1100–1500 h) of the aerodynamic resistances and canopy leaf resistances to water vapour transfer for fairly clear days with wind speeds of about 2–4 m s⁻¹ are shown in Fig. 4. The highest values for R_a and R_l were recorded in the pasture, and the lowest in the

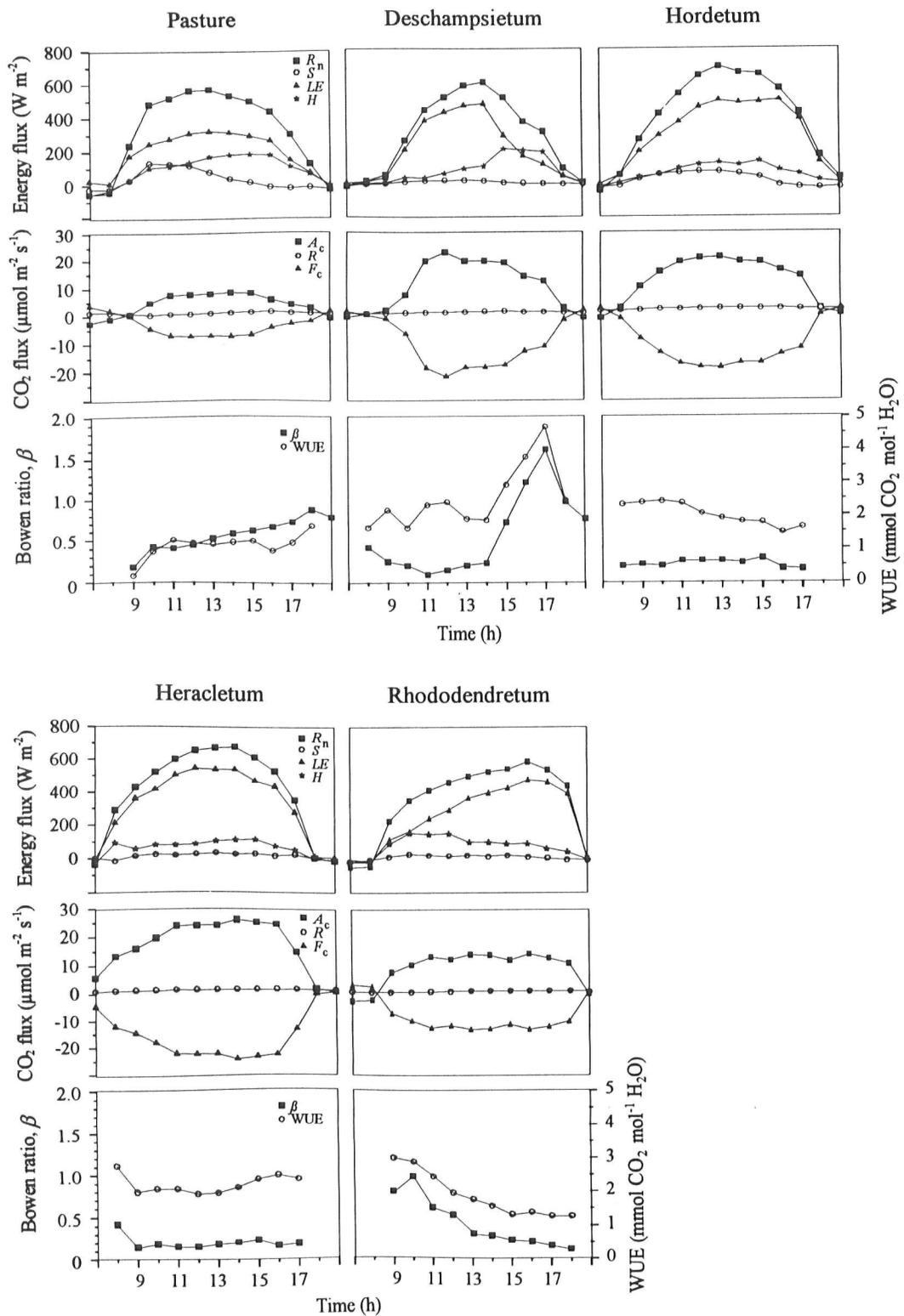


Figure 2. Diurnal patterns of the energy balance components (net radiation R_n , water vapour flux LE , sensible heat flux H and soil heat flux S) and of the CO_2 flux F_c , soil respiration R , apparent whole canopy photosynthesis A_c , the Bowen ratio β and the water use efficiency WUE for the plant communities investigated in the Central Caucasus in July / August 1987 / 1988. Values for comparable clear days were chosen for the figure.

