ELSEVIER

Ecological Modelling 113 (1998) 201–223

ECOLOGICAL MODELLING

Model simulation of spatial distribution of photosynthesis in structurally differing plant communities in the Central Caucasus

Ulrike Tappeiner *, Alexander Cernusca

Institut für Botanik der Universität Innsbruck, Sternwartestr. 15, A-6020 Innsbruck, Austria

---

Abstract

The aim of the present study was to investigate the significance of structural properties for whole canopy photosynthesis (A_{can}). Effects of both classical parameters of canopy structure (vertical distribution of leaf area, plant area and leaf inclination) and of leaf dispersion on A_{can} were analysed by means of a relatively simple canopy photosynthesis model. This model was designed for photosynthetic input parameters based on measured field parameters. Eight structurally different species-rich seminatural and natural plant communities (used and abandoned pastures, hay meadows, tall herbs and dwarf shrubs) in the subalpine belt of the Central Caucasus were investigated. The validation by means of a micrometeorological approach showed that the estimate of A_{can} in the model corresponds well with the measurements in very differently structured, species-rich plant communities. Simulations showed that the significance of canopy properties for canopy photosynthesis essentially depends on the vertical distribution of the leaf area. Therefore this parameter was used for classifying the canopies investigated. Three types of canopies could be distinguished: type 1 with the leaf area amassed near the soil surface and the structural shape of a pyramid with a broad base; type 2 with a gradual increase in leaf area from the canopy surface to the ground (pyramid with a narrow base) and type 3 with a concentration of the leaf area in the upper canopy (inverted pyramid). The significance of the structural properties for A_{can} increases from type 1 to type 3 and is higher when the stand is dominated by a single species. In stands of type 1 canopy structure did not limit A_{can} via light climate, but rather by temperature effects. In stands of type 2 and type 3, mutual shading is an important limiting factor for canopy photosynthesis, but the structural properties of type 3 stands are better optimized for A_{can}. Simulations with assumed equal leaf area index and photosynthetic characteristics showed that in canopies of type 3 the structural properties (leaf inclination, leaf dispersion) are such that the major part of the leaf area in the canopy is supplied with intermediate photosynthetic photon flux densities, thus increasing daily total A_{can}. Sensitivity analysis of A_{can} to non-random leaf dispersions showed effects especially in stands of type 2 and type 3. Clumped leaf dispersions resulted in better light utilization and higher A_{can}. When compared with the leaf dispersions measured in the canopies, the simulation results show that the canopies optimize leaf dispersion with respect to A_{can}. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Canopy structure effects; Dwarf shrub community; Grassland; Leaf area index; Light climate; Non-random leaf dispersion; Tall herb community

---

* Corresponding author. Tel.: +43 512 5075923; fax: +43 512 5072975; e-mail: ulrike.tappeiner@uibk.ac.at

PII S0304-3800(98)00144-6

1. Introduction

Considerable attention has been paid to the relationship between canopy architecture, light interception and photosynthesis since the pioneering work of Monsi and Saeki (1953), de Wit (1965), Duncan et al. (1967). The interactions between canopy structure and function are rather complex, particularly in natural species-rich plant communities (Hesketh and Jones 1980) and can only be assessed by a combination of selected measurements and sufficiently detailed simulations (Caldwell et al., 1986; Tappeiner and Cernusca, 1991).

Many detailed canopy models for homogeneous, continuous canopies (Duncan et al., 1967; Caldwell et al., 1986; Gutschick and Wiegel, 1988; Ryel et al., 1990; Wall and Kanemasu, 1990; Kim and Verma, 1991; De Pury and Farquhar, 1997), for isolated tussocks (Ryel et al., 1993) and for forest canopies (Oker-Blom and Kellomäki, 1982; Grace et al., 1987; Wang and Jarvis, 1990; Leuning et al., 1991; Harley and Baldocchi, 1995) have been developed. They have mostly been applied for single-species canopies. Only few analyses have been performed on mixed-species canopies consisting of two to three species (McMurtrie and Wolf, 1983; Rimmington, 1984; Barnes et al., 1990; Beyschlag et al., 1990). Simulation of whole canopy photosynthesis of natural species-rich plant communities are rare (Kim and Verma, 1991; Tappeiner and Cernusca, 1991). No detailed model assessments of canopy structure effects on canopy photosynthesis have been reported for such stands. This study aims at such a comparative analysis of structurally differing natural mixed-species plant communities. The model consists of an integrated light interception sub-model, based on the classical gap probability approach (Monsi and Saeki, 1953). It includes refinements such as the partitioning of solar radiation into direct beam and diffuse light, varying leaf-angle distribution, non-randomness in leaf dispersion and a phenomenological photosynthesis submodel (Forseth and Norman, 1993). Model predictions are validated at the canopy level using a micrometeorological approach. A methodological aim of the study is to test if and to what extent causal analyses of canopy structure effects in species-rich plant communities are possible by applying relatively simple modelling techniques.

Studies of the CO_2 and energy exchange between the planetary boundary layer and the canopy in the subalpine belt of the Central Caucasus revealed considerable effects of canopy structure on microclimate and energy budget (Tappeiner and Cernusca, 1996). The results from this study and from earlier ones (Salisbury and Spomer, 1964; Cernusca, 1976; Larcher, 1984; Cernusca, 1991) indicate that the density of a canopy as well as accumulation of attached dead material enhance the development of a warm microenvironment that is favourable for dry matter production in mountain ecosystems. On the other hand, the same canopy attributes decrease light availability and therefore may reduce carbon gain. Tappeiner and Cernusca (1996) observed pronounced differences in the CO_2 flux of the investigated plant communities, which, however, could not be explained causally on the basis of the available microclimate measurements. Therefore, in this paper such an analysis is attempted by means of a detailed canopy model.

A further topic to be treated in this paper is not restricted to alpine habitats and is concerned with the effects of non-randomness in leaf dispersion on canopy photosynthesis. Clumped leaf dispersion has been reported for many natural plant communities (Monsi et al., 1973; Ross, 1981; Caldwell et al., 1986; Tappeiner and Cernusca, 1989a). Even though its effects on the light climate within canopies are considerable (Acock et al., 1970), its consequences for canopy photosynthesis are largely unknown (Jarvis and Leverenz, 1983). To address this question a leaf dispersion factor for each canopy layer was included in the model. Carbon gain modelled with observed leaf dispersion relative to various hypothetical dispersions is discussed.

We compare differently structured plant communities in the Central Caucasus on the basis of empirical investigations and a whole canopy photosynthesis model. The general objective is to analyse the effects of canopy structure attributes on canopy photosynthesis. Specific attention is paid to the effects of vertical distribution of structural characteristics, of an accumulation of necromass and of non-random leaf dispersions.

2. Materials and methods

2.1. Sites investigated

The study was conducted in the subalpine belt of the northern slope of the Great Caucasus in the surroundings of the Mountain Research Station Kasbegi of the Georgian Academy of Sciences (Lat 42° 48′N, Long 44° 39′E, altitude 1850 m a.s.l.). Measurements were made during late July and early August 1987, 1988, 1989 and 1990. The following differently structured plant communities were investigated (Table 1): (1) Heavily stocked sheep pasture (HP) with *Festuca rupicola*, *Pulsatilla violacea* and *Carex buschiorum* as the dominant species; (2) Lightly stocked sheep pasture (LP), dominated by *Nardus stricta*, *Carex tristis* and *Ranunculus oreophilus;* (3) Abandoned pasture (AP), dominated by *Festuca woronowii* and *Carex meinshauseniana;* (4) Wet meadow (WM) with *Deschampsia cespitosa* and *Equisetum palustre* as the dominant species, and interspersed with *Phragmites australis;* (5) Hay meadow (HM), dominated by grasses, such as *Hordeum violaceum* and *Poa pratensis* and tall herbaceous species, such as *Anthriscus nemorosa*, *Seseli transcaucasica* and *Heracleum asperum;* (6) Tall herb community (TH) dominated by *Heracleum sosnowskyi*, with an undergrowth consisting only of seven further species; (7) Evergreen *Rhododendron* shrub community (RC), dominated by *Rhododendron caucasicum*, with a very sparse undergrowth mainly consisting of *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Empetrum hermaphroditum;* (8) Deciduous *Rhododendron* shrub community (RL), dominated by *Rhododendron luteum*. A sparse undergrowth mainly consisting of *Festuca rubra* and *Brachypodium sylvaticum* is also present.

During the experimental periods the stands investigated were well supplied with water from precipitation prior to and during the investigation period. Soil water potentials were between -60 and -290 hPa in the main rooting horizon.

2.2. Measurements

The canopy structure of each community was analysed by the stratified clipping method (Monsi and Saeki, 1953) which consisted of harvesting, layer by layer, the above-ground vegetation. Van Dyne et al. (1963), Fliervoet (1984) showed that for a quantitative analysis of the vertical structure of above-ground phytomass of grasslands and tall herb communities, plots (0.25–1 m^2) much smaller than the floristic minimum area are sufficient. Thus, for each stand a representative plot of 1 m^2 was harvested. In order to test to what extent such a plot is representative for the shrub communities two plots were harvested in the RC stand. The results differed by less than 8%. In all harvested plots for each species in each layer the dry mass as well as the area of stems, leaves, inflorescences or fruits and dead plant material were measured. The areas were determined by means of a leaf area meter (LI-3100, LI-COR, Lincoln USA). Leaf area index LAI (= area of leaves per unit ground area, $m^2\ m^{-2}$), plant area index PAI (= area of all above-ground plant parts per unit ground area, $m^2\ m^{-2}$) and plant area density PAD (= area of all above-ground plant parts per unit volume of the canopy, $m^2\ m^{-3}$) were calculated from these measurements.

Field measurements of leaf and stem inclination of the dominant species in each layer were made with a hand inclinometer. Approximately 100 measurements were made for each species in each layer. A total of 35 species was analysed with respect to the inclination of their leaves and axes. For each species the mean leaf and stem inclination and the respective relative variance in 10° classes per layer were calculated, each of the angles measured being weighted with the leaf (stem) area. The mean inclination angle per canopy layer was calculated as a weighted average of the inclination angles of the constituent species where the weighting factors were the relative plant area indices in the respective layer. This procedure is aimed at allowing for the situation encountered in plant stands consisting of a large number of different species, and even differing in species composition from layer to layer. The leaf inclination index x_L was calculated according to Ross

Table 1
Relevant characteristics of the sites investigated in the Central Caucasus

	HP	LP	AP	WM	HM	TH	RC	RL
General characteristics								
Altitude (m a.s.l.)	2050	2350	2000	1750	1850	2200	2200	2200
Exposure	SW	SSW	SW	—	—	N	NNW	SW
Type of management	Heavily stocked sheep pasture	Lightly stocked sheep pasture	Abandoned pasture	Mowed every two years	Mowed once a year	Harvested for silage	—	—
Canopy height (cm)								
Inflorescences	18	12	40	50	120	240	50	100
Leaves	8	8	28	46	80	170	50	110
Degree of cover (%)	80	100	100	100	100	100	100	100
Canopy structure								
Biomass (g DM·m^{-2})	164	231	223	369	580	674	1817	3185
Necromass (g DM·m^{-2})	55	94	468	58	78	94	76	45
Litter (g DM m^{-2})	92	448	447	44	132	70	1066	539
LAI (m^2 m^{-2})	2.4	4.2	2.5	5.8	5.4	6.2	3.8	4.8
PAI (m^2 m^{-2})	3.1	5.7	8.5	6.7	8.4	8.1	4.7	6.9
Mean canopy inclination (°)	47 ± 28	51 ± 26	65 ± 15	66 ± 26	41 ± 20	29 ± 24	36 ± 20	37 ± 22
Inclination index x_L	0.19	0.16	−0.14	−0.26	0.37	0.54	0.39	0.37
Mean dispersion factor *d*	0.93 ± 0.29	1.05 ± 0.27	0.90 ± 0.13	0.75 ± 0.21	0.73 ± 0.24	1.21 ± 0.67	1.03 ± 0.46	0.95 ± 0.41
Leaf layer					0.54 ± 0.21	0.68 ± 0.09	0.75 ± 0.16	0.68 ± 0.26
Stem layer					0.88 ± 0.10	1.99 ± 0.35	1.26 ± 0.54	1.17 ± 0.29

Measurements were taken in the main flowering periods between 1987 and 1990. For some parameters the standard deviation is given.

