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Calculation of daily totals of the gross CO_2 assimilation of leaf canopies

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Summary

Daily totals of gross CO_2 assimilation of leaf canopies have been calculated, based on photosynthesis-light response curves of individual leaves, and on a set of standard conditions. This work is partly a revision of that by de Wit (1965). It is extended for a range of saturation levels of leaf photosynthesis. The influence of leaf angle distribution is small. A set of descriptive equations is developed that gives an adequate description of the daily totals of gross CO_2 assimilation, both of a closed and of a non-closed surface.

Introduction

Often calculations of potential production are based on leaf-canopy models of considerable detail and a fine resolution in time. The problems in handling such large models tend to proliferate exponentially with their size, so that it is worthwhile to try and divide them into submodels. A suitable intermediate level appears the daily total of fluxes of mass and energy, so that the time interval of integration in productivity models can be chosen as large as a day.

De Wit (1965) calculated the gross dry matter production of a leaf canopy, based on the photosynthesis-light response curve for individual leaves and on a set of standard conditions. As it will be explained, some of these data need revision. Moreover, the calculations will be extended for a range of saturation levels of leaf photosynthesis.

A calculation model[1] and its results

In de Wit (1965) the photosynthesis curve for individual leaves was given by

[1] Listings can be obtained at the Department of Theoretical Production Ecology.

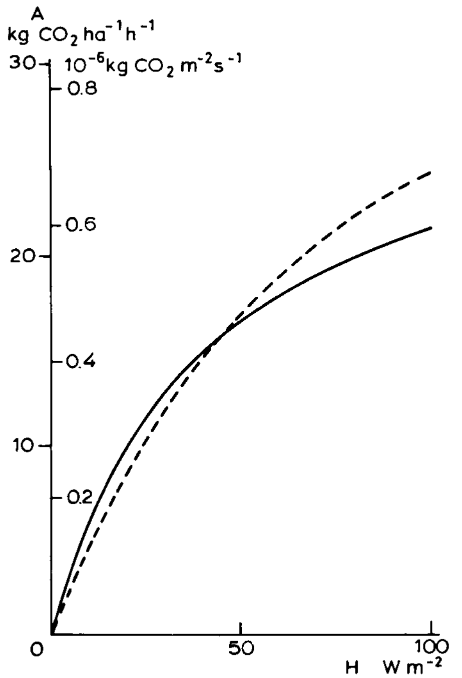

Fig. 1. Gross photosynthesis as a function of absorbed visible radiation:
——— according to Eq. 1;
– – – according to Eq. 2.

$$A = AMAX*H/(H + HH) \quad (1)$$

where AMAX is the rate of leaf photosynthesis at light saturation, H the absorbed photosynthetically active radiation and HH the level of H to reach half the saturation level.

This rectangular hyperbola results in a rather slow and gradual approach of photosynthesis to the saturation level with increasing light intensity. Many more recent measurements (van Laar & Penning de Vries, 1972; Peat, 1970; English, 1976) indicated that the approach is too slow and that a better fit can be obtained with an asymptotic exponential equation such as

$$A = AMAX*(1 - \exp(-H/HH)) \quad (2)$$

The ratio AMAX/HH represents the efficiency of light use at low light intensity. It is the slope of the photosynthesis-absorbed light response curve at the origin. In de Wit (1965) AMAX was taken as 0.8×10^{-6} kg CO_2 m^{-2} s^{-1}* and HH as 39 W m^{-2}* (absorbed photosynthetically active radiation, PAR), so that the efficiency was 21×10^{-9} kg CO_2 J^{-1} (0.75 kg CO_2 m^2 s ha^{-1} h^{-1} J^{-1}). Later evidence has shown that this value is about 30 % too high (de Wit et al., 1978; Björkman & Ehleringer, 1975; van Laar & Penning de Vries, 1972) and that a value of 14×10^{-9} kg CO_2 J^{-1} is in better agreement with reality. In Fig. 1 the asymptotic ex-

* Converted to SI units; de Wit's figures were 20 kg CH_2O ha^{-1} h^{-1} and 0.056 cal cm^{-2} min^{-1}, respectively.

ponential equation with HH = 60 W m^{-2} is compared with the rectangular hyperbola with HH = 40 W m^{-2} (used by de Wit, 1965). The asymptotic exponential equation is more linear at low light than the hyperbolic one. Therefore, even though the initial slope is less, it crosses over at a higher light intensity.