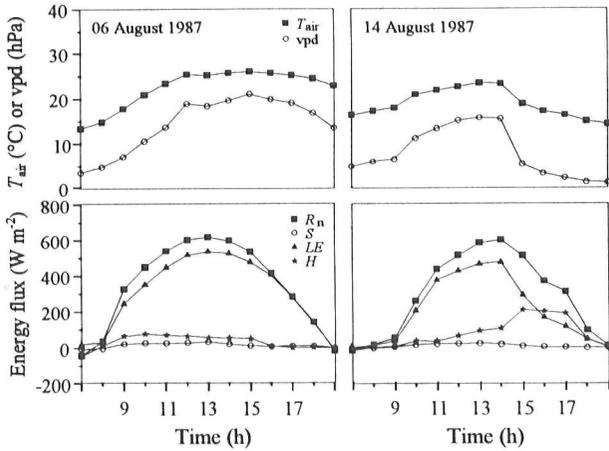


Figure 3. Diurnal patterns of air temperature (T_a) and vapour pressure deficit (vpd) and of energy balance components in the Deschampsietum for two selected days.

Rhododendretum and the Heraclietum. Unlike the canopy resistances, the highest value for r_l occurred in the Deschampsietum ($17.4 \text{ m}^2 \text{ s mol}^{-1}$). In the Hordetum, the pasture, the Rhododendretum and the Heraclietum, r_l was 80, 55, 49 and 36% of this value, respectively. The different ranking orders found for canopy and for leaf resistances can be explained by the different LAI in the canopies.

The R_l/R_a ratio largely determines the degree of coupling between vegetation and the atmosphere, as defined by the ‘omega factor’ Ω (McNaughton & Jarvis 1983; Jarvis & McNaughton 1986). If the vegetation is well coupled to the atmosphere, $\Omega=0$ and transpiration is primarily a function of stomatal conductance and vpd. If vegetation is poorly coupled because of thick leaf and canopy boundary layers, $\Omega=1$ and LE is primarily a function of net radiation (Jarvis 1986). As the results given in Table 2 show, the Heraclietum, the pasture and the Hordetum were only weakly coupled to the atmosphere, whereas the Rhododendretum and, in particular, the Deschampsietum were more strongly coupled to the atmosphere.

CO₂ exchange

Diurnal patterns of CO₂ flux, apparent whole canopy photosynthesis and soil respiration for the investigated stands are shown in Fig. 2. In addition, the daytime totals of these parameters between sunrise and sunset are given in Table 2. It is interesting to note that, except for the Deschampsietum, there was an almost linear relationship between LAI and the daily totals of A_c for the canopies. The diurnal patterns of F_c and A_c followed those of incoming radiation quite closely in all canopies. The dependence of A_c on PPFD is shown more clearly in Fig. 5, which includes data from the entire study period. In all stands, net

