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Physiological aspects of increased CO_2 concentration

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Introduction

The massive use of fossil fuels, to satisfy the energy demands of the industrialized world, leads to the emission of a large amount of C compounds into the atmosphere. Recent estimates place the amount at about 5×10^9 t of C per year. The release of C from soil organic material, following the conversion of forest lands to either grassland or arable land by deforestation in large scale reclamation activities and by shifting cultivation, could be equally important, but there is a continual debate on the magnitude of this source.

Estimates based on soil properties, climatic conditions and changes in land use, lead some authors to figures as high as 5×10^9 t of C released anually from the soil (Buringh, 1979), whereas others claim losses around 1×10^9 t (Loomis, 1979).

Most of the C is released in the form of CO_2. Part of this, it is not certain how much, is absorbed by the oceans, while the remainder leads to increased concentrations of it in the earth's atmosphere.

CO_2 also plays a vital role in the maintenance of human and animal life on earth since these depend on the ability of autotrophic green plants to produce organic material from CO_2, water, nitrogen and mineral nutrients, through the use of the sun's energy. In the light of possible changes in atmospheric CO_2, the influence of the atmospheric CO_2 concentration on the rate of formation of organic compounds is an important subject. Conflicting evidence on its effect is reported in the literature, apparently resulting from different behavior of different plant species under varying environmental conditions.

In this contribution, the quantitative consequences of various plant strategies towards changing external CO_2 concentrations will be considered.

Exchange processes

The formation of organic compounds by plants by photosynthesis and subsequent transformations requires a supply of the inorganic constituents used. Water, nitrogen and mineral nutrients are primarily taken up from the soil, or the nutrient solution in which the plant is placed, and enter it through its root system. CO_2, however, is supplied by the atmosphere and exchange takes place through the stomata. This contact with the atmosphere, necessary to maintain an influx of CO_2, results at the same time in an efflux of water vapour from the water saturated walls of the substomatal cavities. Transpiration and photosynthesis of plants are therefore directly linked and both processes may be considered simultaneously. The exchange of gases between the atmosphere and the substomatal cavity is a diffusion process, governed by the difference in concentrations between the outside air and that in the stomatal cavity and by the diffusion resistance along this pathway. The latter consists of 2 components: a) the resistance of a laminar layer, situated directly above the leaf surface and b) the stomatal resistance. The laminar resistance is a function of the dimensions of the leaf and the windspeed near its surface, typical values ranging between 2 and 50 sec m^{-1}. Stomatal resistances as dictated by the degree of aperture are of the order of 100-300 sec m^{-1} and constitute, therefore, the major hindrance to the exchange of the gases.

Stomatal resistance may be controlled by the internal water status of the plant. Where water is limiting, stomata close thus reducing the rate of transpirational loss. Direct effects of air humidity on stomatal resistance have also been reported (Lange et al., 1971) although light intensity seems to be the main variable controlling the day and night rhythm of opening and closing (Kuiper, 1961). Recent experimental evidence (Raschke, 1975; Goudriaan and van Laar, 1978a) suggests that in a number of cases stomatal resistance is dictated by the CO_2 concentration in the substomatal cavity and hence by the rate of CO_2 assimilation.

Carbon dioxide

The rate of CO_2 assimilation by an individual leaf at low irradiance is determined by the radiant energy available for the formation of energy-carrying substances. With high irradiance, energy is abundantly available and the rates of CO_2 diffusion and absorption become the limiting steps. CO_2-enrichment of the ambient air, resulting in an increased concentration gradient and enhanced diffusion, should then lead to higher assimilation rates. The results from measurements on sunflower leaves illustrate this fact (figure 1). The considerable success of CO_2 fertilization in the production of crops like cucumber and lettuce in glasshouses also indicates this.

Completely different behavior was found when maize was measured by an enclosure method (Louwerse and Eikhoudt, 1975) (figure 2) where the net assimilation rate remained constant above about 200 ppm CO_2 in the external air. This saturation type behavior is probably the result of CO_2-induced stomatal closure. Under certain conditions, plants regulate their stomatal resistance in such a way that the CO_2 concentration inside the stomatal cavity remains approximately constant.