The computer model[1] that is used here is more concise than the one de Wit used for his 1965 publication, and essentially equal to the photosynthesis part of the models described by Goudriaan (1977) and de Wit et al. (1978). However, it is useful to give a brief review of the model here.

The extinction of light in the canopy is exponential with leaf area index reckoned from the top. The effect of multiple scattering is accounted for in the equations by the extinction and reflection coefficient. The calculations for a clear and an overcast sky are done in the same model segment. Similar as in de Wit's publication the incoming radiation under an overcast sky amounts to 20 % of that under a clear sky. The dependence of the incoming PAR under a clear sky on solar height β is expressed as follows:

$$S = 640 \sin(\beta) \exp(-0.1/\sin(\beta)) \qquad (3)$$

which yields a relation practically equal to the one used by de Wit. In this equation the number 640 represents the solar constant for PAR, $\sin(\beta)$ accounts for the angle of incidence on a horizontal surface, and the exponential accounts for extinction of radiation in the atmosphere. De Wit used a scattering coefficient of 0.3 by individual leaves for visible radiation, but we prefer a value of 0.2 (Goudriaan, 1977; Woolley, 1971). Because of multiple scattering the effect of this change is small (Goudriaan, 1977). The leaf area index (LAI) is taken as 5, so that the canopy is practically closed. Apart from photorespiration which shows up in a reduced value of AMAX, respiration losses are not considered here, so that growth and maintenance respiration still have to be subtracted to find the net rate of CO_2 assimilation. For C_4 plants (without photorespiration) a typical value of AMAX of 1.67×10^{-6} kg CO_2 m^{-2} s^{-1} (60 kg CO_2 $ha^{-1}h^{-1}$) can be used and for C_3 plants (with photorespiration) one of 0.83×10^{-6} kg CO_2 m^{-2} s^{-1}. The latter value is practically equal to the 20 kg CH_2O ha^{-1} h^{-1} used by de Wit (1965).

Table 1. Daily total incoming visible (400–700 nm) radiation in 10^6 J m^{-2} for a standard clear day.

North. lat.	15 Jan.	15 Feb.	15 Mar.	15 Apr.	15 May	15 June	15 July	15 Aug.	15 Sep.	15 Oct.	15 Nov.	15 Dec.
0°	14.00	14.72	15.16	14.95	14.26	13.77	13.97	14.68	15.17	14.94	14.23	13.77
10°	12.17	13.44	14.67	15.43	15.48	15.34	15.41	15.51	15.09	13.95	12.55	11.80
20°	10.00	11.73	13.68	15.38	16.22	16.47	16.38	15.84	14.48	12.49	10.50	9.53
30°	7.59	9.65	12.21	14.81	16.45	17.12	16.87	15.64	13.37	10.62	8.17	7.05
40°	5.06	7.30	10.32	13.74	16.18	17.29	16.86	14.93	11.80	8.40	5.67	4.50
50°	2.61	4.80	8.07	12.20	15.44	17.01	16.41	13.75	9.80	5.96	3.19	2.11
60°	0.61	2.34	5.58	10.25	14.31	16.43	15.60	12.15	7.47	3.42	1.00	0.32
70°	0.00	0.38	2.98	7.99	13.06	16.09	14.85	10.28	4.89	1.10	0.00	0.00
80°	0.00	0.00	0.63	5.66	12.87	16.72	15.24	8.81	2.22	0.00	0.00	0.00
90°	0.00	0.00	0.00	4.86	13.02	16.99	15.47	8.73	0.19	0.00	0.00	0.00

Table 2. Calculated daily gross CO_2 assimilation in kg CO_2 ha^{-1} of a closed canopy with a sphreical leaf angle distribution.

