4.1 A simple and universal crop growth simulator: SUCROS87

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4.1.1 Introduction

Pathogen and host mutually affect each other's growth. However, in most phytopathological and entomological studies, fungal and insect epidemics are not considered in relation to their close interaction with the growth of the host plant. To study the complex interference between a crop and its diseases and pests, models that simulate the growth of the crop, the population dynamics of the pathogen, and the interaction between both, are useful.

In this Section, a crop growth model is described, designated SUCROS87 (Simple and Universal CROp growth Simulator, version 1987). SUCROS87 simulates the potential growth of a crop; i.e. its dry matter accumulation under ample supply of water and nutrients in a pest, disease and weed-free environment under the prevailing weather conditions.

The version of SUCROS87 presented here, differs substantially from that published by van Keulen et al. (1982). Canopy photosynthesis is calculated using a different method, which is more mechanistic and more accurate and flexible (Spitters, 1986; Goudriaan, 1986; Spitters et al., 1986). An improved method to simulate leaf area growth of the crop is introduced.

4.1.2 General structure of the model

The model simulates dry matter accumulation of a crop as a function of irradiation, temperature and crop characteristics. The calculation procedure is presented schematically in Figure 45.

The basis for calculating dry matter production, is the rate of gross CO_2 assimilation of the canopy. This rate is dependent on the radiation energy absorbed by the canopy, which is a function of incoming radiation and crop leaf area. From the absorbed radiation and the photosynthetic characteristics of single leaves, the daily rate of CO_2 assimilation of the crop is calculated. Part of the carbohydrates produced (CH_2O) are used to maintain the present biomass. The remaining carbohydrates are converted into structural dry matter. In this conversion, some of the weight is lost as growth respiration. The growth rate (ΔW in kg DM ha^{-1} d^{-1}) is thus obtained as

$$\Delta W = C_f(A - R_m) \qquad \text{Equation 61}$$

in which A is the gross assimilation (kg CH_2O ha^{-1} d^{-1}), R_m the maintenance respiration (kg CH_2O ha^{-1} d^{-1}), and C_f the conversion efficiency (kg DM kg^{-1} CH_2O).

light

photosynthesis parameters

70 GJ PAR $ha^{-1}d^{-1}$

$\longleftarrow$ 8 kg CO_2 GJ^{-1} PAR

assimilation rate

560 kg CO_2 $ha^{-1}d^{-1}$

O_2

x 30/44 kg CH_2O $kg^{-1}CO_2$

380 kg CH_2O $ha^{-1}d^{-1}$

maintenance respiration

x 0.80

growth respiration

300 kg CH_2O $ha^{-1}d^{-1}$

x 0.7 kg DM $kg^{-1}CH_2O$

growth rate

210 kg DM $ha^{-1}d^{-1}$

roots | storage organs | stems | leaves
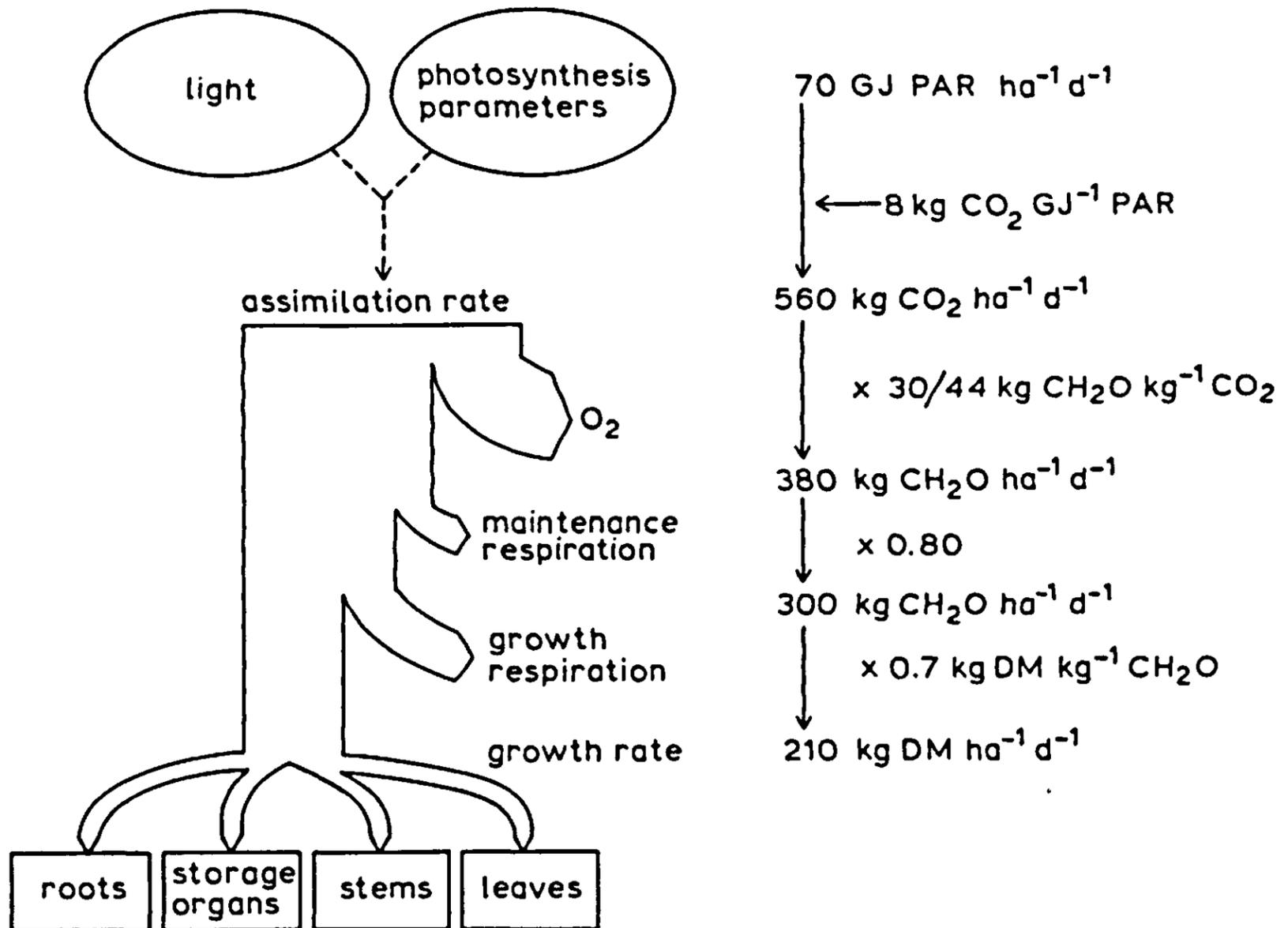
Figure 45. Diagram illustrating schematically the calculation procedure for daily crop growth rate. The numerical values given are typical for a crop that fully covers the ground, growing under average potential conditions in a temperate climate.

The dry matter produced is partitioned amongst the various plant organs, using partitioning factors introduced as a function of the phenological development stage of the crop. The dry weights of the plant organs are obtained by integrating their growth rates over time. The phenological development stage is calculated as a function of ambient temperature.

The model requires as input, data to describe the crop species or cultivar and the site. The site is characterized by its geographical latitude and by daily values of irradiation and temperature.

The computer program (Figure 46; Table 12) is structured in a small main program, followed by a block of parameters and functions to characterize the crop, and another block to characterize the site. Daily CO_2 assimilation and leaf area growth are calculated in separate modules.