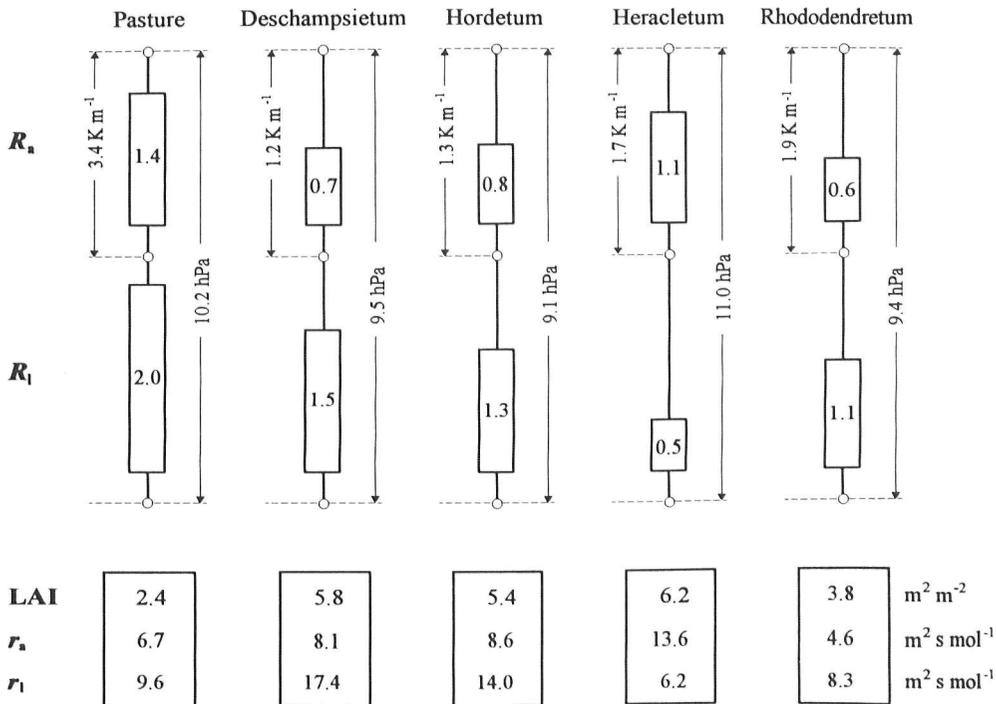


Figure 4. Electrical analogous model for the mean aerodynamic resistances (R_a) and canopy leaf resistances (R_l) to water vapour transfer in the five plant communities investigated. The mean values were calculated from measurements made between 1100 and 1500 h on comparable fairly clear days with a wind velocity of approximately $2\text{--}4 \text{ m s}^{-1}$. In addition to the resistances, the gradients of temperature and water vapour pressure are shown, indicating the main driving forces. Also given are the leaf area indices (LAI), and the calculated exchange resistances (r_a and r_l) for the single leaf.