North. lat.		15 Jan.	15 Feb.	15 Mar.	15 Apr.	15 May	15 June	15 July	15 Aug.	15 Sep.	15 Oct.	15 Nov.	15 Dec.
AMAX = 10 kg CO_2 ha^{-1} h^{-1} (0.28 × 10^{-6} kg CO_2 m^{-2} s^{-1})													
0°	PC	326	334	338	336	329	324	326	333	338	336	329	324
	PO	215	221	225	223	217	213	214	221	225	223	217	213
10°	PC	299	315	332	343	348	348	348	346	338	322	304	294
	PO	194	207	221	229	231	231	231	231	225	213	198	190
20°	PC	266	292	320	347	362	368	366	354	332	303	273	258
	PO	168	188	211	231	241	245	244	236	220	197	174	162
30°	PC	225	262	303	345	372	385	380	358	322	278	236	215
	PO	136	164	196	227	247	256	253	237	210	176	144	128
40°	PC	177	223	279	338	379	399	392	358	305	244	190	165
	PO	99	133	175	219	249	263	258	233	194	149	108	89
50°	PC	121	175	246	325	384	413	402	353	280	201	136	107
	PO	56	95	147	204	247	268	260	225	172	114	67	46
60°	PC	55	119	203	305	388	432	415	344	246	149	76	34
	PO	15	51	110	184	242	271	260	211	141	72	24	8
70°	PC	0	40	149	281	404	488	451	336	202	86	0	0
	PO	0	9	65	156	237	285	265	193	101	26	0	0
AMAX = 20 kg CO_2 ha^{-1} h^{-1} (0.56 × 10^{-6} kg CO_2 m^{-1} s^{-1})													
0°	PC	494	508	517	513	499	490	494	508	517	513	499	490
	PO	269	279	285	282	272	265	268	278	285	282	272	265
10°	PC	448	477	505	525	530	530	530	528	515	488	456	439
	PO	239	258	278	290	292	291	291	292	284	267	245	233
20°	PC	392	436	485	528	553	562	559	541	505	455	405	379
	PO	202	231	263	291	305	310	308	298	276	244	211	194
30°	PC	324	384	453	522	567	587	579	544	484	410	341	308
	PO	160	197	241	284	311	323	318	298	260	214	170	150
40°	PC	246	319	410	506	573	605	593	539	451	353	266	227
	PO	112	155	210	269	311	330	322	290	236	176	124	101
50°	PC	159	242	352	478	573	620	602	524	406	282	181	139
	PO	61	107	171	247	304	331	321	274	204	130	73	50
60°	PC	63	153	280	439	569	637	610	500	346	198	91	37
	PO	15	55	124	216	291	329	314	251	162	79	25	8
70°	PC	0	44	193	390	575	695	643	473	271	102	0	0
	PO	0	10	70	176	277	336	312	222	112	27	0	0
AMAX = 30 kg CO_2 ha^{-1} h^{-1} (0.84 × 10^{-6} kg CO_2 m^{-2} s^{-1})													
0°	PC	623	642	654	648	630	616	622	641	654	648	629	616
	PO	293	305	312	309	297	289	292	304	312	309	297	289
10°	PC	560	600	638	664	670	669	670	669	652	616	572	549
	PO	259	282	304	318	320	318	319	320	311	291	266	252
20°	PC	486	545	610	668	699	711	707	684	637	570	503	469
	PO	217	250	286	318	334	340	338	327	301	264	227	208
30°	PC	396	475	566	657	716	742	732	686	607	510	419	375
	PO	169	211	260	309	341	353	349	325	282	230	181	159
40°	PC	294	389	507	633	721	763	747	676	562	433	321	270
	PO	117	164	225	292	339	360	352	315	254	187	130	105
50°	PC	183	288	429	593	716	776	753	652	499	339	211	158
	PO	63	112	181	265	329	359	348	296	217	137	76	51
60°	PC	66	175	333	536	704	790	756	615	417	230	98	38
	PO	15	57	130	229	312	354	338	268	170	81	25	8
70°	PC	0	45	220	467	699	846	784	572	318	109	0	0
	PO	0	10	72	184	293	357	331	234	116	27	0	0

Table 2. (continued)