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Figure 46. Listing of the program of the model SUCROS87.

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TITLE SUCROS87 SPRING WHEAT

* Dry weights of leaves(green,dead,total), stems, storage organs, roots
* and total above-ground biomass (kgDM/ha) as integrals of growth rates
      WLVG  = INTGRL(0.,GLV-DLV)
      WLVD  = INTGRL(0.,DLV)
      WLV   = WLVG + WLVD
      WST   = INTGRL(0.,GST)
      WSO   = INTGRL(0.,GSO)
      WRT   = INTGRL(0.,GRT)
      TADRW = WLV + WST + WSO

* Leaf area index (ha leaf / ha soil) as integral of leaf area growth rate
      GLAI  = GLA(DAY,DAYEM,DTEFF,DVS,NPL,LAO,RGRL,DELT,SLA,LAI,GLV)
*     LAI   = INTGRL(0.,GLAI - DLAI)
* but in wheat + 0.5 * ear area index:
      LAI   = 0.5 * EAI  +  INTGRL(0.,GLAI - DLAI)

* Development stage: 0 = emergence, 1 = anthesis, 2 = dead ripeness
      DVS = INTGRL(0.,DVR)
      DVR = INSW(DVS-1.,AFGEN (DVRVT,DAVTMP),AFGEN (DVRRT,DAVTMP)) ...
            * INSW(DAY-DAYEM,0.,1.)

* Daily total gross assimilation (DTGA, kg CO2/ha/d)
      DTGA,DSO = DASS(DAY,LAT,DTR,KDF,SCP,LAI,AMAX,EFF)

* Leaf photosynthesis rate at light saturation (kg CO2/ha leaf/h)
      AMAX  = AMX * AMDVS * AMTMP
      AMDVS = AFGEN(AMDVST,DVS)
      AMTMP = AFGEN(AMTMPT,DDTMP)

* Conversion from assimilated CO2 to CH2O
      GPHOT = DTGA * 30./44.

* Maintenance respiration (kg CH2O/ha/d)
      MAINT  = AMIN1(GPHOT, MAINTS * TEFF * MNDVS)
      MAINTS = 0.03*WLV + 0.015*WST + 0.015*WRT + MAINSO*WSO
      MNDVS  = WLVG / (WLV+NOT(WLV))
      TEFF   = Q10**((DAVTMP-25.)/10.)
PARAM  Q10 = 2.

* Fraction of dry matter growth occurring in shoots, leaves, stems,
* storage organs and roots
      FSH = AFGEN(FSHTB,DVS)
      FLV = AFGEN(FLVTB,DVS)
      FST = AFGEN(FSTTB,DVS)
      FSO = 1. - FLV - FST
      FRT = 1. - FSH

* Assimilate requirements for dry matter conversion (kgCH2O/kgDM)
      ASRQ = FSH *(1.46*FLV + 1.51*FST + ASRQSO*FSO) + 1.44*FRT

* Total growth rate (kg DM/ha/d) and
* growth rates of shoots ( leaves, stems, storage organs) and roots
      GTW = (GPHOT - MAINT) / ASRQ
      GSH = FSH * GTW
      GLV = FLV * GSH
      GST = FST * GSH
      GSO = FSO * GSH
      GRT = FRT * GTW
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* Death rate of leaves (DLAI in ha/ha/d, DLV in kg DM/ha/d)
     DLAI = LAI * (1. - EXP(-RDR * DELT))
     DLV  = WLVG * DLAI/(LAI+NOT(LAI))

* Daily global radiation (J/m2/d)
     DTR    = AFGEN(DTRT,DAY) * 1.E6
* Daily temperature (°C): maximum, minimum, average, daytime, effective

     DTMAX  = AFGEN(TMAXT,DAY)
     DTMIN  = AFGEN(TMINT,DAY)
     DAVTMP = 0.5 * (DTMAX+DTMIN)
     DDTMP  = DTMAX - 0.25 * (DTMAX-DTMIN)
     DTEFF  = AMAX1(0.,DAVTMP-TBASE)
* Temperature sum after emergence
     TSUMEM = INTGRL(0.,DTEFF * INSW(DAY-DAYEM,0.,1.))

* Simulation run specifications
     DAY    = AMOD(TIME,365.)
FINISH DVS = 2.
TIMER TIME = 90., FINTIM=271., DELT=1., PRDEL=5.
METHOD RECT
PRINT DVS,TADRW,WLV,WST,WSO,LAI,DTR,DTGA,GPHOT,GTW,MAINT,AMAX
```

***   WEATHER DATA   ***

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* Wageningen 1951 - 1980
* Daily global radiation (MJ/m2/d)
FUNCTION DTRT  = 15,2.1, 46,4.4, 74,7.8, 105,13.0, 135,16.3, ...
     166,17.5, 196,15.6, 227,13.8, 258,10.0, 288,5.8, 319,2.7, 349,1.7
* Daily maximum and minimum temperature (°C)
FUNCTION TMAXT = 15,4.3, 46,5.4, 74,8.9, 105,12.4, 135,17.3, ...
     166,20.5, 196,21.4, 227,21.5, 258,18.9, 288,14.3, 319,8.6, 349,5.5
FUNCTION TMINT = 15,-0.7, 46,-0.6, 74,1.2, 105,3.3, 135,7.3, ...
     166,10.3, 196,12.2, 227,12.0, 258,9.7, 288,6.5, 319,2.9, 349,0.6
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***   FIELD PARAMETERS   ***

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* Latitude of the site
     PARAM LAT = 52.
* Plant density (plants/m2) and day of emergence
     PARAM NPL = 210., DAYEM = 100.
```

***   SPECIES PARAMETERS SPRING WHEAT   ***

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* Initial leaf area (cm2/plant) and relative leaf growth rate (cm2/cm2/°C d)
     PARAM LAO = 0.57, RGRL = 0.0140, TBASE = 0.
* Specific leaf area of new leaves (ha leaf / kg leaf)
     PARAM SLA = 0.0022