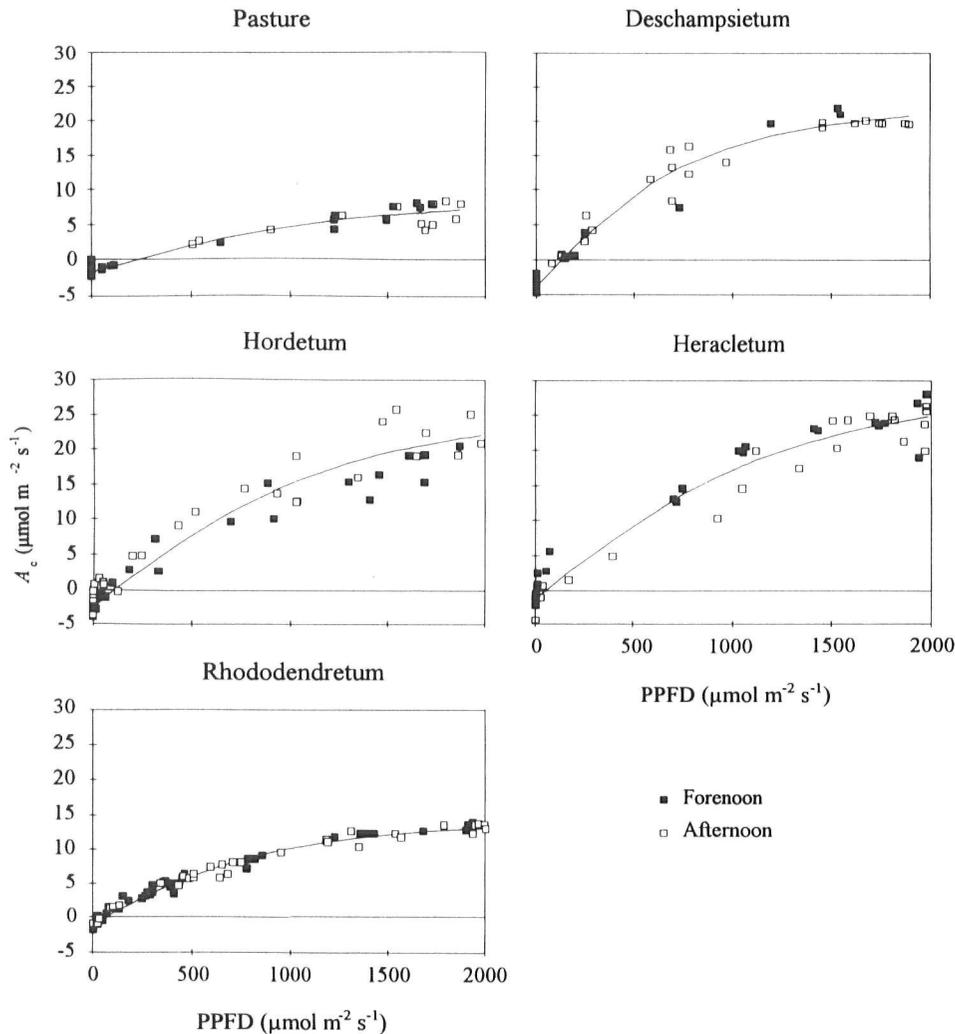


Figure 5. Apparent whole canopy photosynthesis as a function of photosynthetically active radiation (PPFD) above the plant canopies investigated. Data were fitted with a hyperbolic function: $A_c = \alpha \text{PPFD} / [1 + (\alpha^2 \text{PPFD}^2 / A_{c\text{max}}^2)]^{0.5}$, where α is the initial light conversion efficiency and $A_{c\text{max}}$ is the canopy photosynthesis at light saturation.

canopy photosynthesis increased with solar radiation in a curvilinear manner. Pasture, Rhododendretum and Deschampsietum showed a tendency towards saturation at high PPFD.

Daytime mean WUEs for the canopies are given in Table 2; diurnal courses are shown in Fig. 2. There was an increase of WUE in the afternoon in the Deschampsietum and in the pasture, and a decrease in the Hordetum. In the Rhododendretum and the Heraclietum, higher values of WUE occurred in the morning and afternoon and lower values during the middle of the day.

The highest daily total of CO_2 efflux from soil was measured in the Hordetum. The soils of the other stands emitted only two-thirds to half this amount. On all sites the diurnal course of soil respiration described a sinusoidal curve, which followed the diurnal course of temperature in the upper 5 cm of the soil.

DISCUSSION

Canopy structure and microclimate

The extremely heterogeneous climatic and edaphic conditions prevailing in mountains lead to a mosaic of different vegetation units. This natural phenomenon is intensified by anthropogenic management, as can be seen very clearly for the plant stands investigated in the Central Caucasus. Although situated only a few kilometres apart, the plant stands exhibit not only different species composition, but also very different canopy structure and amounts of above-ground phytomass.

The range in total above-ground phytomass reported here coincides with values measured by us and other authors in grasslands, tall herb communities and dwarf shrub communities under comparable site conditions (Cernusca 1976, 1991a; Cernusca & Seeber 1980; Cernusca & Nachuzrišvili 1983; Gisi & Oertli 1981;

Tesarová 1983; Uherčíková & Eliás 1987; Morozov & Belaya 1988; Tappeiner & Cernusca 1989a, b, 1995).

As in earlier investigations on comparable stands (Cernusca 1976, 1991a; Cernusca & Seeber 1980; Cernusca & Nachuzrišvili 1983; Tappeiner & Cernusca 1995), the present studies revealed a strong influence of stand structure on microclimate. On the basis of the effects of stand structure on microclimate, the stands can be grouped into three different structural types (Tappeiner & Cernusca 1990, 1991).

Type 1 is represented by the pasture. Leaf area is amassed near the soil surface, and leaves are mainly erect in the upper part of the canopy and mostly horizontal in the lower part. Such a structure is typical of grazed areas (Cernusca & Nachuzrišvili 1983; Fukuyama 1985; Sala 1988; Tappeiner & Cernusca 1989b, 1995) and is commonly interpreted as an adaptation to grazing. This structure, however, has decisive effects on the microclimate: (1) PPFD is not used very efficiently by assimilatory plant components (53%, Table 2); (2) because of the open structure, air and leaves in the canopy heat up considerably during the day, while they cool considerably during the night; (3) the high radiation absorption near to and at the soil surface causes a high soil heat flux. The daily mean S value of the pasture was twice that of the Hordetum and 4 times that of the other canopies; (4) a low PAI combined with a concentration of phytomass at the soil surface presents only a low resistance to the wind (Shaw & Pereira 1982). Thus, in this type of canopy frictional drag and z_0 are low, which results in relatively large values for R_a , especially at low wind speeds.