HP, heavily stocked pasture; LP, lightly stocked pasture; AP, abandoned pasture; WM, wet meadow; HM, hay meadow; TH, tall herb community; RC, evergreen *Rhododendron* shrub community; RL, deciduous *Rhododendron* shrub community; DM, dry matter; LAI, leaf area index (area of leaves per unit ground area); GAI, green area index (area of assimilating parts of plants per unit ground area); PAI, plant area index (area of all above-ground plant parts per unit ground area).

(1981), and ranges from $+0.6$ (purely horizontal leaves) to -0.4 (purely vertical leaves).

In situ measurements of photosynthetic response to photosynthetic photon flux density (PPFD) were made on the dominant species using a portable, differential gas exchange-system (LCA-2, ADC, Hoddesdon, England). Additionally, the in situ photosynthetic response to temperature was recorded for the dominant species, using a small temperature-controlled glass cuvette (Körner, 1977) and a battery-driven IRGA (BINOS 1, Fa. Leybold–Heraeus, Hanau, Germany). Measurements were carried out at the ambient CO_2–concentrations prevailing at the experimental sites. Gas exchange rates were calculated according to von von Caemmerer and Farquhar (1981) and expressed on a projected leaf area basis.

The parameterisation of the model was carried out using a series of micrometeorological measurements (leaf temperature, incident PPFD). Validation of the model at the canopy level was achieved by a micrometeorological approach, the Bowen-ratio energy-balance (BREB) method (Norman and Hesketh, 1980). In contrast to the cuvette methods, which are commonly used for validation (Hesketh and Jones, 1980), the BREB method causes minimal disturbance and provides fluxes integrated over larger areas (Kim and Verma, 1991). The theory and operation of our BREB-system is described in detail elsewhere (Tappeiner and Cernusca, 1996). Briefly, profiles of soil, air and leaf temperature, of direct and diffuse PPFD, air humidity and CO_2 concentration, within and above the canopy, as well as soil water potential and net radiation, were measured using a portable battery-powered data acquisition system. Calculations of water vapour flux, sensible heat flux and carbon dioxide flux were done using profiles of temperature, water vapour pressure and CO_2 concentration measured at two heights (0.1 and 1.5 m) above the canopy. The BREB measurement of atmospheric CO_2 flux provides the sum of canopy and soil (plus root) CO_2 fluxes. Therefore an estimation of soil (plus root) CO_2 flux is necessary for the computation of canopy photosynthesis. Release of CO_2 from the soil was measured *in situ* by IRGA techniques (for details on the method see Cernusca and Decker, 1989). The whole apparent canopy photosynthesis (A_{can}) results from the difference of the CO_2 flux from the atmosphere and the CO_2 output of the soil (for details see Cernusca, 1982; Tappeiner and Cernusca, 1996).

2.3. Model description

The model consists of integrated light interception and photosynthesis sub-models. A detailed description of the light interception part is given in Tappeiner and Cernusca (1989a, 1991) and only a brief outline is presented here. Penetration of direct and diffuse PPFD is assessed by dividing the canopy into layers, where the leaf and stem surface areas and frequency distribution of inclination angles represent the measured canopy structure for each layer. A gap-probability calculation approach following Monsi and Saeki (1953), Warren Wilson (1960), Duncan et al. (1967) is used to compute both the penetration of direct PPFD into the canopy and the sunlit fraction of leaves (Eq. (1)). In contrast to the classical gap probability function, a non-random dispersion of leaves in the canopy space (i.e. the grouping of foliage, Jarvis and Leverenz, 1983) is taken into account by a dispersion factor (d_i) for each layer, as described in Tappeiner and Cernusca (1991). Independent data sets were used for the calculation of the dispersion factor and the subsequent validation of the light sub-model. Diffuse PPFD penetration into the canopy is calculated in a manner analogous to that for the direct beam. Uniform sky brightness with nine concentric sky bands as the source of diffuse PPFD is assumed. Diffuse PPFD penetration from the different sky segments is calculated and then integrated for the entire sky hemisphere (Duncan et al., 1967). PPFD interception by the leaves of the dominant species is calculated, taking into account the measured frequency curve of inclination in the single layers (Anderson and Denmead, 1969) as well as the diffuse radiation that has been transmitted through and reflected from surrounding foliage according to Caldwell et al. (1986). Sunlit and shaded leaves at each depth are treated separately.

Table 2

Parameter estimates for the photosynthesis sub-model[1,2] of the dominant species of the investigated stands. Parameterisation is based on measurements during the main flowering period. For all species investigated light and temperature response curves were measured for at least 20 and five leaves, respectively.

Species	Φ(mol mol^{-1})	$A_{sat} \pm$ S.E. (μmol m^{-2} s^{-1})	R_d (μmol m^{-2} s^{-1})	r^2	T_{opt} (°C)	a (·10^{-3})	b (·10^{-4})	r^2
Heavily stocked pasture (HP)								
*Festuca rupicola**	0.0172	7.5 ± 1.8	−1.28	0.98	21.8	−4.85	1.23	0.75
Carex buschiorum	0.0185	6.9 ± 2.5	−0.96	0.92	21.2	−4.51	1.17	0.79
Koeleria caucasica	0.0147	10.5 ± 1.1	−0.91	0.82	21.0	−4.93	2.19	0.80
*Pulsatilla violacea**	0.0202	16.1 ± 2.6	−1.57	0.98	22.8	−4.77	1.23	0.78
Alchemilla sericata	0.0211	17.5 ± 2.9	−1.45	0.89	21.8	−3.86	1.22	0.85
Leontodon hispidus	0.0202	18.6 ± 2.4	−1.50	0.94	21.9	−4.82	1.36	0.87
Ranunculus oreophilus	0.0171	15.8 ± 1.9	−1.55	0.95	21.5	−4.90	1.17	0.81
Lightly stocked pasture (LP)								
Nardus stricta	0.0200	13.2 ± 2.6	−1.67	0.79	23.9	−3.01	1.21	0.88
*Agrostis planifolia**	0.0379	8.5 ± 1.7	−1.20	0.96	23.2	−3.51	1.04	0.87
Carex tristis	0.0157	9.4 ± 2.1	−1.46	0.73	24.3	−3.32	0.97	0.90
Alchemilla retinervis	0.0143	11.1 ± 1.2	−0.83	0.90	23.8	−3.50	2.13	0.91
Leontodon danubialis	0.0225	9.8 ± 2.0	−0.85	0.82	23.2	−3.33	1.85	0.89
*Plantago caucasica**	0.0287	14.9 ± 1.8	−2.46	0.94	22.4	−4.35	1.38	0.92
Ranunculus oreophilus	0.0166	11.2 ± 2.0	−0.76	0.85	23.5	−3.62	1.61	0.94
Trifolium ambiguum	0.0167	18.1 ± 3.6	−0.95	0.94	23.6	−3.51	0.82	0.96
Abandoned pasture (AP)								
*Festuca woronowii**	0.0247	11.0 ± 1.2	−0.92	0.95	21.4	−5.32	0.91	0.99
Carex meinshauseniana	0.0229	6.6 ± 1.3	−0.92	0.96	21.1	−4.76	1.25	0.95
*Betonica macrantha**	0.0212	6.6 ± 2.0	−0.85	0.85	20.8	−4.64	0.83	0.95
Polygonum carneum	0.0291	19.6 ± 2.2	−1.02	0.97	20.3	−4.55	1.42	0.85
Wet meadow (WM)								
*Deschampsia cespitosa**	0.0191	10.1 ± 1.1	−1.23	0.96	22.3	−4.01	1.14	0.90
Equisetum palustre	0.0207	10.8 ± 1.7	−1.70	0.92	22.5	−4.02	1.22	0.90
Ranunculus elegans	0.0352	15.1 ± 1.6	−1.03	0.96	22.0	−4.10	0	0.89
Ligularia sibirica	0.0291	5.7 ± 1.4	−0.99	0.86	21.9	−3.82	1.01	0.93
*Gladiolus caucasica**	0.0206	7.3 ± 1.5	−1.64	0.91	22.7	−4.28	2.02	0.93
Hay meadow (HM)								
*Hordeum violaceum**	0.0198	8.1 ± 1.4	−1.16	0.94	20.9	−4.61	0.91	0.82
Festuca pratensis	0.0198	11.4 ± 2.1	−0.98	0.81	20.7	−4.51	1.50	0.90
Poa pratensis	0.0197	8.2 ± 2.0	−1.22	0.95	21.2	−4.78	1.22	0.91
Seseli transcaucasica	0.0273	13.9 ± 0.8	−1.33	0.96	19.9	−3.87	1.01	0.99
*Trifolium ambiguum**	0.0265	12.8 ± 1.2	−0.93	0.96	22.0	−4.52	1.10	0.76
Tall herb community (TH)								
Heracleum sosnowskyi 110–160 cm	0.0407	15.8 ± 3.7	−1.62	0.84	23.9	−3.71	0	0.96
H. sosnowskyi 80–110 cm	0.0295	8.7 ± 1.7	−0.87	0.90	20.2	−3.65	1.01	0.94
H. sosnowskyi 40 –80 cm*	0.0325	5.6 ± 0.7	−0.77	0.94	19.8	−3.50	1.11	0.90
*Alchemilla sp.**	0.0288	3.8 ± 0.4	−0.76	0.99	16.5	−4.12	1.65	0.89

Table 2 (*continued*)

Species	Φ(mol mol^{-1})	A_{sat} ± S.E. (μmol m^{-2} s^{-1})	R_d (μmol m^{-2} s$^{-1)}$	r^2	T_{opt} (°C)	a (·10^{-3})	b (·10^{-4})	r^2
Evergreen *Rhododendron* shrub community (RC)								
Rh. caucasicum 40–60 cm	0.0254	6.3 ± 0.9	−1.13	0.88	19.7	−2.88	1.20	0.85
Rh. caucasicum 20–40 cm	0.0258	5.6 ± 2.1	−0.81	0.98	18.9	−2.73	1.81	0.91
*Vaccinium myrtillus**	0.0210	3.1 ± 0.8	−0.42	0.99	18.6	−2.36	1.50	0.88
Deciduous *Rhododendron* shrub community (RL)								
Rh. luteum 90–110 cm	0.0337	7.5 ± 0.9	−1.09	0.85	19.8	−5.20	1.23	0.83
Rh. luteum 70–90 cm	0.0324	7.1 ± 0.6	−0.95	0.94	18.9	−5.11	1.17	0.78
Rh. luteum 50–70 cm	0.0284	5.7 ± 0.7	−0.65	0.83	18.7	−5.01	0.92	0.83
*Campanula collina**	0.0289	2.8 ± 0.7	−0.83	0.98	17.9	−4.31	1.71	0.86
*Festuca rubra**	0.0193	4.7 ± 0.3	−1.04	0.92	18.3	−4.12	1.50	0.85

[1] Model used to fit photosynthetic response to light: $A = \Phi \mathrm{PPFD}/(1+\Phi^2\mathrm{PPFD}^2/(A_{sat}-R_d)^2)^{1/2}+R_d$, where A is the photosynthetic CO_2 fixation, Φ the slope of the linear proportion of the light response curve, A_{sat} the light saturated photosynthetic rate and R_d the day respiration at 23°C.