* Potential photosynthesis rate at light saturation (kg CO2/ha leaf/h)
     PARAM AMX = 40.
* Effect of DVS on AMX
FUNCTION AMDVST = 0.,1., 1.,1., 2.,0.5, 2.5,0.
* Effect of daytime temperature on AMX
FUNCTION AMTMPT = 0.,0., 10.,1., 25.,1., 35.,0.01, 50.,0.01
* Initial light use efficiency ((kg CO2/ha leaf/h)/(J/m2/s))
     PARAM EFF = 0.45
```

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* Pre-anthesis and post-anthesis development rate(1/d) as a function of temp.
FUNCTION DVRVT = -10.,0., 0.,0., 30.,0.0377
FUNCTION DVRRT = -10.,0., 0.,0., 30.,0.0330

* Extinction coefient for diffuse PAR
    PARAM KDF = 0.6
* Scattering coefficient for PAR
    PARAM SCP = 0.20

* Maintenance coeficient for storage organs (kg CH2O/kg DM/d)
    PARAM MAINSO = 0.01
* Assimilate requirement for d.m. conversion in storage organs (kgCH2O/kgDM)
    PARAM ASRQSO = 1.41

* Fraction of total dry matter growth allocated to shoots (FSH)
* fraction of shoot d.m. growth allocated to leaves (FLV) and stems (FST)
* as a function of DVS
FUNCTION FSHTB = 0.,.50, .10,.50, .20,.60, .35,.78, .40,.83,       ...
    .50,.87, .60,.90, .70,.93, .80,.95, .90,.97, 1.,.98, 1.1,.99,  ...
    1.20,1.0, 2.5,1.0
* Leaf blades:
FUNCTION FLVTB = 0.,.65, .10,.65, .25,.70, .50,.50, .70,.15, .95,0.,...
    2.5,0.
* Stems + leaf sheaths + chaff:
FUNCTION FSTTB = 0.,.35, .10,.35, .25,.30, .50,.50, .70,.85,   ...
    .95,1.0, 1.05,0., 2.5,0.

* Relative death rate of green leaf area (1/d)
* due to developmental ageing (RDRDV) and self-shading (RDRSH)
    RDR = AMAX1(RDRDV, RDRSH)
    RDRDV = INSW(DVS-1.0, 0., AFGEN(RDRT,DAVTMP))
    RDRSH = LIMIT(0., 0.03, 0.03 * (LAI-LAICR) / LAICR)
FUNCTION RDRT = 0.,.03, 10.,.03, 15.,.04, 30.,.09
PARAM LAICR = 4.

* Ear area index (ha ears/ha ground)
    EAI = INTGRL(0., EAR * TADRW *   ...
    INSW(DVS-0.8,0.,1.) * INSW(-EAI,0.,1.) - INSW(DVS-1.3,0.,RDR*EAI))
* Ear area ratio (ha ears (2* one-sided projection) /kg shoot)
    PARAM EAR = 6.3E-5
* EAR: awnless 6.3 and awned cultivars 11.0 cm2/g shoot at anthesis

* Main references to the crop characteristics of wheat:
* van Keulen & Seligman (1987): AMTMPT,FSHTB,FLVTB,FSTTB,DVRVT,DVRRT
* Spitters & Kramer (1986): LAO,RGRL,SLA,FLVTB,FSTTB,EAR,DVRVT
* Groot (1987): FLVTB,FSTTB; van Keulen & de Milliano (1984): RDRT
END
STOP


* ------------------------------------------------------------------
* Subroutine GLA:
* computes daily increase of leaf area index (ha leaf/ ha ground/ d)
* ------------------------------------------------------------------
    FUNCTION GLA (DAY,DAYEM,DTEFF,DVS,NPL,LAO,RGRL,DELT,SLA,
    $             LAI,GLV)
    IMPLICIT REAL (A-Z)
*   during mature plant growth:
    GLA = SLA * GLV
*   during juvenile growth:
    IF ((DVS.LT.0.3).AND.(LAI.LT.0.75)) THEN
        GLA = LAI * (EXP(RGRL * DTEFF * DELT) - 1.)
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          ENDIF
*         at day of seedling emergence:
          IF ((DAY.GE.DAYEM).AND.(LAI.EQ.O.))  GLA = NPL * LAO * 1.E-4
*         before seedling emergence:
          IF (DAY.LT.DAYEM)  GLA = 0.
          RETURN
          END


* ---------------------------------------------------------------------
* Subroutine DASS
* computes potential daily assimilation (DTGA, kg CO2/ha/d)
* ---------------------------------------------------------------------
          SUBROUTINE DASS (DAY,LAT,DTR,KDF,SCP,LAI,AMAX,EFF,
         $                 DTGA,DSO)
          IMPLICIT REAL (A-Z)
          INTEGER T
*         distances and weights in Gaussian integration
          DIMENSION GSDST(3), GSWT(3)
          DATA GSDST /0.112702,  0.5,  0.887298/
          DATA GSWT  /0.277778,0.444444,0.277778/
*         daylength (h) and daily extra-terrestrial radiation (J/m2/d)
          CALL ASTRO (DAY,LAT,
         $            DAYL,SINLD,COSLD,DSINB,DSINBE,DSO)
*         daily radiation above the canopy (J/m2/d)
          CALL DRADIA (DSO,DTR,
         $             FRDF,DPAR)

          DTGA = 0.
          DO T = 1,3
             HOUR = 12. + DAYL*0.5*GSDST(T)
             CALL ASS (HOUR,DAYL,SINLD,COSLD,DSINB,DSINBE,DTR,
         $             FRDF,DPAR,KDF,SCP,LAI,AMAX,EFF,
         $             FGROS)
*         integration of instantaneous assimilation to a daily total (DTGA)
             DTGA   = DTGA  +  FGROS * DAYL * GSWT(T)
          ENDDO
          RETURN
          END


* ---------------------------------------------------------------------
* Subroutine ASTRO
* computes daylength and daily extra-terrestrial radiation
* from daynumber and latitude
*----------------------------------------------------------------------
          SUBROUTINE ASTRO (DAY,LAT,
         $                  DAYL,SINLD,COSLD,DSINB,DSINBE,DSO)
          IMPLICIT REAL (A-Z)
*         conversion factor from degrees to radians
          PI = 3.1416
          RD = PI / 180.
*         declination (DEC, degrees) of the sun as a function of daynumber(DAY)
          DEC   = -ASIN(SIN(23.45*RD) * COS(2.*PI*(DAY+10.)/365.))/RD
          SINLD = SIN(LAT*RD) * SIN(DEC*RD)
          COSLD = COS(LAT*RD) * COS(DEC*RD)
*         daylength (DAYL, h)
          DAYL = 12. * (1.+2. * ASIN(SINLD/COSLD)/PI)
*         daily integral of sine of solar inclination (DSINB)
          DSINB=3600.*(DAYL*SINLD+24.*COSLD*SQRT(1.-(SINLD/COSLD)**2)/PI)
*         daily integral of SINB with a correction for lower
*         atmospheric transmission at lower solar elevations (DSINBE)
          DSINBE=3600.*(DAYL*(SINLD+0.4*(SINLD*SINLD+0.5*COSLD*COSLD)) +
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      $    12.*COSLD*(2.+3.*0.4*SINLD)*SQRT(1.-(SINLD/COSLD)**2)/PI)
*       daily extra-terrestrial radiation (DSO, J/m2/d) from
*       corrected solar constant (SC, J/m2/s)
        SC  = 1370. * (1.+0.033*COS(2.*PI*DAY/365.))
        DSO = SC * DSINB
        RETURN
        END


* -----------------------------------------------------------------
* Subroutine DRADIA:
* computes daily photosynthetically active radiation (DPAR) and
* diffuse fraction of incoming radiation (FRDF)
* from atmospheric radiation transmission
* -----------------------------------------------------------------
        SUBROUTINE DRADIA (DSO,DTR,
      $                    FRDF,DPAR)
        IMPLICIT REAL (A-Z)
*       daily photosynthetically active radiation (J/m2/d)
        DPAR = 0.50 * DTR
*       fraction diffuse radiation(FRDF) from atmospheric transmission(ATMTR)
        ATMTR = DTR / DSO
        FRDF  = 0.23
        IF(ATMTR.LE.0.75) FRDF=1.33-1.46*ATMTR
        IF(ATMTR.LE.0.35) FRDF=1.-2.3*(ATMTR-0.07)**2