Increased CO_2 diffusion rates, due to higher concentration gradients, produce partial stomatal closure which prevents CO_2-enrichment inside the stomatal cavity. The consequence of course is that the net

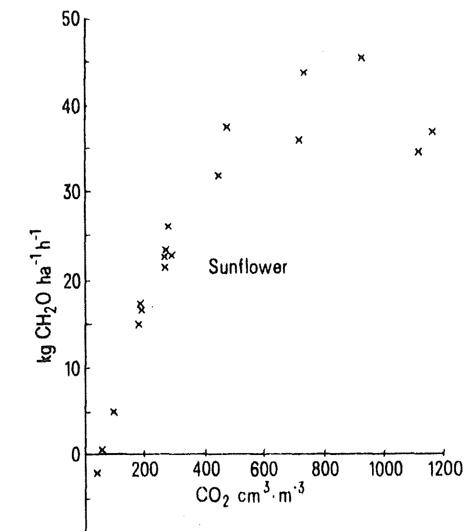

Fig. 1. The relation between net CO_2 assimilation of single sunflower leaves expressed in kg CH_2O ha^{-1} h^{-1} and the CO_2 concentration in the ambient air.

assimilation rate remains constant, while the rate of transpiration decreases as a result of the higher diffusion resistance. Where this type of regulation occurs, the internal CO_2 concentration is fixed near 120 ppm, in plants with the C4-photosynthetic pathway, and near 210 ppm in plants of the C3-type (Goudriaan and van Laar, 1978a).

A type of stomatal behavior intermediate between the 2 mentioned above has been reported for different plant species. In those plants, CO_2-enrichment of the external air leads to both increased net assimilation and a partial closure of the stomata (Raschke, 1975; Goudriaan and van Laar, 1978a). The plants then react in such a way that a constant proportionality is maintained between the CO_2 concentration in the ambient air and that in the stomatal cavity (figure 3). Again there is a difference between C3- and C4-plants, the former stabilizing the internal concentration about 0.7 times the external one, the latter about 0.4 times (Goudriaan and van Laar, 1978a).

The types of stomatal reaction to increased CO_2 concentration in the ambient air (and possibly more intermediate situations) described above have been reported for different plant species grown under identical conditions (Goudriaan and van Laar, 1978a), and for the same plant species grown under different conditions (Louwerse, 1980; Goudriaan and van Keulen, 1979). It is beyond the scope of this paper to speculate on the possible mechanisms that underly these differences. But it is of interest to examine their influence on assimilation and transpiration.

The effect of different CO_2 concentrations on assimilation, transpiration and water-use efficiency of crops

Method. The influence of differences in CO_2 concentration of the ambient air on crop performance is difficult to assess experimentally. Dynamic computer simulation models of crop growth that have been duly validated may be used for this purpose, by carrying out simulation experiments. The simulation model for daily photosynthesis and transpiration described by de Wit et al. (1978) was used for this study. However, their description of stomatal behavior given in the published version (which assumed a constant internal CO_2 concentration) was replaced in subsequent runs by the situation where the stomata were assumed to be fully open during daytime and completely closed during nighttime (absence of any regulation), or where a fixed proportionality was assumed between external and internal CO_2 concentration (see appendix). Runs were carried out for C3-plants, using wheat as an example, and for C4-plants using data representing maize (table 4). As a 'standard' day, the 21st of June was used, with a maximum and minimum temperature of 27.8 °C and 10.8 °C respectively, a water vapour pressure of 17.5 mbar and a windspeed of 1.2 m sec^{-1}. The parameters used for the description of stomatal behavior, were those given in the previous section.

A canopy with a leaf area index of 4, representative of a mature crop, was assumed, while both completely clear and completely overcast days were examined (Goudriaan and van Laar, 1978b). The external CO_2 concentrations assumed in the model were the present level of 330 ppm, and a level of 430 ppm which may be reached within the foreseeable future. To evaluate the influence of canopy water status, runs were made assuming a young active root system or an old suberized one.