[2] Model used to fit photosynthetic response to temperature: $p=(a(T_l-T_{opt})^2)+(b(|T_l-T_{opt}|))+1$, where p is the proportion of A_{sat}(0–1), T_l the leaf temperature and T_{opt} the photosynthetic temperature optimum.

* Averaged response curves used for less abundant species.

Simulated PPFD values and measured leaf temperature values enter the photosynthesis submodel. Single-leaf photosynthesis is predicted by a phenomenological model of leaf photosynthetic response to light and temperature similar to the approach of Forseth and Norman (1993). Photosynthetic response to light of a single leaf was approximated with the relationship (Tenhunen et al., 1987):

$$A = \Phi \mathrm{PPFD}/(1 + \Phi^2\mathrm{PPFD}^2/(A_{sat} - R_d)^2)^{1/2} + R_d \quad (1)$$

where A is the photosynthetic CO_2 fixation, Φ the slope of the linear proportion of the light response curve (mol CO_2 per mol incident photons), A_{sat} the light saturated photosynthetic rate and R_d the interception with the y-axis, which can be denoted as day respiration for the temperature given during the measurements. To estimate R_d at other temperatures, an exponential relationship between R_d and temperature was developed from data for *Rhododendron ferrugineum* (Siegwolf, 1987) and *Ranunculus acris* (Diemer, 1990). This relationship was adjusted by using R_d derived from the light response curves measured at 23°C for the dominant species.

The photosynthetic response to temperature was described by:

$$p = (a(T_l - T_{opt})^2) + (b(|T_l - T_{opt}|)) + 1 \quad \text{with } 0 \leq p \leq 1 \quad (2)$$

where p is the actual rate of photosynthesis relative to A_{sat} (1), T_l the leaf temperature and T_{opt} the photosynthetic temperature optimum.

Model parameters for the dominant species were derived from *in situ* gas exchange measurements and are listed in Table 2. The less abundant species, whose photosynthetic responses were not measured, were classified as grasses or herbs and for each of these groups averaged response curves of the dominant species in the corresponding communities were used for the simulation. These species did not contribute more than 17% to total LAI. For the dwarf shrub communities where stems contribute much more to PAI (25%) than in the investigated grasslands (0.5–5%) the model accounts for the CO_2 uptake and release of stems. Since the photosynthetic responses of stems were not measured in this study, data for the green and brown axes of a closely related shrub species, *Rhododendron ferrugineum*, (Siegwolf, 1987) were used.

The scaling from leaf to canopy level was done by serially integrating the photosynthetic rates of sunlit and shaded leaves (and stems in the dwarf shrub communities) for each species and layer, weighting by the corresponding fractions of sunlit and shaded leaf (and stem) areas:

$$A_{\mathrm{can}} = \sum_{i=1}^{l} \sum_{k=1}^{s} (L_{\mathrm{sun},k,i} \times A_{\mathrm{sun},k,i} + L_{\mathrm{shade},k,i} \times A_{\mathrm{shade},k,i}) \quad (3)$$

where A_{can} is the whole canopy photosynthesis, L_{sun} and L_{shade} are the sunlit and shaded leaf (and stem) area indices, respectively and A_{sun} and A_{shade} are the photosynthetic rate of sunlit and shaded leaves, respectively. The subscripts i and k represent the layer and species, respectively, whereas l and s represent the total number of layers and the total number of species, respectively.

3. Results

3.1. Canopy structure

The stands cover a considerable range of diversities from a 2.4 m high tall herb community with a LAI of 6.2 to a pasture with a maximum height of only 0.18 m and a LAI of 2.4 (Table 1). The diversity in canopy structure of the eight stands is depicted in Fig. 1(a and b). In the grazed communities (HP, LP) two thirds of the phytomass were contained in the lowest 3 cm. Leaf inclination showed an increase with canopy height, the grass leaves with a steep angle of inclination being predominant in the upper half of the canopy. The AP and WM stands showed a more gradual decrease in phytomass with increasing canopy height, with a substantial fraction of necromass (68%) in the abandoned pasture. Both communities formed typically erectophile canopies ($x_L = -0.14$ and -0.26). In the HM more than 80% of the phytomass were distributed quite evenly in the lowest 40 cm of the canopy, with the planophile leaves of the tall herbaceous species dominating between 40 and 20 cm. In the other three stands (TH, RC, RL) canopy structure was characteristically two-layered: the upper half almost contained the entire photosynthetically active leaf surface, while the underlying layer consisted of photosynthetically inactive stems. The TH stand was characterized by strong planophile tendencies ($x_l = 0.54$) and the two dwarf shrub stands (RC, RL) also showed rather small leaf inclination angles.

The mean dispersion factor (d) given in Table 1 compares the stands with respect to spatial arrangement of plant parts: d ranges from 0 (clumped dispersion) to 1 (random dispersion) and 2 (regular dispersion). The RL, RC and TH communities showed a markedly clumped dispersion in the leaf layer and a regular dispersion in the stem layer. The HM and WM stands were characterized by a clumped arrangement of leaves in all canopy layers, which was particularly pronounced in the upper half of the canopy of the HM. The other canopies displayed random dispersion of plant parts.

3.2. Leaf based photosynthetic characteristics of dominant species

The photosynthetic characteristics used in the model (Table 2) were estimated on the basis of *in situ* measurements of PPFD and temperature responses of photosynthesis of the dominant species. Both Φ and A_{sat} considerably varied between the species investigated. As shown by Ehleringer and Björkman (1977), Φ of C_3 plants is dependent on CO_2 and temperature. The comparatively low Φ values of the species investigated (0.014–0.04 mol mol^{-1}) may have resulted from the low CO_2 partial pressure due to elevation (mean intercellular $CO_2 = 17 \pm 1.9$ Pa) and the comparatively high temperatures prevailing during measurements (23–26°C). Light saturated photosynthetic rates of the investigated species are in the range reported for the same genera and species growing under similar environmental conditions (Sawada and Sugai, 1984; Atkinson, 1986; Woledge and Parsons, 1986; Körner and Diemer, 1987; Siegwolf, 1987; Abdaladse, 1988; Gloser, 1993; Abdaladse, 1994; Karlsson, 1994). The different A_{sat}

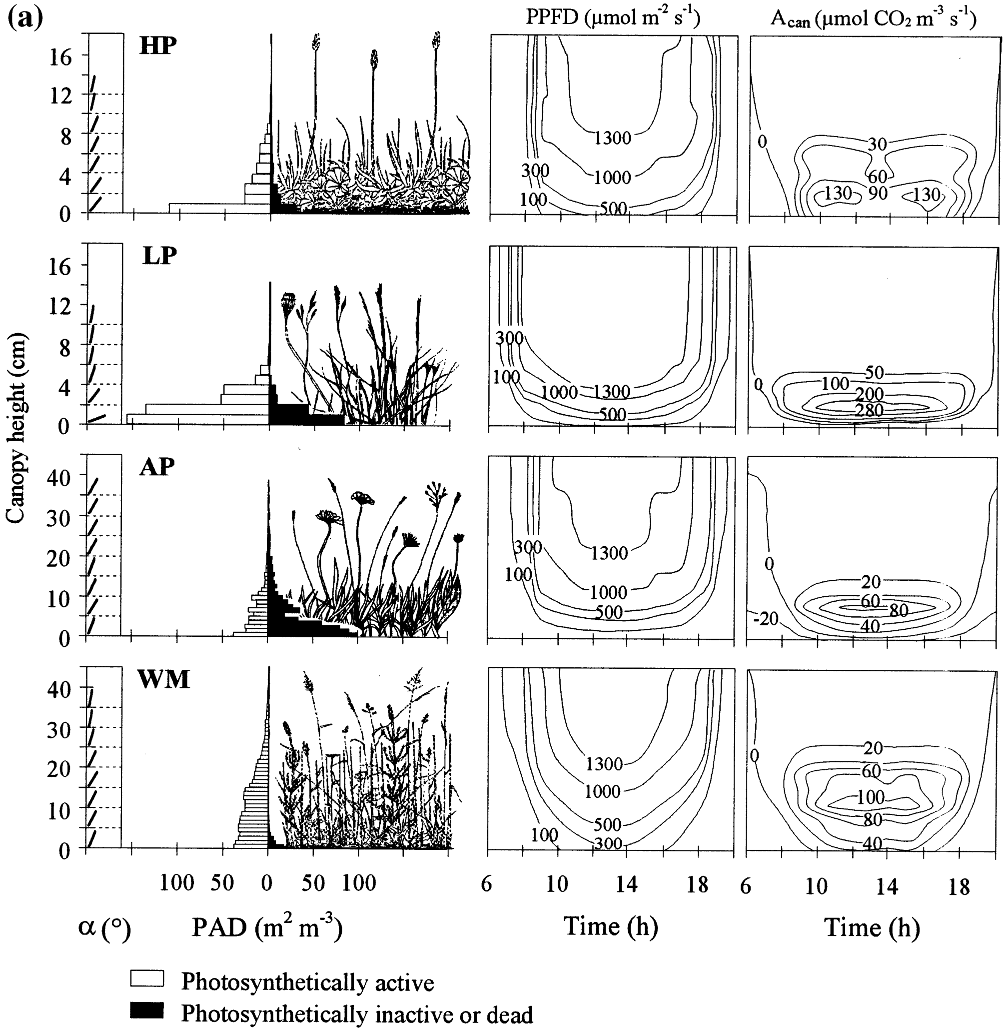

Fig. 1. (a) Stratification of plant area density (PAD), mean leaf inclination angle α (left), contours of simulated photosynthetic photon flux density interception (PPFD) on inclined leaf surface (middle) and contours of simulated apparent canopy photosynthesis (A_{can}) expressed on a volume basis (μmol CO_2 m^{-3} s^{-1}) (right) for the plant communities investigated in the Central Caucasus. For model input a typical diurnal course of microclimatic data for a clear day at the end of July was chosen. Experimental sites: HP, heavily stocked pasture; LP, lightly stocked pasture; AP, abandoned pasture; WM, wet meadow. (b) Experimental sites: HM, hay meadow; TH, tall herb community; RC, evergreen *Rhododendron* shrub community; RL, deciduous *Rhodododendron* shrub community.

values primarily reflect the phenotypic adaptation of the species to the prevailing light climate in the different canopy layers. For example, A_{sat} of *Trifolium ambiguum* is about one third higher in the LP than in the HM, since in the former stand the leaves are mainly situated in layers of higher light availability than in the HM. The tendency of A_{sat} to decrease with a decreasing canopy height could also be clearly observed with *Heracleum sosnowskyi*, *Rh. caucasicum* and *Rh. luteum*. Furthermore, there was a significant correlation between A_{sat} and leaf weight per area (LWA) of all species investigated ($A_{sat} = -3.18 + 0.398$ LWA, $r^2 = 0.69$; data not shown). Since LWA reflects the