        IF(ATMTR.LE.0.07) FRDF=1.
        RETURN
        END


* -----------------------------------------------------------------
* Subroutine ASS
*
* calculates instantaneous assimilation (FGROS, kg CO2/ha/h)
* -----------------------------------------------------------------
        SUBROUTINE ASS (HOUR,DAYL,SINLD,COSLD,DSINB,DSINBE,DTR,
      $                 FRDF,DPAR,KDF,SCP,LAI,AMAX,EFF,
      $                 FGROS)
        IMPLICIT REAL (A-Z)
        INTEGER I,L
        DIMENSION GSDST(3), GSWT(3)
        DATA GSDST /0.112702,  0.5,  0.887298/
        DATA GSWT  /0.277778,0.444444,0.277778/
*       radiation above the canopy: PAR (J/m2/s)
        CALL RADIAT (HOUR,SINLD,COSLD,DSINB,DSINBE,FRDF,DPAR,
      $               PARDF,PARDR,SINB)

*       selection of canopy depths (LAIC from top)
        FGROS = 0.
        DO L = 1,3
           LAIC = LAI * GSDST(L)
*       absorbed radiation fluxes (J/m2/s)
           CALL RADPRF (PARDF,PARDR,SINB,KDF,SCP,LAIC,
      $                  PARLSH,PARLSL,PARLPP,FSLLA)
*       assimilation of shaded leaf area (kg CO2/ha leaf/hr)
           ASSSH = AMAX * (1.-EXP(-EFF*PARLSH/AMAX))
*       assimilation of sunlit leaf area (kg CO2/ha leaf/hr)
           ASSSL = 0.
           DO I = 1,3
              PARLSL = PARLSH + PARLPP * GSDST(I)
              ASSSL = ASSSL + AMAX*(1.- EXP(-PARLSL*EFF/AMAX)) * GSWT(I)
           ENDDO
*       hourly total gross assimilation (kg CO2/ha soil/hr)
           FGROS = FGROS + ((1.-FSLLA)*ASSSH + FSLLA*ASSSL)*LAI*GSWT(L)
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      ENDDO
      RETURN
      END


*     ----------------------------------------------------------------    ----
* Subroutine RADIAT
* computes instantaneous radiation above the canopy (J/m2/s)
*     -----------------------------------------------------------------    ----
      SUBROUTINE RADIAT (HOUR,SINLD,COSLD,DSINB,DSINBE,FRDF,DPAR,
     $                   PARDF,PARDR,SINB)
      IMPLICIT REAL (A-Z)
      PI    = 3.1416
*     sine of solar inclination (SINB)
      SINB  = AMAX1(0.,SINLD+COSLD*COS(2.*PI*(HOUR+12.)/24.))
*     diffuse PAR (PARDF) and direct PAR (PARDR) in J/m2/s
      PAR   = DPAR * SINB * (1.+0.4*SINB) / DSINBE
      PARDF = AMIN1(PAR, FRDF * DPAR * SINB/DSINB)
      PARDR = PAR - PARDF
      RETURN
      END


*     ------------------------------------------------------------------    -
* Subroutine RADPRF
* computes the radiation profile within the canopy and gives
* instantaneous values of absorbed radiation for successive leaf layers
*     ------------------------------------------------------------------
      SUBROUTINE RADPRF (PARDF,PARDR,SINB,KDF,SCP,LAIC,
     $                   PARLSH,PARLSL,PARLPP,FSLLA)
      IMPLICIT REAL (A-Z)
*     canopy reflection coefficient (REFL)
      REFL   = (1. - SQRT(1.-SCP)) / (1. + SQRT(1.-SCP))
*     extinct.coeff. for direct component(KBL) and total direct flux(KDRT)
*     cluster factor as  ratio between empirical and theoretical value of KDF
      CLUSTF = KDF / (0.8*SQRT(1.-SCP))
      KBL    = (0.5/SINB) * CLUSTF
      KDRT   = KBL * SQRT(1.-SCP)

*     absorbed radiation fluxes per unit leaf area (J/m2/s):
*     diffuse flux, total direct flux, direct component of direct flux
      PARLDF = (1.-REFL) * PARDF * KDF * EXP(-KDF *LAIC)
      PARLT  = (1.-REFL) * PARDR * KDRT* EXP(-KDRT*LAIC)
      PARLDR = (1.-SCP)  * PARDR * KBL * EXP(-KBL *LAIC)

*     absorbed fluxes (J/m2 leaf/s) for shaded and sunlit leaves
      PARLSH = PARLDF + (PARLT - PARLDR)
      PARLSL = PARLSH + (1.-SCP) * KBL * PARDR
*     direct par absorbed by leaves perpendicular on direct beam
      PARLPP = PARDR * (1.-SCP)/SINB

*     fraction sunlit leaf area
      FSLLA = EXP(-KBL*LAIC)  *  CLUSTF
      RETURN
      END


ENDJOB
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Table 12. Definition of the abbreviations used in the model SUCROS87, as listed in Figure 46.

Name	Description	Unit
AMAX	actual CO_2 assimilation rate at light saturation for individual leaves	$kg\,ha^{-1}h^{-1}$
AMDVS	factor accounting for effect of development stage on AMX	–
AMTMP	factor accounting for effect of daytime temperature on AMX	–
AMX	potential CO_2 assimilation rate at light saturation for individual leaves	$kg\,ha^{-1}h^{-1}$
ASRQ	assimilate (CH_2O) requirement for dry matter production	$kg\,kg^{-1}$
ASRQSO	assimilate requirement for dry matter production of storage organs	$kg\,kg^{-1}$
ASSSH	CO_2 assimilation rate of shaded leaf area	$kg\,ha^{-1}h^{-1}$
ASSSL	CO_2 assimilation rate of sunlit leaf area	$kg\,ha^{-1}h^{-1}$
ATMTR	atmospheric transmission coefficient	–
CLUSTF	cluster factor	–
COSLD	intermediate variable in calculating solar declination	–
DAVTMP	daily average temperature	°C
DAY	day number since 1 January	d
DAYEM	day of crop emergence	d
DAYL	daylength	$h\,d^{-1}$
DDTMP	daily average daytime temperature	°C
DEC	solar declination	degrees
DLV	death rate of leaves	$kg\,ha^{-1}d^{-1}$
DPAR	daily photosynthetically active radiation	$J\,m^{-2}d^{-1}$
DS0	daily extra-terrestrial radiation	$J\,m^{-2}d^{-1}$
DSINB	integral of SINB over the day	$s\,d^{-1}$
DSINBE	as DSINB, but with a correction for lower atmospheric transmission at lower solar elevations	$s\,d^{-1}$
DTEFF	daily effective temperature	°C
DTGA	daily total gross CO_2 assimilation of the crop	$kg\,ha^{-1}d^{-1}$
DTMAX	daily maximum temperature	°C
DTMIN	daily minimum temperature	°C
DTR	daily total solar radiation	$J\,m^{-2}d^{-1}$
DVR	development rate	d^{-1}
DVRRT	development rate in pre-anthesis phase as a function of temperature	d^{-1}
DVRVT	development rate in post-anthesis phase as a function of temperature	d^{-1}

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DVS	development stage of the crop	–
EFF	initial light use efficiency for individual leaves	$(kg\,ha^{-1}\,h^{-1})$ $(J\,m^{-2}\,s^{-1})^{-1}$
FGROS	instantaneous CO_2 assimilation rate of the crop	$kg\,ha^{-1}\,h^{-1}$
FLV	fraction of shoot d.m. increase allocated to leaves	–
FRDF	diffuse radiation as a fraction of total solar radiation	–
FRT	fraction of total d.m. increase allocated to roots	–
FSH	fraction of total d.m. increase allocated to shoots	–
FSLLA	fraction of sunlit leaf area	–
FSO	fraction of shoot d.m. increase allocated to storage organs	–
FST	fraction of shoot d.m. increase allocated to stems	–
GLA	dummy for GLAI	$ha\,ha^{-1}\,d^{-1}$
GLAI	growth rate of leaf area index of the crop	$ha\,ha^{-1}\,d^{-1}$
GLV	d.m. growth rate of leaves	$kg\,ha^{-1}\,d^{-1}$