Type 2 stands are grassy meadows such as the Deschampsietum. The erect leaves and a gradual increase in phytomass from the canopy surface to the ground have the following effects: (1) there is an almost linear decrease in light availability with canopy height; (2) the difference between maximum and minimum canopy temperature is only half the value observed for type 1; (3) even during the noon hours, leaf temperatures are lower than canopy temperatures. This negative leaf–air temperature difference is favoured by sufficient water and a high vpd (Jackson 1982; Idso *et al.* 1981).

Type 3 is represented by the Heracleum, the Rhododendretum and the Hordetum. In these plant stands the dominant species invest much of their photosynthates in stems which raise their largely horizontal leaves away from the soil surface, thus shading competitors. Similar structure and light use have been reported for a number of shrub communities in the Alps (Cernusca 1976; Tappeiner & Cernusca 1989a, 1991), as well as for tall herb communities in Kamtschatka (Morozov 1974; Morozov & Belaya 1988). The effects on microclimate are: (1) a high PPFD utilization by assimilatory plant components (Table 2); (2) a relatively small difference between maximum and minimum canopy temperature and a small soil heat flux; (3) in the uppermost centimetres of the foliage layer leaves fully exposed to sunlight heat up more than the ambient air; (4)

when the dense layer of the foliage is located close to the canopy surface, as in the case of the Rhododendretum, a very high normalized displacement height is to be expected (Shaw & Pereira 1982; Legg, Long & Zemroch 1981). Values for d/h as high as those found for the Rhododendretum have been reported for a number of forests where dense layers of foliage are also located close to the canopy surface (Jarvis *et al.* 1976).

Shaw & Pereira (1982) theoretically showed the effects of PAI and PAI distribution on wind profile parameters. The values of z_0/h in the stands investigated largely confirmed their model results. For example, the Rhododendretum in spite of a 40% lower PAI has the same normalized roughness length as the Heracleum, since the canopy is very dense near its surface and therefore displays a relatively smooth surface similar to a canopy with high PAI. The d/h values of all stands except the Rhododendretum were, however, 17 to 34% lower than the model values according to Shaw & Pereira (1982). A possible reason for this could be the model assumption of a triangular distribution of plant area density, which occurred only in the Rhododendretum and, to some extent, in the Heracleum.

Energy balance

The average values of LE / R_n observed for the pasture (0.58) are very similar to those reported by Cernusca & Seeber (1980) and Tappeiner & Cernusca (1994) for pastures in the Austrian and Italian Alps (0.53 to 0.61) and for a shortgrass prairie (0.5; Ripley & Redmann 1976), but lower than those (0.58 to 0.83) found for tallgrass prairies (Kim & Verma 1990; Fritschen & Qian 1992). Average values of LE / R_n observed for the other plant stands investigated (0.7 to 0.8) are comparable to those reported for hay meadows (0.71 to 0.74) in the Austrian and Italian Alps (Cernusca & Seeber 1980; Tappeiner & Cernusca 1994), and those (0.7 to 0.9) known for agricultural crops (Kim, Verma & Rosenberg 1989). The LE of the pasture, which is distinctly lower than that in the other canopies investigated, can be explained primarily by the low LAI. Moreover, the concentration of leaves close to the soil surface inhibits the exchange of water vapour, as is evident from the high value of R_a (Fig. 4).

Both the pasture and the Heracleum show a strong coupling between R_n and LE ; this has also been reported in a number of micrometeorological studies for well-watered grasslands and agricultural crops (Ripley & Redmann 1976; Baldocchi, Verma & Rosenberg 1985; Cernusca & Seeber 1989; Kim *et al.* 1989; Kim & Verma 1990). The other plant stands investigated are more comparable to forest canopies, where LE does not follow strictly the diurnal changes in R_n (McNaughton & Jarvis 1983; Verma *et al.* 1986; Valentini *et al.* 1991). The asymmetry in the diurnal courses of LE , H and β is not caused by differences in water supply, and the resultant stomatal reactions. This has been confirmed by ecophysiological measurements

(Sanadiradse, unpublished results). Rather, the asymmetry is caused by the diurnal course of v_{pd} and the higher degree of coupling of the canopies with the atmosphere (low Ω , see Table 2). The lower Ω values can be explained by the relatively low R_a values in these stands.