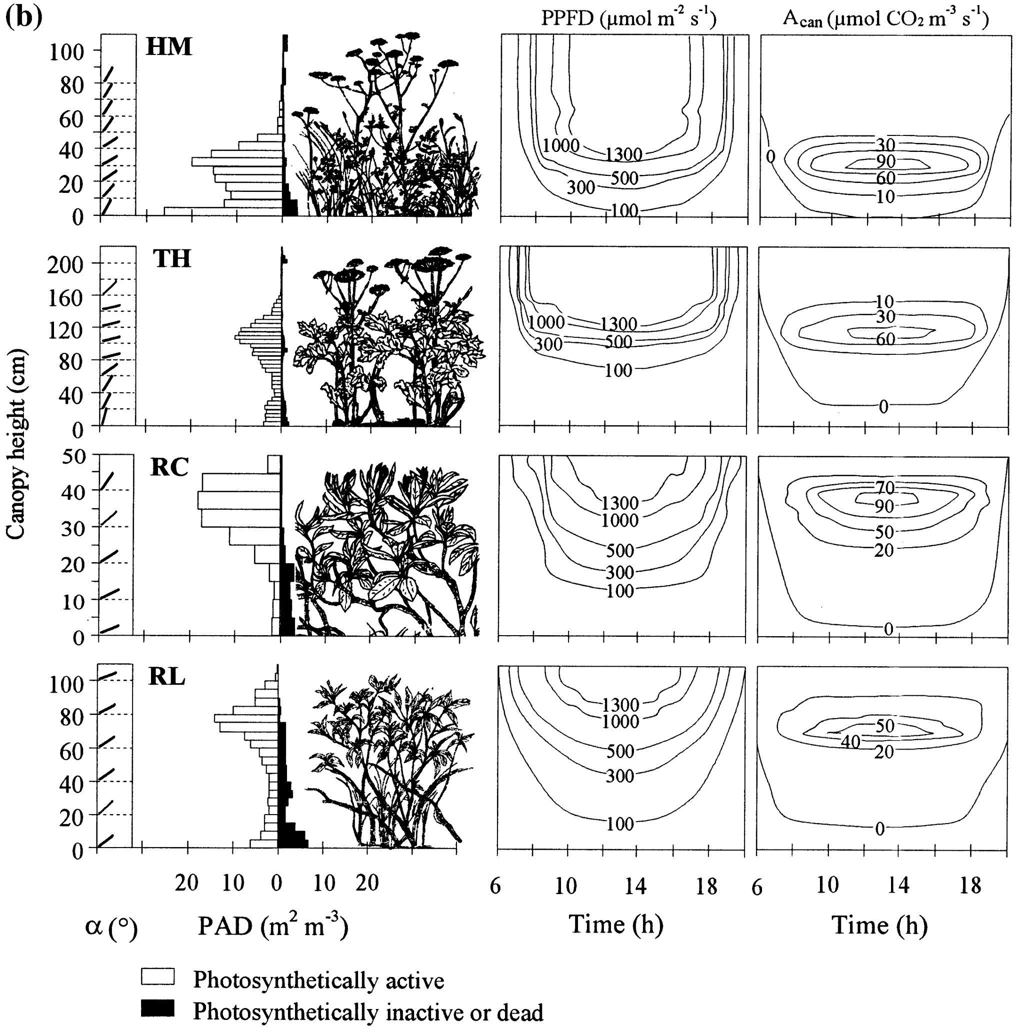

Fig. 1. (*continued*)

prevailing level of photosynthetically active radiation (Björkmann, 1981) this result supports the assumption of an adaptation to the prevailing light climate.

3.3. Model validation

Model results were compared against the measurements of whole canopy CO_2 gas exchange for selected clear days. The measured diurnal courses of environmental conditions (PPFD, leaf temperatures) of these days were used as input values for the model. Results are shown in Fig. 2. Correspondence between the model and measurements was very good in all investigated stands. Only in the HP there was an increasing overestimation of A_{can} by the model observed in the course of the day. This could be caused by limitations related to plant water relations, which are not considered in the model. Control measurements with a porometer revealed reductions in leaf conductance of up to 40% in the upper canopy layers of the HP stand in the early afternoon (Sanadiradze and Kuradze, 1990).

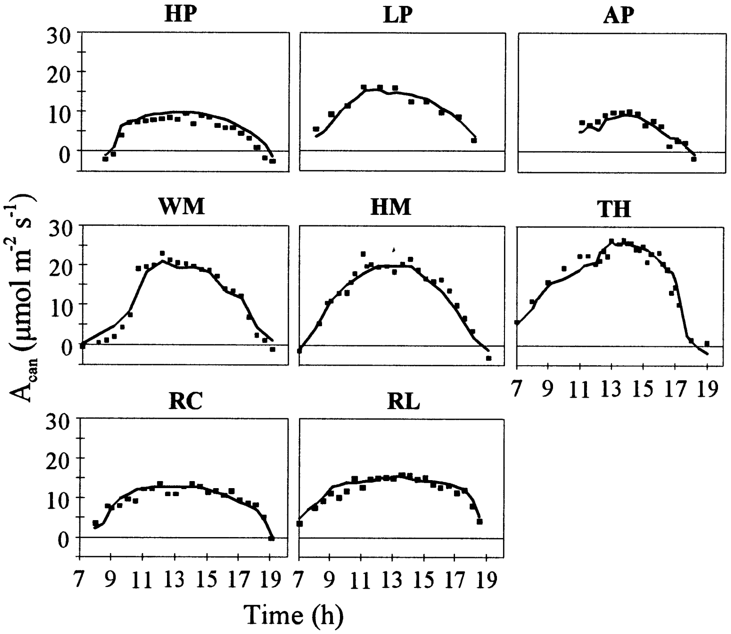

Fig. 2. Model validation for comparable clear days showing diurnal courses of whole apparent canopy photosynthesis (expressed on a ground area basis, A_{can}, μmol CO_2 m^{-2} s^{-1}). Points are values measured, in which A_{can} results from the difference of the CO_2 flux from the atmosphere measured by a micrometeorological approach (Bowen-ratio energy-balance) and the CO_2 output of the soil measured in situ by IRGA techniques. Lines are model predictions using measured structural and microclimatic data as inputs. Experimental sites: HP, heavily stocked pasture; LP, lightly stocked pasture; AP, abandoned pasture; WM, wet meadow; HM, hay meadow; TH-tall herb community; RC, evergreen *Rhododendron* shrub community; RL, deciduous *Rhodododendron* shrub community.

3.4. Diurnal courses of simulated whole canopy photosynthesis

Model simulations were based on a measured diurnal course of incoming PPFD and leaf temperatures on a typical sunny day at biomass maximum (Fig. 3), and on measured canopy structural parameters. The diurnal patterns of simulated whole canopy photosynthesis and sunlit leaf area are shown in Fig. 3. Spatial distribution of mean PPFD on inclined leaf area and of A_{can} (expressed on a canopy volume basis, μmol CO_2 m^{-3} s^{-1}), are presented in Fig. 1(a and b). In the graminoid dominated canopies (WM, AP, LP, HP), which were characterized by erect leaves, PPFD was mainly absorbed by the upper canopy layers in the morning and evening, when solar elevations were relatively low, but penetrated deeper into the canopy during the noon hours. This resulted in a marked diurnal change of sunlit leaf area. In the canopies dominated by tall herbs or dwarf shrubs PPFD was mainly absorbed by the upper half of the canopy throughout the day and the leaf area exposed to direct sunlight was relatively constant during the day. Carbon gain of the different canopy layers was closely related to the intercepted PPFD (Fig. 1(a and b)). In most canopies (HP, WM and to a lesser extent LP, AP, RC, RL), however, a reduction of A_{can} occurred at midday in spite of a high degree of light interception. This was also clearly seen in the diurnal course of total A_{can}, which only in the TH and the HM (Fig. 3) closely followed incoming PPFD. In the other canopies there was either a high degree of saturation of A_{can} during the noon hours (RC, RL) or it followed an asymmetric diurnal course (HP, LP, AP, WM). The causes of this phenomenon were revealed by model analysis: In the two *Rhododendron* stands (RC, RL) the leaves of the dominating species are saturated at relatively low light intensities (PPFD < 1000 μmol m^{-2} s^{-1}) and hardly utilize the higher PPFD values between 10 and 15 h. In the grassland communities leaf temperature is the limiting factor. To quantify this influence the actual leaf temperatures, which were above 20°, were substituted by the optimum temperature for photosynthesis (T_{opt} in Table 2). The result of this analysis is shown in Fig. 4. The high leaf temperatures observed in the HP, LP, WM and AP (data not shown) account for a reduction of daily net photosynthesis of 32, 12, 8 and 4%, respectively.

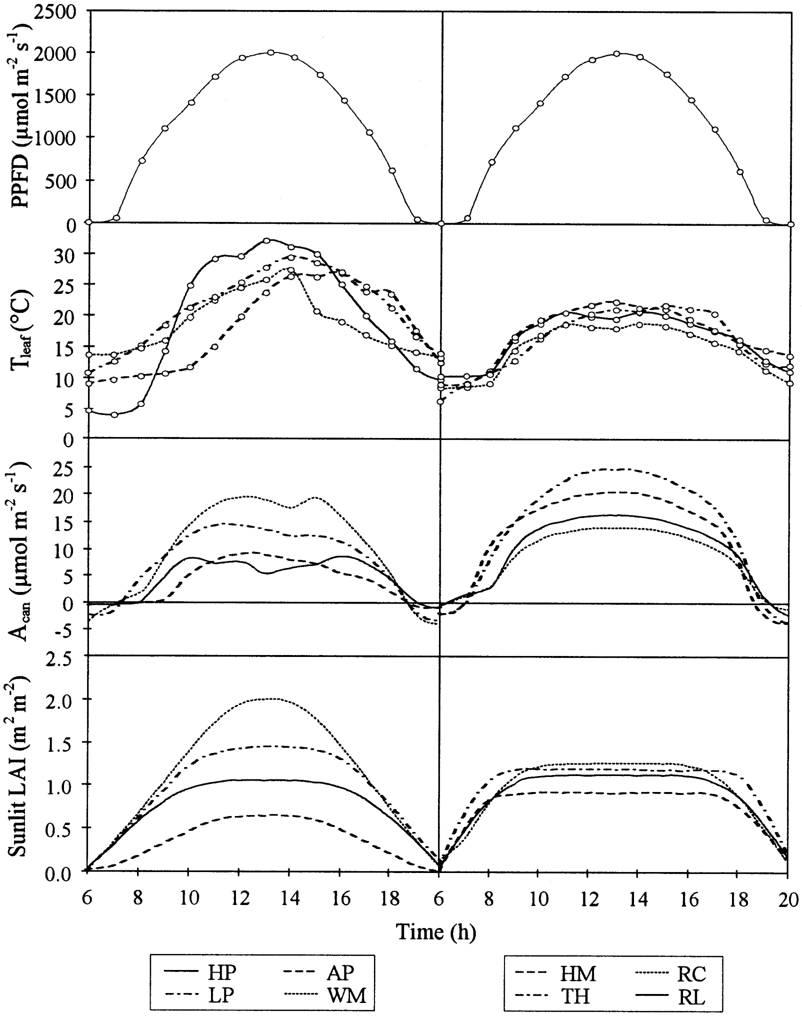

Fig. 3. Diurnal course of microclimatic data (incident photosynthetic photon flux density PPFD and measured leaf temperatures T_{leaf}) used for model input, as well as simulated diurnal patterns of whole apparent canopy photosynthesis (expressed on a ground area basis, A_{can}) and sunlit leaf area index (sunlit LAI) of the plant communities investigated in the Central Caucasus. For experimental sites see Fig. 2.