GPHOT	daily total gross assimilation (CH_2O)	$kg\,ha^{-1}\,d^{-1}$
GRT	d.m. growth rate of roots	$kg\,ha^{-1}\,d^{-1}$
GSDST	distance in Gaussian integration	–
GSH	d.m. growth rate of shoots	$kg\,ha^{-1}\,d^{-1}$
GSO	d.m. growth rate of storage organs	$kg\,ha^{-1}\,d^{-1}$
GST	d.m. growth rate of stems	$kg\,ha^{-1}\,d^{-1}$
GSWT	weighting factor in Gaussian integration	–
GTW	total d.m. growth rate of the crop	$kg\,ha^{-1}\,d^{-1}$
HOUR	hour during the day	h
KBL	extinction coefficient for direct component of direct PAR flux	$ha\,ha^{-1}$
KDF	extinction coefficient for diffuse PAR flux	$ha\,ha^{-1}$
KDRT	extinction coefficient for total direct PAR flux	$ha\,ha^{-1}$
L	counter in DO loop	–
LA0	extrapolated leaf area at field emergence	$cm^2\,plant^{-1}$
LAI	leaf area index	$ha\,ha^{-1}$
LAIC	partial cumulated leaf area index at various canopy depths	$ha\,ha^{-1}$
LAICR	critical LAI beyond which death due to self-shading occurs	$ha\,ha^{-1}$
LAT	latitude of the site	degrees
MAINSO	maintenance respiration coefficient of storage organs (CH_2O per unit d.m.)	$kg\,kg^{-1}$
MAINT	maintenance respiration (CH_2O) of the crop	$kg\,ha^{-1}\,d^{-1}$
MAINTS	maintenance respiration (CH_2O) of the crop at reference temperature	$kg\,ha^{-1}\,d^{-1}$
MNDVS	factor accounting for effect of development stage on maintenance respiration	–
NPL	plant density	$plants\,m^{-2}$

PAR	instantaneous flux of incoming photosynthetically active radiation	$J m^{-2} s^{-1}$
PARDF	instantaneous diffuse flux of incoming PAR	$J m^{-2} s^{-1}$
PARDR	instantaneous direct flux of incoming PAR	$J m^{-2} s^{-1}$
PARLDF	absorbed diffuse PAR per unit leaf area	$J m^{-2} s^{-1}$
PARLDR	absorbed direct component of direct PAR per unit leaf area	$J m^{-2} s^{-1}$
PARLPP	direct PAR absorbed by leaves perpendicular to direct beam	$J m^{-2} s^{-1}$
PARLSH	absorbed PAR for shaded leaves (per unit leaf area)	$J m^{-2} s^{-1}$
PARLSL	absorbed PAR for sunlit leaves (per unit leaf area)	$J m^{-2} s^{-1}$
PARLT	absorbed total direct PAR per unit leaf area	$J m^{-2} s^{-1}$
PI	ratio of circumference to diameter of circle	–
Q10	factor accounting for increase in maintenance respiration with a 10°C rise in temperature	–
RD	factor to convert degrees to radians	radians degree^{-1}
RDR	relative death rate of leaves	d^{-1}
RDRDV	relative death rate due to developmental ageing	d^{-1}
RDRSH	relative death rate due to self-shading at high LAI	d^{-1}
REFL	crop reflection coefficient for PAR	–
RGRL	relative growth rate during exponential leaf area growth	$cm^2 cm^{-2}$ $°C^{-1} d^{-1}$
SC	solar constant, corrected for varying distance sun-earth	$J m^{-2} s^{-1}$
SCP	scattering coefficient of leaves for PAR	–
SINB	sine of solar inclination above the horizon	–
SINLD	intermediate variable in calculating solar declination	–
SLA	specific area of new leaves	ha(leaf) kg^{-1}
T	counter in DO loop	–
TADRW	total above-ground dry weight	kg ha^{-1}
TBASE	base temperature for juvenile leaf area growth	°C
TEFF	factor accounting for effect of temperature on maintenance respiration	–
TSUMEM	temperature sum after emergence	°C d
WLV	dry weight of leaves (green + dead)	kg ha^{-1}
WLVD	dry weight of dead leaves	kg ha^{-1}
WLVG	dry weight of green leaves	kg ha^{-1}
WRT	dry weight of roots	kg ha^{-1}
WSO	dry weight of storage organs	kg ha^{-1}
WST	dry weight of stems	kg ha^{-1}

4.1.3 Description of the model

Daily gross assimilation: an outline of the approach Rates of gross CO_2 assimilation are calculated from the absorbed light energy and the photosynthesis-light response of individual leaves. If illumination intensities, averaged over the day and over the canopy, were applied, daily canopy assimilation would be seriously overestimated, because photosynthesis responds to light intensity in a nonlinear, convex way. In the model, the temporal and spatial variation in illumination intensity over the leaves is, therefore, taken into account.

First, the instantaneous radiation flux at the top of the canopy is derived from measured daily irradiance. A distinction is made between diffuse skylight and direct sunlight because of the large difference in illumination intensity between shaded leaves, receiving only diffuse radiation, and sunlit leaves, receiving both direct and diffuse radiation. Subsequently, the vertical profiles of the radiation fluxes within the canopy are characterized. From these profiles, the absorbed radiation for each horizontal leaf layer is derived. On the basis of the photosynthesis-light response of individual leaves, the assimilation rate in a leaf layer is calculated for sunlit and shaded leaves separately. Daily crop assimilation is obtained by integrating these assimilation rates over the leaf layers and over the day.

This comprehensive approach for calculating crop assimilation rate is discussed here only in general terms. Detailed discussions are given by Spitters et al. (1986) for calculating the diffuse and direct radiation fluxes above the canopy, by Spitters (1986) for calculating assimilation rates from these fluxes, and by Goudriaan (1986) for the Gaussian integration method used to integrate assimilation rates over the canopy and over the day. Simplified approaches for calculating crop assimilation rates are discussed in Subsections 4.2.4 and 4.2.5.

The model SUCROS87 can be applied, without a thorough understanding of the subroutines used, to calculate the daily crop assimilation rate. Readers not interested in the details can, therefore, proceed directly to the section on carbohydrate production.

Radiation fluxes above the canopy Measured daily total irradiance (wavelength 300-3000 nm) is used as input for the model. Incoming radiation is partly direct, with the angle of incidence equal to the angle of the sun, and partly diffuse, with incidence under various angles. The diffuse flux is the result of the scattering of sun rays by clouds, gases and dust in the atmosphere. The proportion of diffuse radiation in the total radiation is, thus, dependent on the degree of scattering. To characterize this, the measured daily total radiation is compared with the quantity that would have reached the earth's surface in the absence of an atmosphere; a value that can be calculated from theoretical considerations. The ratio of both values is called the atmospheric transmission. The proportion of diffuse radiation is derived from the atmospheric transmission on the basis of an empirical relationship.