North. lat.		15 Jan.	15 Feb.	15 Mar.	15 Apr.	15 May	15 June	15 July	15 Aug.	15 Sep.	15 Oct.	15 Nov.	15 Dec.
AMAX = 40 kg CO_2 ha^{-1} h^{-1} (1.11 × 10^{-6} kg CO_2 m^{-2} s^{-1})													
0°	PC	728	753	768	761	737	720	727	752	768	760	736	720
	PO	306	320	328	324	311	302	306	319	328	324	311	302
10°	PC	652	701	748	779	786	784	785	784	765	720	667	638
	PO	270	295	319	334	336	333	335	336	327	305	277	262
20°	PC	562	634	713	783	820	834	829	802	745	665	583	542
	PO	226	261	300	334	351	356	355	343	316	276	236	216
30°	PC	454	549	659	768	839	869	858	804	708	591	481	429
	PO	175	219	271	324	357	371	366	341	295	239	187	163
40°	PC	333	445	586	737	843	892	873	788	652	497	364	304
	PO	120	169	233	304	354	377	368	329	264	193	133	107
50°	PC	202	324	491	686	833	904	877	757	574	384	234	172
	PO	63	114	187	275	343	375	363	307	224	140	77	52
60°	PC	68	191	375	615	813	915	875	708	474	255	102	39
	PO	15	57	132	236	323	368	351	277	175	83	25	8
70°	PC	0	46	240	527	798	967	896	649	353	114	0	0
	PO	0	10	73	189	302	369	341	240	118	27	0	0
AMAX = 50 kg CO_2 ha^{-1} h^{-1} (1.39 × 10^{-6} kg CO_2 m^{-2} s^{-1})													
0°	PC	817	846	864	856	828	808	816	845	864	855	827	808
	PO	315	329	338	334	320	310	315	329	338	334	320	310
10°	PC	730	786	841	877	884	881	882	882	860	809	747	714
	PO	277	303	328	344	346	343	345	346	337	314	285	269
20°	PC	626	709	799	880	923	938	932	902	837	744	650	603
	PO	231	268	308	344	362	367	366	354	325	284	241	221
30°	PC	502	611	737	862	943	977	965	903	793	659	533	474
	PO	178	223	278	333	368	382	377	351	303	244	191	166
40°	PC	364	491	652	824	945	1001	980	883	727	550	398	331
	PO	121	172	239	312	364	388	379	338	271	197	135	108
50°	PC	216	353	542	764	931	1012	981	844	636	421	252	183
	PO	64	115	190	281	352	386	372	315	229	142	78	52
60°	PC	70	203	409	679	904	1019	974	785	520	273	105	39
	PO	15	58	134	241	331	377	359	283	178	84	25	8
70°	PC	0	46	256	575	880	1067	988	713	380	117	0	0
	PO	0	10	73	191	307	376	348	244	119	28	0	0
AMAX = 60 kg CO_2 ha^{-1} h^{-1} (1.67 × 10^{-6} kg CO_2 m^{-2} s^{-1})													
0°	PC	894	926	946	937	906	883	892	925	947	937	904	883
	PO	321	336	345	341	327	316	321	335	345	341	326	316
10°	PC	796	859	920	960	967	964	966	966	941	884	815	777
	PO	282	309	335	351	353	350	352	353	344	320	290	274
20°	PC	680	773	873	963	1010	1027	1021	988	915	812	707	654
	PO	234	272	314	351	369	375	373	361	332	289	245	224
30°	PC	543	663	803	942	1032	1070	1056	987	865	716	576	511
	PO	180	227	283	340	376	390	385	358	309	248	194	168
40°	PC	389	529	707	898	1033	1095	1071	964	790	595	427	354
	PO	122	174	242	318	372	396	387	344	275	199	137	109
50°	PC	227	377	584	829	1014	1104	1069	918	688	451	266	192
	PO	64	116	193	286	358	393	379	320	232	144	78	52
60°	PC	71	212	437	733	980	1107	1057	850	558	289	107	40
	PO	15	58	135	244	336	383	365	287	180	84	25	8
70°	PO	0	47	268	615	948	1151	1066	766	403	119	0	0
	PO	0	10	74	193	311	381	353	247	120	28	0	0

Table 2. (continued)