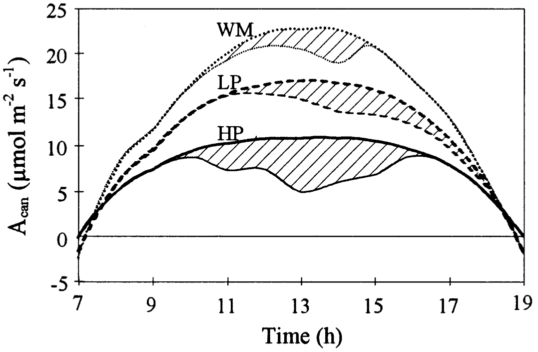

Fig. 4. Reduction *(hatched area)* of whole apparent canopy photosynthesis (expressed on a ground area basis, A_{can}) in the diurnal course, due to high leaf temperatures measured on a clear day on the wet meadow (WM), the lightly (LP) and the heavily (HP) stocked pasture. Simulations were performed with measured *(thin line)* and hypothetical *(bold line)* leaf temperatures. Leaf temperatures above 20° were substituted by the optimum temperature of single leaf photosynthesis.

3.5. Sensitivity analysis of daily total A_{can}

In order to examine the significance of the structural and photosynthetic characteristics for daily total A_{can} a sensitivity analysis was conducted (Fig. 5). Parameter values (PAI and LAI, leaf inclination, dispersion factor, A_{sat} and R_d) were individually changed for all canopy layers and species in the range from 0.7 to 1.3 of their average values. The resulting A_{can} was plotted as a relative value against the control A_{can} (measured environmental and canopy structure conditions, factor = 1; Fig. 5). A_{can} was highly dependent on PAI and LAI in the canopies with a high portion of necromass (LP 29%, AP 68%). In the other stands LAI and PAI had a markedly smaller influence on A_{can}: a further increase of PAI and LAI resulted in an increase of A_{can} in less dense canopies (HP, RC), but in a reduction of A_{can} in the denser canopies (WM, HM, TH, RL). In a series of further simulations LAI was kept constant and PAI was varied in such a manner that the portion of the area of necromass varied from zero to the measured value. In both the LP and the AP, A_{can} strongly decreased in an exponential manner with increasing portion of necromass. Simulations without necromass resulted in an increase of A_{can} by 1.3 and even 2.5 in the LP and the AP, respectively.

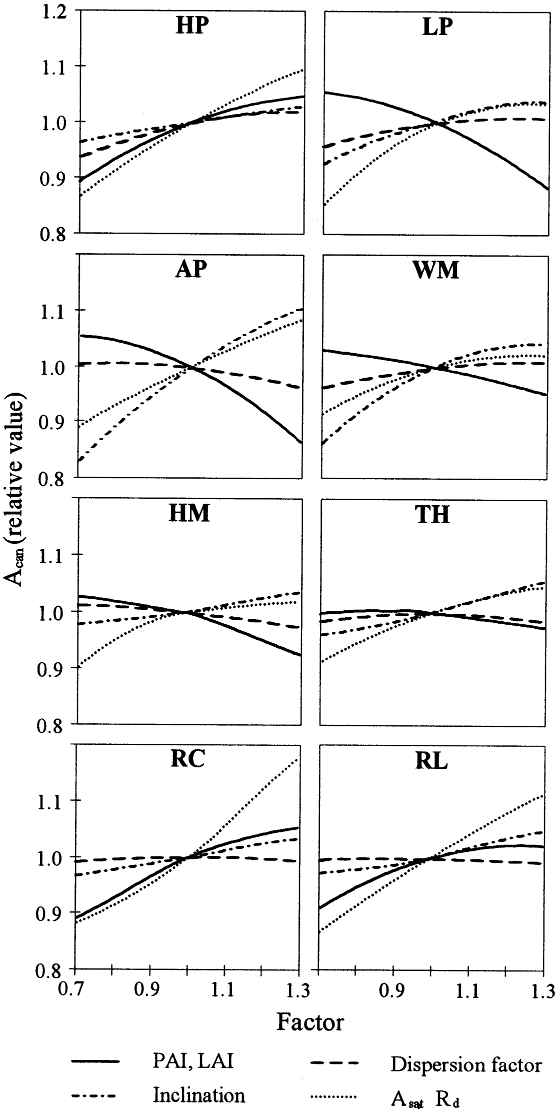

Fig. 5. Sensitivity of whole apparent canopy photosynthesis to plant and leaf area index, leaf inclination angle, dispersion factor, light saturated photosynthetic rate (A_{sat}) and day respiration (R_d) of the dominant species of the plant communities investigated in the Central Caucasus. To examine the sensitivity to plant area index (PAI) and leaf area index (LAI), both PAI and LAI were multiplied in all layers and for all species by a factor ranging from 0.7 to 1.3 *(abscissa)*; all other parameters were kept as measured. Sensitivity to leaf inclination angle and dispersion factor were examined by multiplying the respective parameter in all layers and for all species by a factor, with all other parameters kept as measured. Sensitivity to A_{sat} and R_d was examined by multiplying both A_{sat} and R_d by a factor, with all other parameters kept as measured. For experimental sites see Fig. 2.

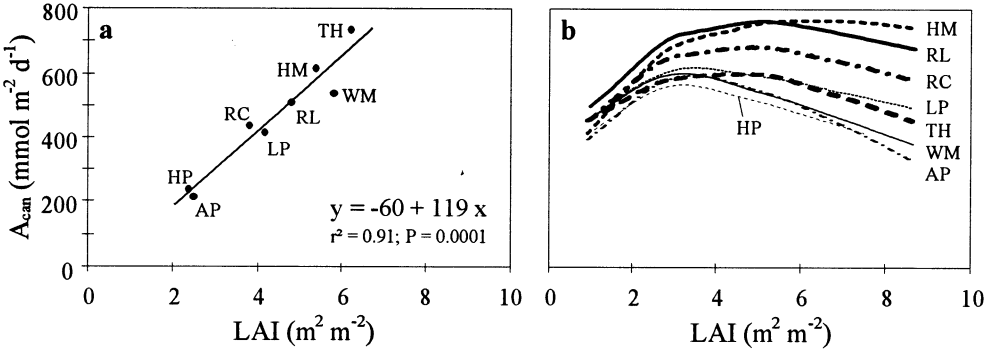

Fig. 6. (a,b) Relationship between daily total apparent canopy photosynthesis (expressed on a ground area basis, A_{can}) and leaf area index (LAI) of the plant communities investigated in the Central Caucasus. a Simulation performed with measured microclimatic data and structural parameters. The constant of the linear regression is not significant ($t = -0.9$, sig $t = 0.37$). (b) Analysis of effects of the vertical distribution of structural parameters (leaf area, leaf inclination, dispersion factor). For each stand simulations were performed by changing LAI from 1–8.5. For the input parameters equal values were chosen for all stands: ratio leaf area/attached dead area (1:0.17), single leaf photosynthetic parameters ($\Phi = 0.3$, $A_{sat} = 13$, $R_d = -1.3$, $T_{opt} = 20$, $a = -0.0045$, $b = 0.00012$), and measured values for incoming PPFD. Leaf temperatures below 20° were used as measured, higher values were substituted by 20°. In these simulations the only parameters differing between the stands are the measured vertical distribution of leaf area, and the profiles of leaf inclination angles and foliage dispersion factors.

The effects of changes in leaf inclination were similar in all canopies: decreasing leaf inclination decreased A_{can}, the effect being marked in the dense graminoid dominated stands (AP, WM) and less pronounced in less dense canopies (LP, HP) and stands dominated by dwarf shrubs and tall herbs (HM, TH, RC, RL). This is in good agreement with calculations by Duncan (1971), Barnes et al. (1990), Ryel et al. (1993), who found that in dense stands canopy photosynthesis was decreased by more planophile leaves.

Altering the dispersion factor revealed different responses in the canopies. A decrease in d_i (more clumped dispersion) caused a decrease in A_{can} in the HP, the LP and to a lesser extent in the WM. In the other canopies an increase in d_i (more regular dispersion) contributed to a decrease in A_{can}.

As it is the objective of this paper to analyse canopy structure effects, only a rough sensitivity analysis was performed for the photosynthetic parameters. It is known from different studies (Kira et al., 1978; Caldwell et al., 1986) that in natural plant communities R_d and A_{sat} of leaves decrease concomitantly with a decreasing canopy height, which often results in a close correlation. Therefore A_{sat} and R_d were concomitantly altered for this analysis. In all canopies investigated A_{can} increased with increasing A_{sat} and R_d and decreased with decreasing A_{sat} and R_d, the effect being most pronounced in the RC and the RL. In these canopies higher light intensities, which occur between 11^{00} and 15^{00}, cannot be utilized by sunlit leaves for an increase of A_{can} (Fig. 3). A concomitant increase of A_{sat} and R_d means that single leaf photosynthesis is saturated at higher light intensities and reaches higher rates, which particularly affects canopies dominated by species that are saturated at rather low PPFD.

3.6. *Effects of leaf area index and structural characteristics*

In Fig. 6(a) daily total A_{can} is plotted against LAI. The highly significant linear correlation suggests the conclusion that for the daily net carbon gain of the investigated plant canopies LAI, rather than the structural characteristics, is the determining factor. In order to test this a number of simulations of diurnal courses of A_{can} were made by changing LAI from 1–8.5. The following input parameters were kept equal in all stands: ratio leaf area/attached dead plant area (1:0.17), single leaf photosynthetic parameters ($\Phi = 0.3$,

$A_{\mathrm{sat}} = 13$, $R_{\mathrm{d}} = -1.3$, $T_{\mathrm{opt}} = 20$, $a = -0.0045$, $b = 0.00012$) and incoming PPFD (values as measured). Vertical distribution of leaf area, and the profiles of leaf inclination angles and foliage dispersion factors were used as measured in the respective stand. Leaf temperatures below 20° were used as measured, higher values were taken to be 20°. Fig. 6(b) clearly shows that these structural parameters play an important role for A_{can}. The canopies investigated can be grouped into stands dominated by dwarf shrubs or tall herbs (HM, RC, RL, TH) and graminoid dominated stands (HP, LP, AP, SM). The first group reaches the maximum A_{can} at LAI values of about 5–6 (optimum LAI). The second group is characterized by an optimum LAI of 3 and displays somewhat lower values of daily total A_{can} than the first group (except TH). In the TH stand, which is extremely planophile, a slight increase of leaf inclination (by 25%) results in daily total A_{can} values comparable to those of the other stands of the first group.

3.7. Effects of non-random leaf dispersion

The determination of foliage grouping revealed a clumped dispersion in the leaf layers and a regular dispersion in the stem layers of the HM, TH, RL, RC and WM stands, which was considered in the model. In order to analyse the effects of leaf dispersion on light absorption and canopy photosynthesis, simulations based on observed leaf dispersion were compared with simulations assuming random dispersion in all layers. As Fig. 7 shows, the measured clumped dispersion in the HM, TH, RC and RL stands resulted in a shift of sunlit leaf area and maximum photosynthesis to somewhat lower canopy layers, where the maximum LAI occurred. In the WM stand the measured clumped dispersion resulted in a markedly higher photosynthesis in the layers with the highest LAI than in the case of random dispersion. In all canopies investigated the measured clumped dispersion resulted in a higher daily total canopy photosynthesis of up to 6%. The grouping of foliage is primarily determined by the morphology of the species and may not necessarily be a strategy of maximizing the carbon gain. Thus, in a further step a sensitivity analysis was performed to test if the dispersion of leaves measured in all canopies is near optimum for canopy photosynthesis. For this sensitivity analysis all parameters except d_{i} were kept as measured. The dispersion factors were varied according to the following equation: $d_{\mathrm{i}}^{\mathrm{variation}} = ((d_{\mathrm{i}} - 1)v_2 + 1)v_1$, for $0.5 < v_1, v_2 < 1.5$. Variation of v_1 causes changes of the level of d_{i} (in all layers more clumped when $v_1 < 1$ and more regular when $v_1 > 1$). Variation of v_2 has the effect that differences of d_{i} between the layers are increased ($v_2 > 1$) or decreased ($v_2 < 1$). Fig. 8 shows two typical results. In all canopies investigated there was an optimum range of d_{i} for A_{can}, which also includes the actually measured dispersion of leaves. In the LP, as well as the HP, AP and RC stands (not shown), A_{can} was insensitive to a wide range of variations of d_{i}. In these canopies the differences of d_{i} between the layers had no effect, A_{can} was only determined by the occurrence of foliage clumping. In the other stands (TH, HM, RL, WM) A_{can} was much more sensitive to d_{i}, both with respect to its levels and the differences between the layers (profile). The optimum in these canopies was the result of an optimized combination of levels and profile of d_{i}. The resulting matrix of these stands is characterized by a more or less triangular structure (see TH in Fig. 8). This structure shows particularly well that the actually measured dispersion of leaves is near optimum for canopy photosynthesis.