Irradiance intensity changes during the day according to the sine of the elevation of the sun above the horizon (sin β). On the basis of this relation, the instantaneous flux densities of diffuse and direct radiation are calculated from their daily totals.

Only half the incoming radiation is photosynthetically active (PAR, wavelength 400-700 nm). This visible fraction, usually called 'light', is used to calculate CO_2 assimilation.

Radiation profiles within the canopy Incoming radiation is partly reflected by the canopy. The reflection coefficient (ρ) of the canopy is a function of solar elevation, leaf angle distribution, and reflection and transmission properties of the leaves. The complementary fraction ($1 - \rho$) is potentially available for absorption by the canopy.

Radiation fluxes decrease more or less exponentially with increasing leaf area within the canopy:

$$I_L = (1 - \rho)I_0 e^{-kL}$$

Equation 62

in which I_0 is the flux at the top of the canopy (J m^{-2} ground s^{-1}), L the cumulative leaf area index (counted from the top of the canopy downwards) (m^2 leaf m^{-2} ground), I_L the net flux at depth L, and k the extinction coefficient. The diffuse and direct fluxes each attenuate at a different rate, i.e. they are characterized by radiation-specific extinction coefficients. The extinction coefficients are calculated as a function of solar elevation, leaf angle distribution, and the scattering coefficient of individual leaves.

Part of the direct flux intercepted by the leaves is scattered (i.e. reflected or transmitted). Hence, the direct flux segregates inside the canopy into a scattered, diffused component and a direct component. Both are treated separately in the model.

The decline of the radiation flux is a measure for its absorption. The rate of absorption at a depth L in the canopy is obtained by taking the derivative of Equation 62 with respect to cumulative leaf area index in the canopy:

$$I_{aL} = -dI_L/dL = k(1 - \rho)I_0 e^{-kL}$$

Equation 63

in which the subscript a refers to absorbed radiation (J m^{-2} leaf s^{-1}).

Instantaneous assimilation rate per leaf layer The photosynthesis-light response of individual leaves can be described by the exponential function:

$$A_L = A_m(1 - e^{-\varepsilon I_{aL}/A_m})$$

Equation 64

in which A_L is the gross assimilation rate (kg CO_2 m^{-2} leaf s^{-1}), A_m the gross assimilation rate at light saturation (kg CO_2 m^{-2} leaf s^{-1}), and ε the initial slope or light use efficiency (kg CO_2 J^{-1} absorbed). Substituting the appropriate value for the absorbed photosynthetically active radiation (I_{aL} in Equation 63) yields the assimilation rate for each specific leaf layer.

Instantaneous assimilation rates for each leaf layer are calculated for shaded leaf area and sunlit leaf area separately. The shaded leaf area receives the diffuse flux and the scattered component of the direct flux. The sunlit leaf area receives both diffuse and direct flux. Illumination intensity of sunlit leaves varies strongly with leaf angle. In the model, the assimilation rate of the sunlit leaf area is, therefore, integrated over the leaf angle distribution.

The assimilation rate per unit leaf area in a canopy layer, is the sum of the assimilation rates of sunlit and shaded leaves, taking into account their proportion in each layer. The proportion of sunlit leaf area at depth L in the canopy equals the proportion of the direct component of the direct flux reaching that depth. This proportion is calculated in analogy to Equation 62, introducing the extinction coefficient of the direct radiation component.

Daily gross assimilation of the canopy The daily rate of CO_2 assimilation of the crop is obtained by integrating the instantaneous rates per leaf layer over the canopy leaf area index and over the day. This is achieved by using the Gaussian integration method, a simple and fast method of numerical integration (Scheid, 1968). The Gaussian integration method specifies the discrete points at which the value of the function to be integrated has to be calculated, and the weighting factors that must be applied to these values to attain minimum deviation from the analytical solution. To integrate numerically a continuous function over the standardized interval (0,1) of the independent variable, using the 3-point algorithm, the function value is calculated at the discrete points $0.5 - \sqrt{0.15}, 0.5$ and $0.5 + \sqrt{0.15}$. The integrated value is obtained by applying a weighting factor of 1.6 to the value at 0.5 and 1.0 to both other values. (In Figure 46, the Gaussian distances and weighting factors are implemented as DATA statements). For calculating daily total assimilation, the 3-point method performs very well (Goudriaan, 1986; Spitters, 1986). The assimilation rates at three depths in the canopy are calculated three times daily (Figure 47).

The three canopy depths selected according to the Gaussian criteria are:

$$L = (0.5 + p\sqrt{0.15})LAI \qquad p = -1,0,1 \qquad \text{Equation 65}$$

where LAI is the total leaf area index of the crop. The assimilation rates (A′) at these depths are calculated according to Equation 64. The weighted average of these assimilation rates is:

$$A_h = LAI(A'_{-1} + 1.6A'_0 + A'_1)/3.6 \qquad \text{Equation 66}$$

where A_h is the hourly canopy assimilation rate (kg CO_2 ha^{-1} h^{-1}).

To integrate over the day, three points in time are selected in the period from noon to sunset:

$$t_h = 12 + 0.5D(0.5 + p\sqrt{0.15}) \qquad p = -1,0,1 \qquad \text{Equation 67}$$

where D is the daylength (h). Daily total canopy assimilation is obtained as the

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PAR$_0$
Jm^{-2}s^{-1}

200

100

0

12   24
                      solar time (h)

relative intensity (PAR$_L$/PAR$_0$)
0   0.5   1.0

A$'_{-1}$ 1.0   26.39   21.14   5.58 kg CO$_2$ ha^{-1}(leaf)h^{-1}

A$'_0$ 16   9.86   6.39   1.24

2.5

A$'_1$ 1.0   2.95   1.62   0.31   x 5/3.6 LAI

A$_h$ 62.67   45.81   10.95 kg CO$_2$ ha^{-1}(ground) h^{-1}

W   10   16   1.0

5.0
LAI

↓ x 14.22/3.6   daylength
580.3   kg CO$_2$ ha^{-1}(ground)d^{-1}
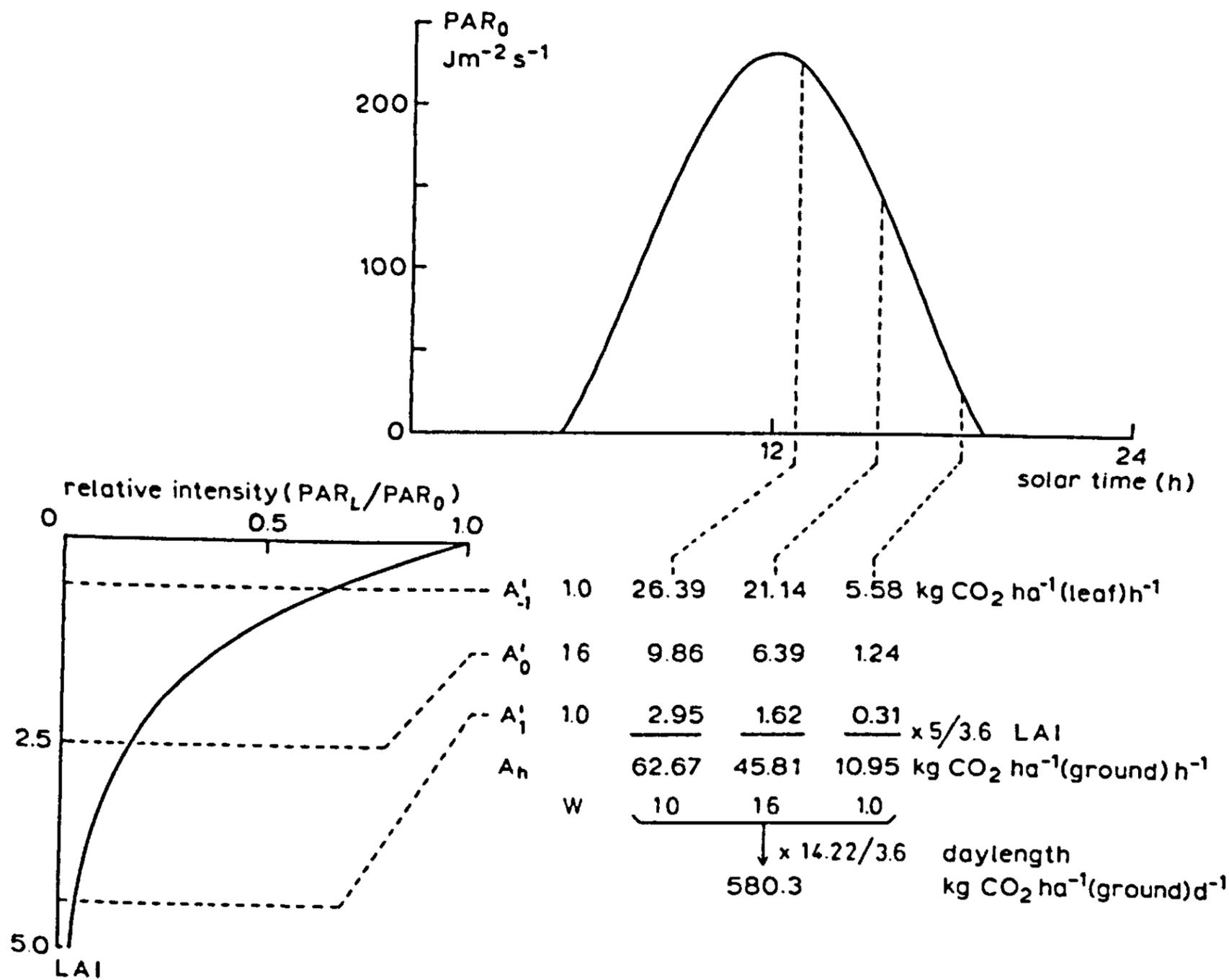
Figure 47. Summary of the Gaussian integration procedure. At three selected moments of the day, incident photosynthetically active radition (PAR$_0$) is computed. Using this radiation, assimilation is computed at three selected depths in the canopy. Integration is performed following the Gaussian algorithm, i.e. a summation using certain weighting factors (w) (Equations 65-68). The daily assimilation rate of a standard crop (LAI = 5, k = 0.72, A$_m$ = 40 kg ha^{-1}h^{-1}, ε = 0.45 kg ha^{-1}h^{-1} (J m^{-2}s^{-1})$^{-1}$ is presented for an average day in the Dutch growing season (18 August, 52° NL, PAR = 7.07 MJ m^{-2}d^{-1}).