North. lat.		15 Jan.	15 Feb.	15 Mar.	15 Apr.	15 May	15 June	15 July	15 Aug.	15 Sep.	15 Oct.	15 Nov.	15 Dec.
AMAX = 70 kg CO_2 ha^{-1} h^{-1} (1.95 × 10^{-6} kg CO_2 m^{-2} s^{-1})													
0°	PC	959	995	1017	1007	973	947	958	993	1018	1007	971	947
	PO	326	341	350	346	331	321	325	340	351	346	331	321
10°	PC	852	922	989	1032	1039	1035	1037	1038	1012	949	873	832
	PO	285	313	340	357	358	356	357	359	349	324	294	277
20°	PC	726	827	937	1035	1086	1103	1097	1062	983	870	755	698
	PO	237	276	319	356	375	381	379	366	336	292	248	226
30°	PC	577	707	860	1011	1109	1149	1134	1060	927	765	613	542
	PO	182	229	287	345	381	396	391	363	313	251	195	170
40°	PC	410	562	755	962	1108	1175	1150	1033	845	633	452	372
	PO	123	176	245	322	377	402	392	349	278	201	138	110
50°	PC	236	397	620	885	1086	1183	1145	982	733	477	278	198
	PO	65	117	194	289	362	398	384	324	234	145	78	53
60°	PC	71	220	460	779	1046	1182	1129	905	591	301	109	40
	PO	15	58	136	246	340	388	369	290	181	85	25	8
70°	PC	0	47	277	649	1006	1222	1132	810	421	121	0	0
	PO	0	10	74	195	314	385	356	249	120	28	0	0

Table 3. As Tables 1 and 2, but for a horizontal leaf angle distribution. For comment, see text.

North. lat.		AMAX = 30 kg CO_2 ha^{-1} h^{-1} (0.84 x 10^{-6} kg CO_2 m^{-2} s^{-1})						AMAX = 60 kg CO_2 ha^{-1} h^{-1} (1.67 x 10^{-6} kg CO_2 m^{-2} s^{-1})					
		15 Jan.	15 Mar.	15 May	15 July	15 Sep.	15 Nov.	15 Jan.	15 Mar.	15 May	15 July	15 Sep.	15 Nov.
0°	PC	596	614	600	595	615	600	871	903	878	870	903	877
	PO	295	313	299	295	314	299	334	358	340	334	358	339
20°	PC	494	586	659	666	607	507	708	856	968	978	889	729
	PO	222	289	336	339	303	231	246	327	383	387	345	257
40°	PC	341	520	694	715	564	365	455	742	1012	1045	812	493
	PO	122	230	342	355	259	135	130	254	387	402	288	145
60°	PC	74	391	721	767	471	113	79	515	1027	1096	639	125
	PO	16	135	319	344	177	27	17	144	352	382	190	27

Tables 1 and 2 give the results for AMAX values ranging from 0.28 to 1.95 $\times 10^{-6}$ kg CO_2 m^{-2} (leaf) s^{-1}. AMAX $= 0.84 \times 10^{-6}$ is comparable to the one given by de Wit (1965). Our table gives lower values for overcast skies, especially in winter. For clear skies in summer our values are somewhat higher. These differences are mainly due to the changed photosynthesis-light response curve for individual leaves. In particular the light use efficiency is lower.

A question that deserves special attention is the influence of the leaf angle distribution. Therefore we also made some calculations for a horizontal leaf angle distribution. In Table 3 some results are presented. For an overcast sky the performance is always slightly better than that of a spherical leaf angle distribution. For a clear sky two regions can be distinguished, separated by the dashed line in Table 3. Generally spoken, for high solar altitudes the spherical leaf angle distribution is better and for low solar altitudes the horizontal one. Since the spherical leaf angle distribution is quite close to the vertical one, probably the same applies to the erect leaf angle position. Still, even under tropical conditions the differences are not impressive, this was also concluded by de Wit (1965), in spite of many references to the opposite.

Descriptive equations[1]

The results presented in Tables 1 and 2 can be used in a model with a time interval of one day to simulate crop production over a growing season. Tabulated input is cumbersome to handle, and an equation describing the tabulated results is certainly more convenient. A formal description might be obtained in a polynomial form with all relevant variables, but the number of terms required will then probably be almost as large as the number of data to be represented. There is better scope for an equation based on the description of the process itself. It should contain only a few parameters that must be found by curve fitting.