4. Discussion

In the absence of limiting environmental conditions (e.g. clear day, no moisture stress, no lack of mineral nutrition) canopy net photosynthesis is determined by the ability of the stand to intercept light and by its effectiveness in utilizing light for photosynthesis. Whether a stand can capture and use incident PPFD will ultimately be controlled by its structural properties (vertical distribution of leaf area, density, spatial dispersion and orientation of plant elements; (Duncan, 1971; Roberts and Miller, 1977; Myneni et al., 1989)). On the basis of the vertical distribution of the leaf area (Fig. 1(a and b)) the investigated stands can be roughly divided into three types (Tappeiner and Cernusca, 1991, 1996): a pyramid with a broad base (type 1), a pyramid with a narrow base (type 2) and an inverted pyramid (type 3). These obvious structural characteristics are linked to a number of functional parameters.

Type 1 is represented by grazed areas, such as the HP and the LP. Its structure is commonly interpreted as an adaptation to grazing (Cernusca and Nachuzrisvili, 1983; Fukuyama, 1985, Sala, 1988; Tappeiner and Cernusca, 1989b). Leaf area is amassed near the soil surface, leaf inclination varies from predominantly vertical in the upper canopy to predominantly horizontal in the lower canopy. The simulations show that PPFD penetrates deep into the stand throughout almost the

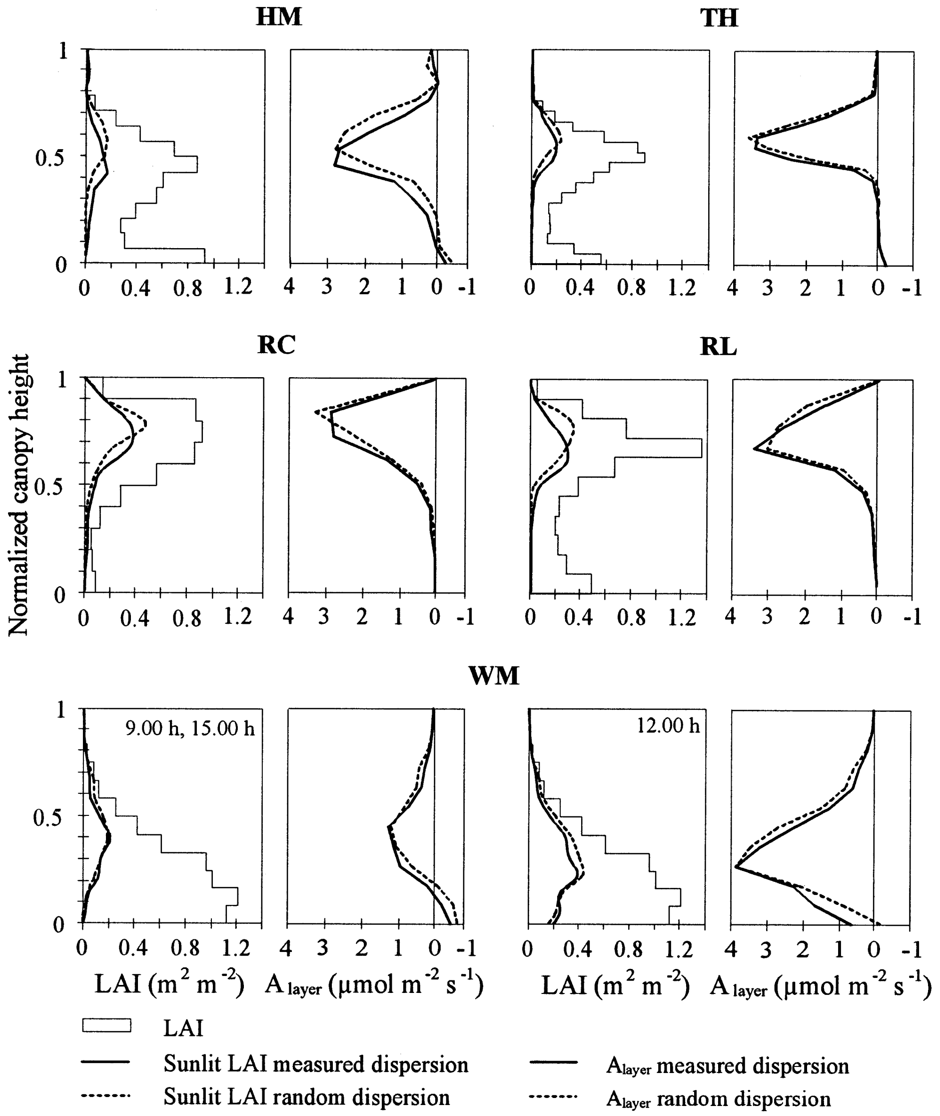

Fig. 7. Measured profiles of the leaf area index (LAI) and simulated profiles of sunlit leaf area (sunlit LAI) for measured and random foliage dispersion (left), and simulated profiles of apparent photosynthesis in the respective layers of the canopy (A_{layer}) for measured and random foliage dispersion (right). For the HM, TH, RC, RL sites daily means are given, whereas for the WM site hourly means for different times of the day are shown. For experimental sites see Fig. 2.

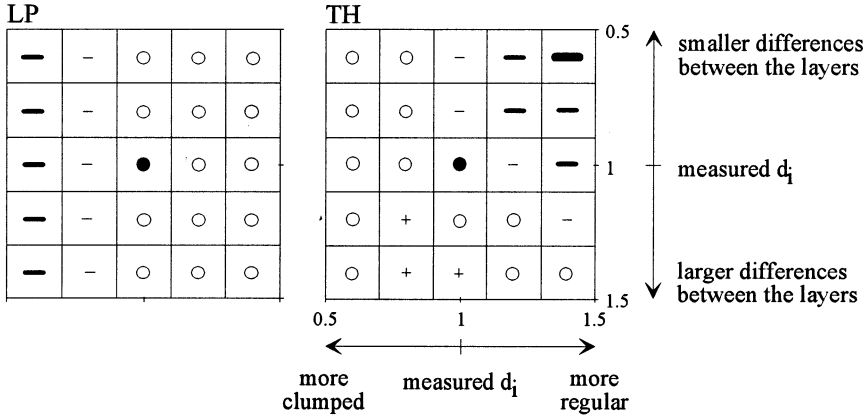

Fig. 8. Sensitivity of daily total whole canopy photosynthesis to variations of the level of dispersion factors (d_i) per layer (columns) and the profile of d_i (lines) for the lightly grazed pasture (LP) and the tall herb community (TH). For this sensitivity analysis all parameters except d_i were kept as measured. The levels of d_i were increased or decreased in the same proportion in all layers and the profiles of d_i were changed by systematically increasing or decreasing the measured differences of d_i between the layers (for further explanations see text). , A_{can} at measured d_i; , deviation = 1%; +, increase 2–5%; —, decrease 2–5%; —, decrease 6–10%, —, decrease > 10%.

entire day (Fig. 1(a)) and that a low LAI results in a loss of PPFD to the soil surface of up to 17% (HP). In stands of type 1 canopy structure exerts only little influence on canopy photosynthesis via light climate. Canopy photosynthesis is generally not limited by light but by other factors. (1) The dense leaf layers near the soil surface absorb a major part of the incoming radiation, but on the other hand they also slow down the exchange processes with the atmosphere (high aerodynamic resistance). On clear summer days this results in high canopy and leaf temperatures during the noon and early afternoon hours (Tappeiner and Cernusca, 1996), leading to a pronounced reduction in canopy photosynthesis (Fig. 4). Similarly high leaf temperatures combined with low canopy photosynthesis during clear midday periods in August were also measured by Ripley and Redmann (1976) in a short grass prairie. Beyschlag et al. (1990) showed for a mixture of wheat and wild oat that even small increases in foliage temperatures lead to substantial reductions in (A_{can}. Such temperature effects may not be restricted to direct effects, as considered by the model, but may also include indirect effects on photosynthesis via stomata responses to high water vapour pressure deficits (Tenhunen et al., 1990). (2) Grazing removes part of the photosynthetic surface, thus reducing LAI and A_{can}, on the other hand it also indirectly increases the photosynthetic capacity by favouring the development of young leaves in an environment with high light availability (Woledge and Parsons, 1986). Extensification and abandonment result in an increase of necromass and a slow change of the structure of canopies of type 1 from a pyramid with a broad base to one with a narrow base (AP).

Type 2 is represented by meadows such as the WM and the AP. The erect leaves and a gradual increase in leaf area from the canopy surface to the ground result in an almost linear decrease in light availability with canopy height and a pronounced diurnal course of light availability in all canopy layers (Fig. 1(a)). Mutual shading plays an important role in canopy photosynthesis. A large proportion of the foliage (80%) is in shade most of the time (Fig. 7) and contributes only up to 15% of canopy carbon gain. This is only half the value found for the dwarf shrub- and tall herb communities investigated by the author, or for a *Quercus coccifera* stand investigated by Caldwell et al. (1986). A high portion of necromass, as observed in the AP, increases the effects of mutual shading and exerts a markedly negative influence on A_{can} (Tappeiner and Cernusca, 1989b, 1995). As Fig. 5 shows, in such stands canopy photosynthesis is very sensitive to variations of PAI. In general, the structural properties have a more pronounced effect on photosynthesis in stands of type 2, as compared to stands of type 1. This can be clearly seen from the sensitivity of A_{can} with respect to decreasing leaf inclination (see AP, WM in Fig. 5) and variations in the profile of d_{i} (WM). The large amount of sunlit leaf area during the midday hours (Fig. 3) results in rather high temperatures in the active layer, which causes somewhat smaller reductions in canopy photosynthesis (Fig. 4) than in stands of type 1.

Type 3 is represented by the dwarf shrub communities (RC, RL) and the tall herb dominated stands (TH, HM). The inverted pyramid shape of the canopy results from the morphology of the dominating species, which raise their largely horizontal leaves away from the soil surface. The effects on microclimate are a high attenuation of PPFD by the upper half of the canopy and a relatively small diurnal course of leaf temperatures (Fig. 3). This results in a characteristic spatial distribution of canopy photosynthesis, with the highest A_{can} occurring in layers with the highest LAI (Fig. 1(b)), and very low A_{can} in the underlying layers. The simulation results presented in this paper support the contention of other authors (Küppers, 1985; Caldwell, 1987; Barnes et al., 1990) that plant architecture plays an important role in competition: canopies of type 3 are dominated by plants that have succeeded in spreading out their leaves in the upper half of the stand, thus effectively exploiting PPFD to suppress competition from species in the lower layers. Due to lack of light A_{can} is negative in the lowest canopy layers in the TH, RC and RL stands throughout the whole day. In this type canopy structure plays an important role for canopy photosynthesis, as is proved by the simulations of effects of the structural characteristics (Fig. 6(b)). In a comparison of all stands on the basis of assumed equal single leaf photosynthetic parameters, stands of type 3 display a higher carbon gain and a higher optimum LAI than stands of types 1 and 2. This is not the result of higher attenuation of PPFD by the canopy but rather results from the distribution of intercepted PPFD in the canopy which is such that a great part of the leaves are exposed to intermediate, non-saturating PPFD. This maximizes the ratio A_{can}/absorbed PPFD (Jarvis and Leverenz, 1983; Wall and Kanemasu, 1990). This favourable distribution of light is partly due to the clumped dispersion of leaves in the upper canopy. Sensitivity analysis of A_{can} with respect to variation in the level and profile of leaf dispersion clearly revealed the particular importance of the differences in d_{i} between the layers in canopies with high LAI. It could also be shown that in such stands the observed leaf dispersions follow a pattern which allows for an optimization of carbon gain of the whole stand (Figs. 7 and 8).