weighted average of the instantaneous assimilation rates (Equation 66) at the three points in time:

$$A_d = D(A_{h, -1} + 1.6A_{h, 0} + A_{h, 1})/3.6 \qquad \text{Equation 68}$$

where A_d is the total daily gross assimilation (kg CO_2 ha^{-1} d^{-1}).

Carbohydrate production In the photosynthesis process, CO_2 is reduced to carbohydrates (CH_2O) using the energy supplied by the absorbed light. This reaction can be written as:

$$CO_2 + H_2O \rightarrow CH_2O + O_2$$

For each kg of CO_2 absorbed, 30/44 kg of CH_2O is formed, the numerical values representing the molecular weights of CH_2O and CO_2, respectively.

Maintenance respiration Some of the carbohydrates formed are respired to provide energy for maintaining the existing biostructures. The maintenance processes include resynthesis of degraded proteins (especially enzyme turnover) and maintenance of ionic gradients across cell membranes. The higher the metabolic activity of the plant, the higher the maintenance costs (Penning de Vries, 1975); probably due to a higher enzyme turnover and higher transport costs.

The maintenance costs may be estimated on the basis of the quantities of proteins and minerals present in the biomass, and crop metabolic activity, as presented by de Wit et al. (1978). This method, however, requires information on the nitrogen and mineral contents of the vegetation.

Based on the results of this analysis, typical values for the maintenance coefficients of various plant organs have been derived by Penning de Vries & van Laar (1982). In the model SUCROS87, these coefficients are used to calculate the maintenance requirements of the crop according to:

$$R_{m,r} = 0.03 \, W_{lv} + 0.015 \, W_{st} + 0.015 \, W_{rt} + 0.01 \, W_{so} \qquad \text{Equation 69}$$

in which $R_{m,r}$ is the maintenance respiration rate (kg CH_2O ha^{-1} d^{-1}) at a reference temperature of 25 °C, and W is the organ dry weight (kg ha^{-1}) with the subscripts referring to leaves, stems, roots and storage organs, respectively. The numerical values in Equation 69, representing the maintenance coefficients, have the dimension kg CH_2O kg^{-1} DM d^{-1}.

Higher temperatures accelerate the turnover rates in plant tissue and hence the costs of maintenance. An increase in temperature of 10 °C increases maintenance respiration by a factor of about 2 ($Q_{10} = 2$) (Penning de Vries & van Laar, 1982; Kase & Catský, 1984). The rate of maintenance respiration at temperature, T, is thus:

$$R_m(T) = R_{m,r} \cdot 2^{(T-T_r)/10} \qquad \text{Equation 70}$$

The reference (T_r) is assumed to be 10 °C higher for tropical species than for

species from temperate climates, because the maintenance requirements of a crop are likely to be adapted to the growth temperatures.

When the crop ages, its metabolic activity and, therefore, its maintenance requirements decrease. This effect could be accounted for by relating the maintenance coefficients to the N content of the tissues (van Keulen & Seligman, 1987). However, N contents are not simulated in the model. Therefore, maintenance respiration is assumed to be proportional to the fraction of the accumulated leaf weight that is still green. This reduction factor is also applied to the maintenance respiration of the other plant organs, as it is assumed that dying of stem tissue and roots proceeds simultaneously to dying of leaves.

For the storage organs, a storage component and a non-storage component are distinguished. The storage component (mainly carbohydrates) is metabolically inactive and does not require maintenance. For the non-storage component, the maintenance coefficient is assumed to be identical to that of the stem. For instance, in sugar beet, the sugar content is about 80% on a dry weight basis, so the maintenance coefficient of the beet is $(1 - 0.80) \cdot 0.015 + 0.80 \cdot 0 = 0.003$ $kg \, CH_2O \, kg^{-1} \, DM \, d^{-1}$.

It should be emphasized that modelling of maintenance respiration is still in a preliminary phase. The physiological basis is rather weak and measurements of maintenance costs are scarce and inaccurate.

Growth respiration The primary assimilates in excess of the maintenance costs, are available for conversion into structural plant material (Equation 61). In this conversion process of the glucose molecules, CO_2 and H_2O are released. This is a partial combustion of glucose to provide energy required in the various biochemical pathways. Hence, biosynthesis of the various structural compounds can be considered as a process of cut and paste, the scraps representing the weight lost in growth respiration.

Each structural compound is formed along a distinct, non crop-specific pathway. Following these reactions, the weight of glucose required to produce a unit weight of the compound can be calculated (Penning de Vries et al., 1974). The transport costs of the molecules are included. Two active passages of membranes are assumed. Each active passage requires 1 ATP, which is provided by respiring 1/38 molecule of glucose. The assimilate requirements are presented in Table 13 for the following groups: structural carbohydrates, proteins, lipids (including fats and oils), lignin and organic acids. Minerals require assimilates only for uptake and transport. The data in Table 13 show, for example, that lipids are more expensive to produce than proteins.

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Table 13. Average chemical composition of leaves, stems, roots and wheat grains, and the assimilates required to form the distinguished groups of compounds (top line) and to form a unit weight of the various plant organs (right column). The assimilate requirement of leaves, for example, is calculated as:

$0.52 \cdot 1.275 + 0.25 \cdot 1.887 + 0.05 \cdot 3.189 + 0.05 \cdot 2.231 + 0.05 \cdot 0.954 + 0.08 \cdot 0.120 = 1.46 \ kg \ CH_2O \ kg^{-1} \ DM$. (Modified after Penning de Vries & van Laar, 1982, according to Penning de Vries, pers. commun.).

	Carbo-hydrates	Proteins	Lipids	Lignin	Organic acids	Minerals	Assim. req.
Assim. req.	1.275	1.887*	3.189	2.231	0.954	0.120	$kg \ CH_2O$ $kg^{-1} \ DM$
% Composition							
Leaves	52	25	5	5	5	8	1.46
Stems	62	10	2	20	2	4	1.51
Roots	56	10	2	20	2	10	1.44
Wheat grain	76	12	2	6	2	2	1.41

* 2.784 for leguminous crops with N_2 fixation by Rhizobium.