Mean noon values of R_a observed in this study (0.6–1.4 $\text{m}^2 \text{ s mol}^{-1}$) are slightly higher than those of grassland communities in the Alps (0.4–0.5 $\text{m}^2 \text{ s mol}^{-1}$; Cernusca & Seeber 1980), but are similar to those reported for a tallgrass prairie (0.4 to 3.4 $\text{m}^2 \text{ s mol}^{-1}$; Kim & Verma 1990) and lower than the range for grasslands (1.2 to 2.4 $\text{m}^2 \text{ s mol}^{-1}$) given by Jarvis (1981). Such differences are probably the result of differences in wind speed regimes and the aerodynamic roughness of the vegetation. Values of R_1 (1.3 to 2.0 $\text{m}^2 \text{ s mol}^{-1}$) for the grassland communities studied here are slightly lower than those for the grasslands in the Alps (1.8 to 2.5 $\text{m}^2 \text{ s mol}^{-1}$; Cernusca & Seeber 1980), but very similar to those of a tallgrass prairie (1.0–2.4 $\text{m}^2 \text{ s mol}^{-1}$; Kim & Verma 1990), whereas the lower values of the Rhododendretum and the Heracleum are comparable to those reported for agricultural crops (0.5–1.2 $\text{m}^2 \text{ s mol}^{-1}$; Jarvis 1981). All R_1 values except those for the pastures are below the critical value, defined by McNaughton & Spriggs (1989) as 60 s m^{-1} (1.8 $\text{m}^2 \text{ s mol}^{-1}$), which means that LE is primarily a function of equilibrium evaporation. Thus the classical Priestly & Taylor equation (Priestly & Taylor 1972) could be applied for large-scale estimation of LE of all canopies investigated except the pasture. The low R_1 values of the tall herb and dwarf shrub communities are caused by the low stomatal resistances of single leaves (Fig. 4). However, this is not true for the grass-dominated stands. Whereas the high R_1 of the pasture is correlated with a low r_1 , the comparatively low R_1 in the Deschampsietum is correlated with a high r_1 . This also explains why LE for the pasture was only 20% lower than that for the Deschampsietum, even though the leaf area of the Deschampsietum is more than twice as large: transpiration is facilitated by both lower boundary layer resistance and lower leaf resistance. This is in good agreement with ecophysiological investigations by Körner (1980), who observed that plants in a comparable pasture in the Caucasus transpire twice as much as plants in a hay meadow, on account of the much lower stomatal diffusion resistances.

Leaf resistances, as well as the coupling of the vegetation to the atmosphere, affect the WUE and CWFR of a canopy to a considerable extent (Baldocchi *et al.* 1981; Jarvis 1986). The values of CWFR observed in this study (0.9 to 2.1 mmol mol^{-1}) coincide with values measured by several authors in crops and in an oak-hickory forest (Baldocchi *et al.* 1981, 1985; Anderson *et al.* 1984; Verma *et al.* 1986). Because of complex interactions it is, however, difficult to compare the canopies investigated with respect to WUE. The Heracleum had the same mean WUE as the Deschampsietum, even though the former displayed the lowest and the latter the highest r_1 of all canopies investigated. This trend of stomatal resistance is opposed by the degree of coupling of the canopy with the atmosphere. A

well-coupled canopy has a higher WUE than a poorly coupled canopy with a similar structure (Jarvis 1986).