5. Conclusions

(1) The relatively simple whole canopy photosynthesis model used requires photosynthetic input parameters which are readily measurable. The successful validation shows that such a model is well suited for species-rich plant communities of very different structures. The correspondence between model results and measurements is comparable to that obtained by Kim and Verma (1991), Ryel et al. (1993), both of which groups used a more complex photosynthesis sub-model (Farquhar and Von Caemmerer, 1982; Tenhunen et al., 1987). However, the slight overestimation of A_{can} in one stand reveals limitations of the model under conditions of moisture stress.

(2) The significance of canopy properties (density, spatial dispersion and inclination of plant elements) for canopy photosynthesis essentially depends on the vertical distribution of the leaf area. The canopies investigated in the Central Caucasus could be grouped into three types, their structural shape ranging from a pyramid with a broad base (type 1) to a pyramid with a narrow base (type 2) and finally to an inverted pyramid (type 3) (Fig. 9). The significance of the structural properties for A_{can} increases from the pyramid with a broad base to the inverted pyramid and is higher when the stand is dominated by a single species.

(3) The simulations have shown (Fig. 6(b)) that in canopies of type 3 the structural properties are better optimized for canopy photosynthesis than in the other canopy types. In a comparison of all canopies with assumed equal LAI and photosynthestic characteristics, canopies of this type obtain higher total daily stand photosynthesis and reach the maximum of A_{can} at LAI values between 5 and 6 (optimum LAI). Stands of the other two types have an optimum LAI of only 3.

(4) High A_{can} is not achieved by the optimization of a single structural property but is the result of an optimized combination of several properties. This is exemplified by TH in Fig. 8 (optimum is the result of suitable level and profile of d_{i}), but is also valid for the combination of leaf inclination and density of the stand (Fig. 5). A high efficiency of utilization of incoming radiation for canopy photosynthesis can be achieved by (a) adapting canopy structural properties (leaf inclination, leaf dispersion) so that the major part of the leaf area is supplied with intermediate PPFD, and (b) physiological and anatomical adaptations of species to the low PPFD in lower layers of the canopy (Jarvis and Leverenz, 1983). Such complex processes of optimization can be seen from the relatively constant ratio A_{can}/LAI in the investigated stands (Fig. 6(a)), which is the result of an interplay between structural properties of the canopy and leaf based photosynthetic properties. In a comparison of all investigated stands the most effective use of both possibilities occurs in the stands of type 3.

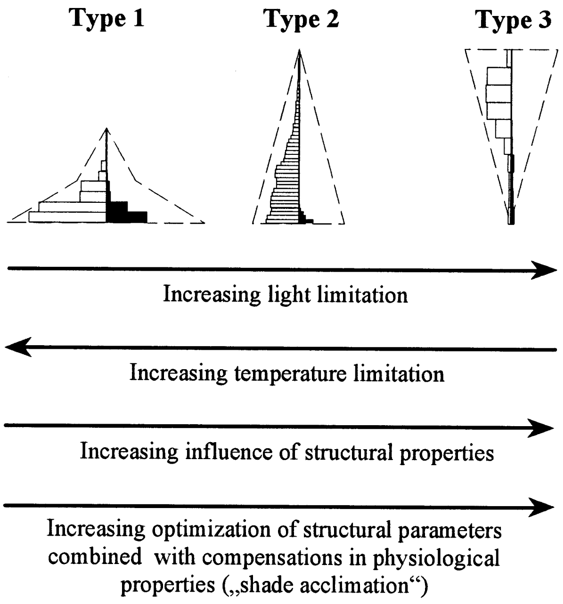

Fig. 9. The significance of canopy properties for whole apparent canopy photosynthesis (A_{can}) in dependence of canopy architecture. According to the vertical distribution of the leaf area the investigated stands were divided into three types: (1) pyramid with a broad base (HP, LP), (2) pyramid with a narrow base (AP, WM), (3) inverted pyramid (HM, TH, RC, RL). Characteristic effects of structural parameters on daily total A_{can} are indicated by arrows. For experimental sites see Fig. 2. For further explanation see text.

(5) The simulation results indicate that the above-mentioned optimization of canopy photosynthesis does not imply maximization. Rather, the structural properties only adapt to give a satisfying strategy for carbon gain (e.g. TH in Fig. 8). However, in a general approach optimization and maximization of canopy structure can not be conclusively discussed without considering the availability and distribution of nitrogen in the canopy (Hirose and Werger, 1987; Badeck, 1995) and leaf turnover and phenology (Field, 1983).

(6) In mountain ecosystems structural properties of the canopy (dense leaf layers, accumulation of attached dead plant material) can enhance the development of a warm microenvironment. Simulations showed that in the investigated stands the arrangement of dense leaf layers near the soil surface and the accumulation of attached dead plant material can reduce carbon gain of the canopy as a result of heating effects and of decreased light availability. On the other hand, a high portion of leaf area in the upper canopy (inverted pyramid stands) allows much better optimization of structural characteristics favouring a high carbon gain (Fig. 9).

Acknowledgements

This investigation was supported in part by the Austrian Academy of Science. The authors warmly acknowledge the support and assistance of G. Nakhutsrishvili and his staff during the investigations in the Caucasus. The authors wish to thank Joy Wieser for correcting the English text.

Appendix A. Abbreviations

a		Constant in Eq. (2)
A	μmol CO_2 m^{-2} leaf area s^{-1}	Photosynthetic CO_2 fixation of a single leaf
A_{can}	μmol CO_2 m^{-2} ground area s^{-1}	Whole apparent canopy photosynthesis
A_{layer}	μmol CO_2 m^{-2} ground area s^{-1}	Apparent photosynthesis in the different canopy layers
AP		Abandoned pasture
A_{sat}	μmol CO_2 m^{-2} leaf area s^{-1}	Light saturated photosynthetic rate of a single leaf
b		Constant in Eq. (2)
BREB		Bowen-ratio energy-balance method
d_i		Foliage dispersion factor for layer i
$d_i^{variation}$		Variations of d_i for sensitivity analysis
GAI	m^2 m^{-2}	Green area index
HM		Hay meadow
HP		Heavily stocked pasture
I_o	μmol photons m^{-2} ground area s^{-1}	Incident direct PPFD on a horizontal plane
I_x	μmol photons m^{-2} ground area s^{-1}	Simulated direct PPFD on a horizontal plane at the surface of a layer x in the canopy
$I_x^{observed}$	μmol photons m^{-2} ground area s^{-1}	Measured direct PPFD on a horizontal plane at the surface of a layer x in the canopy
LAI	m^2 m^{-2}	Leaf area index
LP		Lightly stocked pasture
LWA	g dry matter m^{-2}	Leaf weight per area
p		Actual rate of photosynthesis relative to A_{sat}
PAD	m^2 m^{-3}	Plant area density
PAI	m^2 m^{-2}	Plant area index
PPFD	μmol photons m^{-1} ground area s^{-1}	Photosynthetic photon flux density
RC		Evergreen *Rhododendron* shrub community
R_d	μmol CO_2 m^{-2} leaf area s^{-1}	Interception of the light response curve of a single leaf with the y-axis
RL		Deciduous *Rhodododendron* shrub community
TH		Tall herb community
T_l	°C	Leaf temperature
T_{opt}	°C	Optimum temperature of leaf based photosynthesis
$v1$, $v2$		Factors for variation of levels and profile of d_i
WM		Wet meadow
x_L		Leaf inclination index
α	°	Frequency distribution of leaf inclination angles
β	°	Solar elevation
Φ	mol CO_2 mol^{-1} photons	Slope of the linear proportion of the light response curve of a single leaf

References

Abdaladse, O., 1988. On field research plant CO_2 gas exchange in high mountains of the Caucasus. In: Nakhutsrishvili, G.S. (Ed.), The Ecology of High Mountains. Mezniereba, Tbilisi, pp. 63–75.

Abdaladse, O., 1994. CO_2 gas exchange in high mountain plants of Georgia (Central and Minor Caucasus). Doctoral Thesis, Georgian Academy of Sciences.

Acock, B., Thornley, J.H.M., Warren Wilson, J., 1970. Spatial variation of light in the canopy. Prediction and measurement of photosynthetic productivity. Central Agricultural Publishers, Wageningen, pp. 91–102.

Anderson, M.C., Denmead, T., 1969. Short wave radiation on inclined surfaces in model plant communities. Agron. J. 6, 867–871.

Atkinson, C.J., 1986. The effect of clipping on net photosynthesis and dark respiration of plants from an upland grassland, with reference to carbon partitioning in *Festuca ovina*. Ann. Bot. 58, 61–72.

Badeck, F.W., 1995. Intra-leaf gradient of assimilation rate and optimal allocation of canopy nitrogen: a model on the implications of the use of homogeneous assimilation functions. Austral. J. Plant Physiol. 22, 425–439.

Barnes, P.W, Beyschlag, W., Ryel, R.J., Flint, S.D., Caldwell, M.M., 1990. Plant competition for light analyzed with a multispecies canopy model. III. Influence of canopy structure in mixtures and monocultures of wheat and wild oat. Oecologia 82, 560–566.

Beyschlag, W., Barnes, P.W., Ryel, R.J., Caldwell, M.M., Flint, S.D., 1990. Plant competition for light analyzed with a multispecies canopy model. II. Influence of photosynthetic characteristics on mixtures of wheat and wild oat. Oecologia 82, 374–380.

Björkmann, O., 1981. Responses to different quantum flux densities. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Encyclopedia of Plant Physiology, vol. 12A. Springer, Berlin, pp. 57–107.

Caldwell, M.M., 1987. Plant architecture and resource competition. In: Schulze, E.D., Zwölfer, H. (Eds.), Ecological Studies, vol. 61. Springer, Berlin, pp. 164–179.

Caldwell, M.M., Meister, H.P., Tenhunen, J.D., Lange, O.L., 1986. Canopy structure, light microclimate and leaf gas exchange of *Quercus coccifera* L. in a Portuguese macchia: measurements in different canopy layers and simulations with a canopy model. Trees 1, 25–41.

Cernusca, A., 1976. Bestandesstruktur, Bioklima und Energiehaushalt von alpinen Zwergstrauchbeständen. Oecol. Plant 11, 71–102.

Cernusca, A., 1982. Standardmeteorologie und Mikrometeorologie. In: Janetschek, H. (Ed.), Ökologische Feldmethoden. Verlag Eugen Ulmer, Stuttgart, pp. 9–27.

Cernusca, A., 1991. Ecosystem research on grassland in the Austrian Alps and in the Central Caucasus. In: Esser, G., Overdiek, V. (Eds.), Facets of Modern Ecology. Elsevier, Amsterdam, pp. 233–271.

Cernusca, A., Decker, P., 1989. Vergleichende Atmungsmessungen an Graslandökosystemen. In: Cernusca, A. (Ed.), Struktur und Funktion von Graslandökosystemen im Nationalpark Hohe Tauern. Universitätsverlag Wagner, Innsbruck, pp. 405–417.