A useful notion for such a description is that crop photosynthesis, just like individual leaf photosynthesis, exhibits a light response curve of a saturation type. The actual crop photosynthesis amounts to a fraction of the saturation level LAI $\times$ AMAX. This fraction can be represented by a rectangular hyperbola according to

$$P = X/(X+1)$$

where X is a dimensionless variable defined as

$$X = RAD \times EFFE/(AMAX \times LAI)$$

RAD is the incoming visible radiation (PAR) averaged over the day and EFFE is the light use efficiency for incoming PAR. Since about 8 % of PAR is reflected by a closed canopy, an efficiency of 14 $\times 10^{-9}$ for individual leaves means a value of 12.9 $\times 10^{-9}$ kg CO_2 J^{-1} for EFFE. With an LAI of 5 and an AMAX of 0.83 $\times 10^{-6}$, actual photosynthesis is 50 % of the saturation value at 323 W m^{-2} of incoming PAR.

Both incoming PAR and actual crop photosynthesis are calculated as averages over the day. The effective daylength is shorter than the astronomical daylength and was found to be best estimated as the duration of time that solar height exceeds 8 degrees. The equations for the astronomical daylength DAYL (which we will need later) and the effective daylength DAYLE are

$$\delta = -23.45 \cos(360 \times (\text{DAY}+10)/365)$$
$$\text{SSIN} = \sin\delta \sin\lambda$$
$$\text{CCOS} = \cos\delta \cos\lambda$$
$$\text{DAYL} = 43200 \{ \pi + 2 \times \arcsin(\text{SSIN}/\text{CCOS}) \}/\pi$$
$$\text{DAYLE} = 43200 \{ \pi + 2 \times \arcsin((-\sin 8 + \text{SSIN})/\text{CCOS})\}/\pi$$

Here λ stands for the latitude of the site and δ for the declination of the sun. DAY is the number of the day in the year counted from 1 January onwards. These equations are valid for both hemispheres. The equation for RAD is

$$\text{RAD} = 0.5 \times \text{DRO}/\text{DAYLE}$$

DRO is the daily total of incoming short-wave radiation under an overcast sky, which consists for 50 % of PAR. The daily total crop photosynthesis for an overcast sky is given by

$$\text{PO}_f = \text{LAI} \times \text{AMAX} \times \text{DAYLE} \times \text{P}.$$

The equations given so far can be used to describe daily crop photosynthesis under an overcast sky. Under a clear sky some modification is necessary to account for the more unequal light distribution. Two classes of leaves are distinguished, sunlit and shaded. The average daily sunlit leaf area SLLAE is estimated as the sine of the solar height angle at noon ($90 + \delta - \lambda$). The basis for this estimation is that for a spherical leaf angle distribution the sunlit leaf area is given by $2 \times \sin(\beta)$ where β is the actual solar height. As a rough estimate the average sine of the solar height is half of that at noon, so that the factor 2 cancels. By searching the best fit it was found that 45 % of the incoming PAR is allotted to this average sunlit leaf area. A second effect of the unequal light distribution is that the saturation level is approached more gradually than under an overcast sky. Such a phenomenon can be represented by replacing the dimensionless variable X by $\ln(1+X)$ before substitution into the rectangular hyperbola (Goudriaan, in prep.). The equations are now given by

$$\text{X} = 0.45 \times \text{EFFE} \times \text{RADC}/(\text{SLLAE} \times \text{AMAX})$$
$$\text{X}' = \ln(1+\text{X})$$
$$\text{P} = \text{X}'/(1+\text{X}')$$
$$\text{PS} = \text{SLLAE} \times \text{DAYLE} \times \text{AMAX} \times \text{P}$$
$$\text{X} = 0.55 \times \text{EFFE} \times \text{RADC}/((\text{LAI-SLLAE}) \times \text{AMAX})$$
$$\text{X}' = \ln(1+\text{X})$$
$$\text{P} = \text{X}'/(1+\text{X}')$$
$$\text{PSH} = (\text{LAI-SLLAE}) \times \text{DAYLE} \times \text{AMAX} \times \text{P}$$
$$\text{PC}_f = \text{PS}+\text{PSH}.$$

Finally a linear regression was made between the model results and the results of the descriptive equations:

$$\hat{PC}_m = 0.95 \times PC_f + 2.05 \times 10^{-3} \qquad s = 0.96 \times 10^{-3}$$
$$\Delta_{max} = 3.23 \times 10^{-3} \qquad \text{kg } CO_2 \text{ m}^{-2} \quad (4)$$

$$\hat{PO}_m = 0.9935 \times PO_f + 0.11 \times 10^{-3} \qquad s = 0.055 \times 10^{-3}$$
$$\Delta_{max} = 0.26 \times 10^{-3} \qquad \text{kg } CO_2 \text{ m}^{-2} \quad (5)$$