CO₂ exchange

The range of daily total soil respiration reported here (95.9–169.2 $\text{mmol m}^{-2} \text{ d}^{-1}$) is within the range of values obtained by us and other authors in grasslands and dwarf shrub communities in the Alps (81.8–247.7 $\text{mmol m}^{-2} \text{ d}^{-1}$; Cernusca & Decker 1989; Tappeiner & Cernusca 1994) and in temperate grasslands (38.1–169.1 $\text{mmol m}^{-2} \text{ d}^{-1}$; Ripley & Redmann 1976; 92–260 $\text{mmol m}^{-2} \text{ d}^{-1}$; Gale *et al.* 1990). The ratio R / F_c (7 to 19%, averaged between sunrise and sunset, with a maximum of 43% in certain hours) indicates that caution should be exercised when attempting to calculate the net carbon dioxide exchange of a plant stand from the CO₂ flux in the atmosphere alone (cf. also Denmead 1976; Gale *et al.* 1990).

The canopy photosynthesis of the subalpine grasslands reported in this study is, with the exception of the pasture, in good agreement with the mean value reported by Woledge & Parsons (1986) for temperate grasslands with a wide range of management and LAI (545 $\text{mmol m}^{-2} \text{ d}^{-1}$). The markedly lower value of daily total A_c on the pasture compares well with that of a shortgrass prairie in Canada (225 $\text{mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$, LAI=1.5; Ripley & Redmann 1978). The relationships between maximum A_c and maximum surface conductance G_s ($= 1/R_c$) in this study correspond very well with values in the literature and fit the regression calculated by Schulze *et al.* (1994), in a world-wide comparison of plant canopies.

The maximum values of F_c for the Heracleum (–24 $\mu\text{mol m}^{-2} \text{ s}^{-1}$), the Deschampsietum (–22 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) and the Hordetum (–19 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) are in the range reported by Kim & Verma (1990) for a tallgrass prairie during the peak growth stage (–13 to –30 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, LAI=3), but lower than those for crops such as alfalfa, wheat and soybean under similar environmental conditions (–22 to –45 $\mu\text{mol m}^{-2} \text{ s}^{-1}$; Baldocchi *et al.* 1981; Anderson *et al.* 1984; Wall & Kanemasu 1990; Baldocchi 1994b). The maximum values of F_c for the Rhododendretum (–13 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) and the pasture (–7 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) are comparable to those for a shortgrass prairie (–6 to –13 $\mu\text{mol m}^{-2} \text{ s}^{-1}$; Ripley & Redmann 1976, 1978) and a tallgrass prairie (–8 to –15 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) with low LAI (1.2–1.7; Gale *et al.* 1990).

Besides the LAI, the canopy structure plays an important role in determining the level of canopy photosynthesis; high canopy photosynthesis is achieved by a canopy structure that provides optimal capture and use of incident PPFD (Woledge & Parsons 1986; Wall & Kanemasu 1990). This conclusion is strongly supported by our investigations. A comparison of the canopy photosynthesis, on a leaf area basis (A_c/LAI), of all canopies investigated shows clearly that canopies of type 3 (Heracleum, Rhododendretum and Hordetum) exhibit a somewhat higher canopy photosynthesis per leaf area (108 to 122 $\text{mmol m}^{-2} \text{ d}^{-1}$) than the canopies of types 1 and 2

($A_c/LAI \sim 85 \text{ mmol m}^{-2} \text{ d}^{-1}$). This is probably an effect of canopy structure rather than of differences in the ecophysiology of species in the stands investigated. For example, the leaves of *Rhododendron caucasicum*, which is the dominant species of the Rhododendretum, have a mean photosynthetic capacity of only $6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and are light-saturated at a PPFD of $900 \mu\text{mol m}^{-2} \text{ s}^{-1}$, while the dominant species of the Deschampsietum, *Deschampsia cespitosa* and *Equisetum palustre*, have a mean photosynthetic capacity of 10 and $11 \mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively, and saturate at a PPFD of more than $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Tapeiner 1996).

In conclusion, canopy structure was found to have decisive effects on microclimate, photosynthetic light use, CO₂ exchange and surface resistances. Structure affects the energy budget mainly via the LAI and indirectly via the degree of coupling of the canopy to the atmosphere.

ACKNOWLEDGMENTS

This study was supported by the Austrian Academy of Science. Our sincere thanks are due to G. Nakhutsrishvili and his staff for their support and assistance during our investigations in the Caucasus and to Paul G. Jarvis and two anonymous referees for their valuable comments on this paper.

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Received 17 January 1995; received in revised form 27 July 1995; accepted for publication 15 August 1995

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