Results and discussion. In table 1, the values for total daily net assimilation and total daily transpiration, both over a 24-h period, and their ratios are given for 3 latitudes and 2 external CO_2 concentrations for a canopy with C3-type photosynthesis. The same data are presented in table 2 for a canopy with a C4-type photosynthesis. The transpiration/assimilation ratio is used here as a measure for water-use efficiency to avoid difficulties associated with the conversion of primary photosynthates into structural plant material.

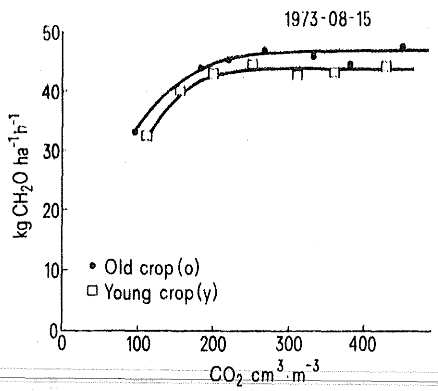

Fig. 2. The relation between net CO_2 assimilation expressed in kg CH_2O ha^{-1} h^{-1} and the CO_2 concentration in the ambient air for a young (y) and an old (o) maize crop as measured in crop enclosures (van Laar et al., 1977).

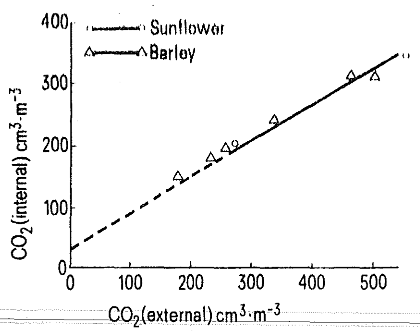

Fig. 3. The relation between the internal CO_2 concentration and the CO_2 concentration in the ambient air for sunflower and barley as measured in crop enclosures (Louwerse, 1980).

As an approximation, the water-use efficiency in terms of dry matter may be found by assuming an average conversion efficiency of 0.7 (Penning de Vries, 1974). The absolute values found in the presence of stomatal regulation and normal external CO_2 concentration of ±90 kg H_2O kg^{-1} (dry matter) for C3-plants and ±60 for C4-plants are very low when compared with values normally reported. Comparison of measured rates of CO_2 assimilation and transpiration in the field with those predicted by the model (de Wit et al., 1978) support, however, the conclusion that under certain conditions such values are realistic.

The data show firstly that the net assimilation rate of C4-plants exceeds that of C3-plants under favourable conditions of temperature and irradiance, but that potential hardly expresses itself under low light. Under such conditions, however, the daily transpiration of C4-plants is substantially lower since at these low assimilation rates the lower internal CO_2 concentration of the C4 species permits further closure of the stomata. The water-use efficiency of plants of this type is therefore substantially higher over the full range of irradiances (de Wit and Alberda, 1961; Downes, 1969). There is in fact very little difference

Table 1. Simulated values of total daily net CO_2 assimilation, total daily transpiration and their ratios for a C3-canopy of LAI = 4, growing at different latitudes on completely clear and completely overcast days at 2 levels of external CO_2 concentration