In these equations $\hat{PC}_m$ and $\hat{PO}_m$ are the best estimates for the model results, PC_f and PO_f the results of the descriptive formulas, s the square root of the residual variance and Δ_{max} the maximum difference ever observed between model and its estimate, all over the range of 8 latitudes (0-70 degrees in ten degree intervals), 7 AMAXs (10-70 in intervals of 10), and 12 months, a total of 672 data points. The latitudes above 70 degrees are excluded, because they cause a severe deterioration of the goodness of fit the descriptive formulas.

For low values of the LAI, when the canopy does not form a closed crop surface, radiation is lost to the soil and the photosynthesis is reduced. The reduction can be estimated by the fraction intercepted

$$FINT = (1 - \exp(-0.8 \times LAI)) \qquad (6)$$

in which an extinction coefficient for PAR of 0.8 is assumed. The value 0.8 holds for a spherical leaf angle distribution, for a horizontal one the value 1.0 is better. Multiplication of $\hat{PC}_m$ and $\hat{PO}_m$ with FINT gives an estimate of the photosynthesis

Table 4. Gross CO_2 assimilation of a canopy with LAI = 1 and a spherical leaf angle distribution. The upper values have been calculated with the model, the lower values with the descriptive equations.

North. lat.		AMAX = 30 kg CO_2 ha^{-1} h^{-1} (0.84×10^{-6} kg CO_2 m^{-2} s^{-1})				AMAX = 60 kg CO_2 ha^{-1} h^{-1} (1.67×10^{-6} kg CO_2 m^{-2} s^{-1})			
		Dec.	Feb.	Apr.	June	Dec.	Feb.	Apr.	June
0°	PC	252.4	257.1	258.2	252.4	397.0	406.9	409.4	397.0
		238.9	244.2	245.5	238.9	391.9	402.4	404.8	391.9
	PO	138.7	145.4	147.0	138.7	161.6	170.9	173.2	161.6
		124.4	148.2	149.6	142.4	171.5	181.4	183.7	171.5
20°	PC	209.5	230.8	256.6	281.5	321.0	359.1	420.2	445.8
		197.7	217.8	253.9	269.7	313.7	354.6	418.6	445.1
	PO	102.8	121.7	151.4	161.4	116.0	139.9	178.4	190.4
		107.7	126.0	154.4	164.6	122.7	148.3	189.3	202.2
40°	PC	144.0	187.6	256.6	308.2	206.4	280.4	414.0	485.0
		134.9	177.3	251.6	295.4	188.8	268.2	410.6	486.2
	PO	53.9	82.6	141.5	172.2	57.9	91.2	163.2	201.7
		57.2	87.5	146.6	177.3	60.4	95.9	173.2	214.5
60°	PC	20.9	102.8	254.4	345.1	22.1	134.9	381.7	529.7
		—	91.9	241.8	334.5	—	113.5	368.5	533.0
	PO	4.4	29.8	144.7	173.7	4.4	31.1	127.3	197.8
		—	31.3	121.5	183.7	—	32.3	134.0	210.2

for a non-closed crop surface. However, for low values of AMAX photosynthesis is better related to leaf area than to intercepted radiation. In the extreme situation all leaves are photosynthesizing at the maximal rate all day long. Then the daily total is given by DAYL × AMAX × LAI. In fact, both estimates FINT × $\hat{P}$ and DAYL × AMAX × LAI, give an upper limit to the rate of photosynthesis. When these estimates are not much different it means that saturation with light gives a considerable reduction and that photosynthesis is less than predicted by FINT × $\hat{P}$. The best transition from the one situation to the other is obtained by:

```
C1 = P̂C × (1 — exp(—0.8 × LAI))
C2 = LAI × AMAX × DAYL
IF(C1.GT.C2) GO TO 2                                              (7)
C0 = C1
C1 = C2              interchange the values of C1 and C2
C2 = C0
2 PCR = C2 × (1 — exp(—C1/C2))
```

and likewise for overcast conditions.

In Table 4 the results of this descriptive procedure are compared to the model results for LAI of 1 and a spherical leaf angle distribution. The agreement is so good that the use of the descriptive equations is well justified.

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