Cernusca, A. and Nachuzrisvili, G.S., 1983. Untersuchung der ökologischen Auswirkungen intensiver Schafbeweidung im Zentral-Kaukasus, Verh Gesell Ökol X: 183–192.

De Pury, D.G.G., Farquhar, G.D., 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant Cell Environm. 20, 537–557.

De Wit, C.T., 1965. Photosynthesis of leaf canopies. Agric. Res. Rep. 663, Ctr. Agric. Publ. Docu., Wageningen.

Diemer, M., 1990. Die Kohlenstoffbilanz von Blättern krautiger Arten aus dem Hochgebirge und der Niederung. Thesis, Univ. Innsbruck.

Duncan, W.G., 1971. Leaf angles, leaf area and canopy photosynthesis. Crop Sci. 11, 482–485.

Duncan, W.G., Loomis, S., Williams, W.A., Hanau, R., 1967. A model for simulating photosynthesis in plant communities. Hilgardia 38, 181–205.

Ehleringer, J., Björkman, O., 1977. Quantum yield for CO_2 uptake in C3 and C4 plants. Plant Physiol. 59, 86–90.

Farquhar, G.D., Von Caemmerer, S., 1982. Modelling of photosynthetic response to environmental conditions. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Encyclopedia of Plant Physiology, New Series 12B. Springer Verlag, Berlin, pp. 549–587.

Field, C., 1983. Allocating leaf nitrogen for the maximisation of carbon gain: Leaf age as a control on the allocation program. Oecologia 56, 341–347.

Fliervoet, L.M., 1984. Plot size, representativeness, diversity and phytomass structure of some grasslands. L.M. Fliervoet, 'Canopy structure of dutch grasslands. Stichting Studentenpers, Nijmegen, pp. 63–82.

Forseth, I.N.and, Norman, J.M., 1993. Modelling of solar irradiance, leaf energy budget and canopy photosynthesis. In: Hall, D.O., Scurlock, J.M.O., Bolhàr-Nordenkampf, H.R., Leegood, R.C., Long, S.P. (Eds.), Photosynthesis and production in a changing environment: a field and laboratory manual. Chapman and Hall, London, pp. 207–219.

Fukuyama, M., 1985. Production characteristics of short grass pastures. JARQ 19 (3), 202–211.

Gloser, J., 1993. Photosynthesis and limiting factors. In: Rychnovská, M. (Ed.), Structure and functioning of seminatural meadows. Developments in agricultural and managed-forest ecology. Elsevier, Amsterdam, pp. 193–210.

Grace, J.C., Jarvis, P.G., Norman, J.M., 1987. Modelling the interception of solar radiant energy in intensively managed stands. New Zealand J. For. Sci. 17, 193–209.

Gutschick, V.P., Wiegel, F.W., 1988. Optimizing the canopy photosynthetic rate by patterns of investment in specific leaf mass. Am. Natural. 132, 67–86.

Harley, P.C., Baldocchi, D.D., 1995. Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. I. Leaf model parametrization. Plant Cell Environm. 18, 1146–1156.

Hesketh, J.D., Jones, J.W., 1980. What is modelling and why model photosynthesis? In: Hesketh, J.D., Jones, J.W. (Eds.), Predicting Photosynthesis for Ecosystem Models, vol. I. CRC, Bota Raton, FL, pp. 1–9.

Hirose, T., Werger, M.J.A., 1987. Maximising daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. Oecologia 72, 520–526.

Jarvis, P.G., Leverenz, J.W., 1983. Productivity of temperate, deciduous and evergreen forests. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Encyclopedia of Plant Physiology, New Series 12D. Springer, Berlin, pp. 233–280.

Karlsson, P.S., 1994. Photosynthetic capacity and photosynthetic nutrient-use efficiency of *Rhododendron lapponicum* leaves as related to leaf nutrient status, leaf age and branch reproductive status. Funct. Ecol. 8, 694–700.

Kim, J., Verma, S.B., 1991. Modelling canopy photosynthesis: scaling up from a leaf to canopy in temperate grassland ecosystem. Agric. Forest. Meteorol. 57, 187–208.

Kira, T., Ono, Y., Hosokawa, T., 1978. Biological Production in a Warm-Temperate Evergreen Oak Forest of Japan. Univ. Tokyo Press, Tokyo.

Körner, Ch., 1977. Der CO_2 Gaswechsel verschiedener Pflanzen im alpinen Grasheidegürtel. I. Der Einsatz einer neuen teilklimatisierten Meßkammer für in situ Messungen an kleinwüchsigen Gebirgspflanzen. In: Cernusca, A. (Ed.), Alpine Grasheide Hohe Tauern, Veröff. Österr. MaB-Hochgebirgsprogrammes Hohe Tauern, Bd. 1. Universitätsverlag Wagner, Innsbruck, pp. 47–68.

Körner, Ch., Diemer, M., 1987. In situ photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. Funct. Ecol. 1, 179–194.

Küppers, M., 1985. Carbon relations and competition between woody species in a Central European hedgerow. IV. Growth form and partitioning. Oecologia 66, 343–352.

Larcher, W., 1984. Klima und Pflanzenleben im Gebirge. Universitas 39, 629–637.

Leuning, R., Wang, Y.P., Cromer, R.N., 1991. Model simulations of spatial distributions and totals of photosynthesis in *Eucalyptus grandis* canopies. Oecologia 88, 494–503.

McMurtrie, R., Wolf, L., 1983. A model of competition between trees and grass for radiation, water and nutrients. Ann. Bot. London 52, 449–458.

Monsi, M., Saeki, T., 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Jpn. J. Bot. 14, 22–52.

Monsi, M., Uchijima, Z., Oikawa, T., 1973. Structure of foliage canopies and photosynthesis. Ann. Rev. Ecol. Syst. 4, 301–327.

Myneni, R.B., Ross, J.and, Asrar, G., 1989. A review of photon transport in leaf canopies. Agric. Forest. Meteorol. 45, 1–153.

Norman, J.M., Hesketh, J.D., 1980. Micrometeorological Methods for Predicting Environmental Effects on Photosynthesis. In: Hesketh, J.D., Jones, J.W. (Eds.), Predicting Photosynthesis for Ecosystem Models, vol. I. CRC, Boca Raton, FL, pp. 9–35.

Oker-Blom, P., Kellomäki, S., 1982. Theoretical computations on the role of crown shape in the absorption of light by forest trees. Math. Biosci. 59, 291–311.

Rimmington, G.M., 1984. A model of the effect of interspecies competition for light on dry-matter production. Aust. J. Plant Physiol. 11, 277–286.

Ripley, E.A., Redmann, R.E., 1976. Grassland. In: Monteith, J.H.M. (Ed.), Vegetation and the Athmosphere 2. Academic Press, London, pp. 349–398.

Roberts, S.W., Miller, P.C., 1977. Interception of solar radiation as affected by canopy organization in two mediterranean shrubs. Oecol. Plant 12, 273–290.

Ross, J., 1981. The Radiation Regime and Architecture of Plant Stands. Junk, The Hague.

Ryel, R.J., Barnes, P.W., Beyschlag, W., Caldwell, M.M., Flint, S.D., 1990. Plant competition for light analyzed with a multispecies canopy model. I. Model development and influence of enhanced UV-B conditions on photosynthesis in mixed wheat and wild oat canopies. Oecologia 82, 304–310.

Ryel, R.J., Beyschlag, W., Caldwell, M.M., 1993. Foliage orientation and carbon gain in two tussock grasses as assessed with a net canopy gas exchange model. Funct. Ecol. 7, 115–124.

Sala, O.E., 1988. The effect of herbivory on vegetation structure. In: Werger, M.J.A., Van der Aart, P.J.M., During, H.J., Verhoeven, J.T.A. (Eds.), Plant Form and Vegetation Structure. Academic Publishing, The Hague, pp. 317–330.

Salisbury, F.B., Spomer, G.G., 1964. Leaf temperatures of alpine plants in the field. Planta 60, 497–505.

Sanadiradze, G., Kuradze, T., 1990. Water relations of plants and phytocenoses. In: Nakhutsrishvili, G. (Ed.), Ecological and geobotanical studies at the Kazbegi high-mountain station (Central Caucasus). Georgian Academy of Science, Tbilisi, pp. 38–42.

Sawada, S., Sugai, M., 1984. Responses of transpiration and CO_2 exchange characteristics to soil moisture stress in four *Plantago* species. Photosynthetica 18, 34–42.

Siegwolf, R., 1987. CO_2-Gaswechsel von *Rhododendron ferrugineum* L. im Jahresgang an der alpinen Waldgrenze. Thesis, Univ. Innsbruck.

Tappeiner, U., Cernusca, A., 1989a. Canopy structure and light climate of different alpine plant communities: Analysis by means of a model. Theor. Appl. Climatol. 40, 81–92.

Tappeiner, U., Cernusca, A., 1989b. Auswirkungen des Auflassens einer Almweide auf die Bestandesstruktur und das Lichtklima. In: Cernusca, A. (Ed.), Struktur und Funktion von Graslandökosystemen im Nationalpark Hohe Tauern. Universitätsverlag Wagner, Innsbruck, pp. 531–548.

Tappeiner, U., Cernusca, A., 1991. The combination of measurements and mathematical modelling for assessing canopy structure effects. In: Esser, G., Overdieck, V. (Eds.), Modern Ecology, Basic and Applied Aspects. Elsevier, Amsterdam, pp. 161–194.

Tappeiner, U., Cernusca, A., 1995. Analysis of changes in canopy structure and microclimate in abandoned alpine grassland ecosystems. In: Bellan, D., Bonin, G., Emig, C. (Eds.), Functioning and Dynamics of Natural and Perturbed Ecosystems. Lavoisier, Paris, pp. 49–62.

Tappeiner, U., Cernusca, A., 1996. Microclimate and fluxes of water vapour, sensible heat and carbon dioxide in structurally differing subalpine plant communities in the Central Caucasus. Plant Cell Environ. 19 (4), 403–417.

Tenhunen, J.D., Harley, P.C., Beyschlag, W., Lange, O.L., 1987. A model of net photosynthesis for leaves of the sclerophyll Quercus coccifera. In: Tenhunen, J.D., Catarino, F., Lange, O.L., Oechel, W.C. (Eds.), Plants responses to stress–functional analysis in mediterranean ecosystems. Springer, Berlin, pp. 339–354.

Tenhunen, J.D., Sala Serra, A., Harley, P.C., Doughtery, R.L., Reynolds, J.F., 1990. Factors influencing carbon fixation and water use by mediterranean sclerophyll during summer drought. Oecologia 82, 381–393.

Van Dyne, G.M., Vogel, W.G., Fisser, H.G., 1963. Influence of small plot size and shape on range herbage production estimates'. Ecology 44, 746–759.

Von Caemmerer, S., Farquhar, G.D., 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153, 376–387.

Wall, G.W., Kanemasu, E.T., 1990. Carbon dioxide exchange rates in wheat canopies. Part I. Influence of canopy geometry on trends in leaf area index, light interception and instantaneous exchange rates. Agric. Forest. Meteorol. 49, 81–102.

Wang, Y.P., Jarvis, P.G., 1990. Description and validation of an array model-MAESTRO. Agric. Forest. Meteorol. 51, 257–280.

Warren Wilson, J., 1960. Inclined point quadrats. New Phytol. 59, 1–8.

Woledge, J., Parsons, A.J., 1986. Temperate grasslands. In: Baker, N.R., Long, S.P. (Eds.), Photosynthesis in Contrasting Environments. Elsevier, Amsterdam, pp. 173–197.