Latitude north			Internal CO_2 concentration fixed			Constant proportionality between external and internal CO_2 concentrations			Non-regulating stomata		
			Total daily net assimilation ($kg\ CO_2 \cdot ha^{-1}\ day^{-1}$)	Total daily transpiration ($mm \cdot day^{-1}$)	Transpiration/assimilation ratio ($kg\ H_2O \cdot kg\ CO_2^{-1}$)	Total daily net assimilation ($kg\ CO_2 \cdot ha^{-1}\ day^{-1}$)	Total daily transpiration ($mm \cdot day^{-1}$)	Transpiration/assimilation ratio ($kg\ H_2O \cdot kg\ CO_2^{-1}$)	Total daily net assimilation ($kg\ CO_2 \cdot ha^{-1}\ day^{-1}$)	Total daily transpiration ($mm \cdot day^{-1}$)	Transpiration/assimilation ratio ($kg\ H_2O \cdot kg\ CO_2^{-1}$)
10	Clear	330	659	4.2	64.2	672	4.6	68.2	771	8.0	104.2
	Overcast	-	298	1.9	62.7	304	2.2	73.0	408	7.0	172.9
30	Clear	-	753	4.8	64.3	769	5.2	68.1	873	8.5	97.2
	Overcast	-	330	2.0	61.8	337	2.4	72.2	450	7.3	162.0
50	Clear	-	785	5.0	63.2	803	5.4	67.0	919	9.2	100.0
	Overcast	-	329	2.1	63.2	335	2.5	73.5	453	8.0	177.2
10	Clear	430	663	2.6	39.8	805	4.2	52.3	942	8.0	82.5
	Overcast	-	298	1.2	40.3	317	1.9	58.9	456	7.0	154.5
30	Clear	-	759	3.0	39.8	927	4.8	52.2	1073	8.5	82.5
	Overcast	-	330	1.3	39.1	352	2.0	57.6	503	7.3	144.6
50	Clear	-	791	3.1	39.1	959	5.0	51.7	1122	9.2	81.8
	Overcast	-	329	1.3	40.7	348	2.1	59.2	502	8.0	159.4

Table 2. Simulated values of total daily net CO_2 assimilation, total daily transpiration and their ratios, for a C4-canopy of LAI = 4, growing at different latitudes on completely clear and completely overcast days, at 2 levels of external CO_2 concentration

Latitude north			Internal CO_2 concentration fixed			Constant proportionality between external and internal CO_2 concentrations			Non-regulating stomata		
			Total daily net assimilation ($kg\ CO_2 \cdot ha^{-1}\ day^{-1}$)	Total daily transpiration ($mm \cdot day^{-1}$)	Transpiration/assimilation ratio ($kg\ H_2O \cdot kg\ CO_2^{-1}$)	Total daily net assimilation ($kg\ CO_2 \cdot ha^{-1}\ day^{-1}$)	Total daily transpiration ($mm \cdot day^{-1}$)	Transpiration/assimilation ratio ($kg\ H_2O \cdot kg\ CO_2^{-1}$)	Total daily net assimilation ($kg\ CO_2 \cdot ha^{-1}\ day^{-1}$)	Total daily transpiration ($mm \cdot day^{-1}$)	Transpiration/assimilation ratio ($kg\ H_2O \cdot kg\ CO_2^{-1}$)
10	Clear	330	874	3.6	41.7	916	3.9	43.0	1185	9.6	81.4
	Overcast	-	321	1.3	39.6	324	1.3	41.0	464	7.9	171.2
30	Clear	-	1008	4.2	42.0	1057	4.6	43.2	1362	10.3	75.8
	Overcast	-	356	1.4	38.4	360	1.45	40.2	514	8.2	160.3
50	Clear	-	1039	4.3	41.1	1087	4.6	42.4	1408	11.0	78.5
	Overcast	-	351	1.4	39.6	354	1.45	40.9	506	9.0	178.3
10	Clear	430	874	2.7	31.3	1028	3.5	34.4	1400	9.6	68.7
	Overcast	-	321	1.0	30.5	332	1.1	34.0	503	7.9	158.0
30	Clear	-	1008	3.2	31.5	1189	4.1	34.6	1615	10.3	63.7
	Overcast	-	356	1.1	29.7	369	1.2	33.0	558	8.2	147.5
50	Clear	-	1039	3.2	30.9	1217	4.1	34.0	1661	11.0	66.4
	Overcast	-	351	1.1	30.7	362	1.2	34.3	547	9.0	164.9

between the tropical (10° NL) and temperate regions (50° NL) both in terms of total net assimilation and in terms of daily transpiration. A somewhat higher radiation level on completely clear days and a better light distribution, due to more daylight hours, results in both higher assimilation and higher transpiration rates farther north, and no change in the transpiration/assimilation ratio.

The effect of differences in stomatal behavior on crop performance shows up dramatically with both photosynthetic pathways: absence of CO_2-induced regulation leads to higher net assimilation rates accompanied, however, with an even greater proportional increase in transpiration rate, resulting in an increase of the transpiration/assimilation ratio by about 60%. The calculated transpiration rates in the absence of regulation are very high, amounting to between 60 and 70% of the total global radiation. It should, however, be borne in mind that they were obtained under the following assumptions:

a) Transport of moisture in the soil towards the root system and through the plant were nonlimiting. If such high rates were encountered under field conditions, it is likely that transport would be rate-limiting and the plants would suffer from moisture shortage at least during part of the day, leading to stomatal closure and reduced assimilation and transpiration.

b) All stomata over the entire canopy profile are fully open in the daytime, while in most cases some regulation occurs, so that the stomata of the lower leaves are likely to be more closed.

c) There is no feedback to the microclimate inside the canopy. Transport out of the canopy could in the field become a limiting factor (Goudriaan, 1977).

The effect of increased CO_2 concentration in the external air depends completely on the assumed stomatal behavior. When indeed CO_2-governed stomatal regulation is present, increased CO_2 concentration in the air hardly influences net assimilation rate, but it leads to considerably reduced transpiration rates and hence to a much more favorable transpiration/assimilation ratio. The difference between the situation with a fixed internal CO_2 concentration and that with a constant ratio between external and internal concentrations increases at higher CO_2 levels. The proportionality leads to substantially higher internal CO_2 concentrations in the latter case. It is obvious that the 'blessing' is shared here between

Table 3. Simulated values of total daily net CO_2 assimilation, total daily transpiration and their values for a C4-canopy of LAI=4, at different latitudes on clear days, at 2 levels of external CO_2 concentration, under water stress

Latitude north		Internal CO_2-concentration fixed			Constant proportionality between external and internal CO_2 concentrations			Non-regulating stomata		
		Total daily assimilation ($kg\ CO_2 \cdot ha^{-1}\ day^{-1}$)	Total daily transpiration ($mm \cdot day^{-1}$)	Transpiration/assimilation ratio ($kg\ H_2O \cdot kg\ CO_2^{-1}$)	Total daily assimilation ($kg\ CO_2 \cdot ha^{-1}\ day^{-1}$)	Total daily transpiration ($mm \cdot day^{-1}$)	Transpiration/assimilation ratio ($kg\ H_2O \cdot kg\ CO_2^{-1}$)	Total daily assimilation ($kg\ CO_2 \cdot ha^{-1}\ day^{-1}$)	Total daily transpiration ($mm \cdot day^{-1}$)	Transpiration/assimilation ratio ($kg\ H_2O \cdot kg\ CO_2^{-1}$)
10	Clear 330	810	3.3	40.6	822	3.4	41.0	859	5.4	62.6
30	Clear 330	929	3.8	40.6	942	3.9	42.0	982	5.8	58.8
50	Clear 330	988	4.0	40.2	1005	4.1	40.9	1062	6.55	61.7
10	Clear 430	873	2.7	31.4	960	3.2	33.0	1032	5.4	52.3
30	Clear 430	1004	3.15	31.4	1105	3.65	33.0	1185	5.8	48.9
50	Clear 430	1039	3.2	30.9	1164	3.8	32.9	1272	6.6	51.6

Table 4. Characteristics of the most important variables used to calculate photosynthesis and transpiration

Variable	Description	C3 plant	C4 plant	Unit
EFF	Efficiency of CO_2-assimilation derivative of CO_2-assimilation versus absorbed visible radiation	0.5	0.5	$kg\ CO_2\ ha^{-1}h^{-1}J^{-1}m^2sec$
PROP	EFF at saturating internal CO_2 concentration	0.98	0.917	$kg\ CO_2\ ha^{-1}h^{-1}J^{-1}m^2sec$
RCO2IM	Maximum internal CO_2 concentration	210	120	ppm
CO2C	CO_2 compensation point	50	10	ppm
CIEQ	Michaelis-Menton constant for internal CO_2 concentration, governing the efficiency	200	100	ppm
RMES	Mesophyll resistance for CO_2 diffusion	274	107	$sec\ m^{-1}$
RA	Resistance of boundary layer for heat	12	19	$sec\ m^{-1}$
$SRW_{minimum}$	Minimum stomatal resistance for transpiration, as determined by water potential	125	70	$sec\ m^{-1}$
WDL	Average width of leaves	0.02	0.05	m
DPL	Dissimilation rate of leaves that photosynthesize in daytime	0.2-1.2	0.2-1.2	$kg\ CO_2\ ha^{-1}h^{-1}$

assimilation and transpiration. The former increases, especially at high radiation levels, whereas the latter decreases by about 10%. The result is again a decrease in the transpiration/assimilation ratio by about 25%. Where stomatal regulation is completely absent, the higher CO_2 concentration is completely reflected in increased net assimilation, transpiration being at its maximum value. Also in this case, the transpiration/assimilation ratio changes to more favorable values.

In situations where plants are under moisture stress, the stomatal opening is governed by the degree of dehydration of the plant, whatever its normal type of behavior. Both assimilation and transpiration are then affected. In table 3 some simulation results are summarized, obtained under the assumption that the conductivity of the root system was too low to allow unrestricted uptake of moisture from the soil. Under the influence of stomatal closure, the CO_2 concentration inside the stomatal cavity is lower than without water stress. The diffusion of CO_2 into the intercellular space is therefore higher at the same stomatal conductance. This situation thus leads to a somewhat lower transpiration/assimilation ratio, as was also observed by Lof (1976) in container experiments. The effects are strongest in the originally non-regulating situation and they are virtually identical at low and high external CO_2 concentrations. The differences in total daily assimilation and transpiration among the different types of stomatal behavior are due to the fact that the imposed moisture stresses are not of the same duration and degree in all types.

Conclusions

Effects of increased CO_2 assimilation in the atmosphere on plant performance, and through that on agricultural production cannot be described by one general rule. The crucial factor is the plant's stomatal behavior and that may be different for different species or under different environmental conditions. Where CO_2-induced stomatal regulation is present, increased CO_2 concentration will result directly in lower daily rates of water loss, rather than in higher daily rates of production. This phenomenon may indirectly lead to higher production levels over the season under conditions where water is the main limiting factor for plant growth, since the available moisture is used more efficiently. Where CO_2-induced stomatal regulation is absent, plants may benefit from higher CO_2 levels through increased assimilation rates, which can be maintained only, however, when the moisture supply can also be maintained at near-optimum levels. In that case, water is used with very low efficiencies.

The fact that in the same species regulation is found to be present to a greater or lesser extent justifies the expectation that the trait may be manipulated. This would suggest that either through plant breeding or through management practices different properties could be induced for plants growing under different environmental conditions.

To much optimism with regard to the beneficial effects of increased CO_2 in the atmosphere seems unwarranted, however, since under natural conditions in many cases nutrient supply is the main limiting factor for primary production (van Keulen, 1977; Penning de Vries, 1978). That limitation will remain, whatever improvements in the momentary growth rates or water-use efficiencies may be achieved.

Appendix

In the published version of the simulation program used in this study (de Wit et al., 1978), stomatal behavior was described assuming full regulation at a constant internal CO_2-concentration. In the framework of the present paper the model was adapted to handle also the non-regulating situation and the one in which a constant ratio between external and internal CO_2 concentration is maintained. The necessary changes are described below.

Description. Practically all the changes are in MACRO called TRPH (de Wit et al., 1978, p. 97) (the program will be found on p. 792).

The parameter REGPAR indicates whether regulation is assumed (+1) or not (−1). When it is assumed (+1) and the stomatal resistance is not governed by the moisture status of the canopy (SRW) the calculation proceeds as previously. If SRW is larger than the resistance calculated on the basis of the regulatory mechanism or the minimum resistance in the case of absence of regulation (SRESL), the latter is set equal to SRW (line 10). The total diffusion resistance for CO_2 is calculated next and the internal CO_2 concentration is obtained through a series of successive better approximations (lines 13 through 20). A first estimate (GCI) follows from the assumption that the assimilation is light-saturated, and diffusion rate and assimilation rate are equal. On the basis of this value the light-saturated assimilation rate (AM) and the initial light-use efficiency (EFFE) are recalculated. The net assimilation rate follows from these values and the level of irradiance (VIS). Next a new value for the internal CO_2 concentration is calculated (FCI) and the procedure is repeated until a preset accuracy criterion (ERROR) has been satisfied.

The distinction between a fixed internal CO_2 concentration and a constant ratio between internal and external CO_2 concentration is described in section 7.1. The line defining RCO2I now reads:

RCO2I = INSW (RGPAR1, RIECO2*ECO2C, RCO2IM)

When RGPAR1 equals −1, a constant ratio is assumed, whereas a fixed concentration results for RGPAR1 = +1.

```
MACRO    TEHL, TSHL,AVTCP,NCRL=TRPH(VIS,NIR,LWR,AREA)
         ABSRAD=VIS+NIR+LWR
         IF (REGPAR.LT.1) GOTO 600
         EVA    =AMIN1 (EFF*VIS/AMAX,46.)
*        PREVENTS UNDERFLOW
         NCRIL =(AMAX+DPL)*(1.-EXP(-EVA) )-DPL
         SRESL = (68.4*(ECO2C-RCO2I)-RA*1.32*NCRIL)/AMAX1(0.001,NCRIL)/1.66
         IF (SRESL.GT.SRW.OR.SRESL.LT.0.) GO TO 700
    600  CONTINUE
         SRESL = SRW
         TSR=1.66*SRESL+RA*1.32
         GCI=(ECO2C/TSR+CO2C/RMES)/(1./RMES+1./TSR)
         ESTIM=AMIN1(1., (100./SRW)**2)
         CI=IMPL(GCI,ERROR,FCI)
         AM=(CI-CO2C)*68.4/RMES
         EFFE=PROP*CI/(CI+CIEQ)
         EVAE=AMIN1(EFFE*VIS/AM,46.)
         NCRIL=(AM+DPL)*(1.-EXP(-EVAE))-DPL
         FFCI=ECO2C-TSR/68.4*NCRIL
         FCI=CI+(FFCI-CI)*ESTIM
    700  SRES   =AMIN1 (RESCW,SRESL)
         ENP    =0.3*NCRIL
         EHL    =(SLOPE*(ABSRAD-ENP)+DRYP)/(PSCH*(RA*0.93+SRES)/RA+SLOPE)
         SHL    = ABSRAD-EHL-ENP
         TL     =TA+SHL*RR
         TEHL   =TEHL +AREA*EHL
         TSHL   =TSHL +AREA*SHL
         AVTCP  =AVTCP+AREA*TL
         NCRL   =NCRL +AREA*NCRIL
ENDMAC
```

Finally the non-regulating situation is defined by the value of the minimum stomatal resistance (70 sec m^{-1} for C4-plants, 125 sec m^{-1} for C3-plants) and that of SRW which assumes a very high value at night and is governed by the crop water status in daytime.

The description presented here implies that the values of the light saturated assimilation rate, AMAX, and the initial light use efficiency, EFF, defined in section 7.1 of the program are obtained from measurements on leaves with regulating stomata. Therefore transpiration rates should be measured concurrently with the determination of the photosynthesis-light response curve, so that the internal CO_2 concentration can be calculated (Goudriaan and van Laar, 1978a). The measured values of AMAX and EFF can then be adapted when conditions other than the assumed ones occur.

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