The assimilates required to produce a unit weight of a certain plant organ can now be calculated from its chemical composition and the assimilate requirements of the various chemical compounds. Typical values for leaves, stems and roots are given in Table 13. Storage organs (grains, tubers, etc.) vary too much in composition among species for one general value of their assimilate requirements to be given. The conversion efficiency (Equation 61, $kg \ DM \ kg^{-1} \ CH_2O$) represents the inverse of the assimilate requirement ($kg \ CH_2O \ kg^{-1} \ DM$).

At higher temperatures, the conversion processes are accelerated, but the pathways are identical. Hence, the assimilate requirements do not vary with temperature.

Phenological development The pattern of dry matter distribution over the various plant organs is closely related to the development stage of the crop. Development is defined as progression in the successive phenological stages. It is characterized by the formation rate of the various vegetative and reproductive organs and their order of appearance.

For many annual crops, the development stage can conveniently be expressed in a dimensionless variable, having the value 0 at seedling emergence, 1 at flowering and 2 at maturity. The development stage (D) is calculated as the integral of the development rate (D_r). The development rate has the unit d^{-1}, and is equal to the inverse of the time, in days, required to complete one unit

development. If it takes 100 days from emergence (D = 0) to flowering (D = 1), the average development rate over that period equals 1/100 or 0.01 d^{-1}.

Temperature is the main environmental factor affecting the rate of development. This rate responds to temperature according to a curvilinear relationship. It has, however, often been demonstrated, that over a wide range of temperatures, the development rate increases more or less linearly with temperature (van Dobben, 1962; van Keulen & Seligman, 1987). Within this linear region, the rate of development can be defined as a function of average daily temperature:

$$D_r = (\bar{T} - T_b)/\Sigma(\bar{T} - T_b) \hspace{3cm} \text{Equation 71}$$

in which $\bar{T}$ is the average temperature, T_b the base temperature below which the development rate equals zero, and $\Sigma(\bar{T} - T_b)$ the temperature sum or 'heat sum' (°C d) required to complete a unit development. The periods from emergence to flowering and from flowering to maturity are each characterized by their own temperature sum.

When temperatures fall partly outside the linear region, the rate of development is introduced in the model as a non-linear function of temperature (Figure 46: wheat, Figure 51: maize), or accumulated effective temperatures are used (Figure 51: potato, sugar beet).

For certain species or cultivars, effects of photoperiod and vernalization must also be taken into account. Approaches that describe such effects quantitatively are given by, among others, Weir et al. (1984), Hadley et al. (1984) and Reinink et al. (1986).

Pattern of dry matter distribution In the model, total dry matter growth is partitioned over the various plant organs according to fixed distribution factors, defined as a function of the development stage. Dry matter is first partitioned between shoots and roots, and then the shoot fraction is further subdivided between leaves, stems and storage organs.

The growth rate of a certain plant organ is thus obtained by multiplying the overall growth rate of the crop (Equation 61) by the fraction allocated to that organ. Its dry weight is obtained by integrating this growth rate over time.

This approach to the partitioning of dry matter is descriptive, as the distribution keys are defined as a function of the development stage of the crop only. The influence of environmental factors could be included by applying modification factors to these keys, depending on temperature, water and nutrient status of the crop, and its reserve level (Loomis et al., 1979; van Keulen & Seligman, 1987). In more mechanistic models, one or more reserve pools of free sugars are defined. Primary photosynthates enter these reserve pools, which are depleted by respiration and structural growth of the various organs, differing in sink strength (Thornley, 1972; Fick et al., 1973; Cooper & Thornley, 1976; Ng & Loomis, 1984). It is emphasized, however, that modelling of assimilate partitioning is still in a preliminary phase.

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Redistribution of dry matter within the plant (sink-source relationships) Storage organs may not only be filled from current assimilates but also from carbohydrates and proteins that have been stored temporarily in other organs. Neglecting this relocation may lead to a substantial underestimate of the yield of storage organs. A simple procedure is discussed to elaborate the basic model to take into account the influence of carbohydrate reserves on the rate of kernel growth in cereals.

During the pre-anthesis phase, and in the early phase of kernel growth, not all primary assimilates are converted into structural plant material. Reserves in the form of non-structural carbohydrates (starch, fructans, di- and monosaccharides) are accumulated, especially in the stems. Together with the current assimilates, these temporary reserves form the carbohydrate 'source' available for kernel growth.

Dry matter accumulation in the grains proceeds according to an S-shaped curve, in which three phases can be distinguished: (1) the lag phase, in which cell division takes place and growth is about exponential, (2) the linear phase with an approximately constant growth rate and (3) the maturation phase with a gradual decline in the growth rate (Figure 48). Growth rate of the grains is relatively independent of the current rate of assimilation, as long as sufficient reserves are available. The growth rate of the grains is then determined by their demand for carbohydrates; i.e. by their 'sink' size. When the reserves are exhausted, the size of the 'source' limits growth rate. For further discussions on the sink-source relations in grain yield formation in cereals, see Tollenaar (1977) and Spiertz & van Keulen (1980).

A simple calculation procedure for grain yield formation is presented in Figure 49. The demand of the grains for carbohydrates (the size of the sink) and the availability of carbohydrates as the sum of current assimilates and reserves (the size of the source) are defined. The actual growth rate of the kernels is then calculated as the minimum of the potential growth rate (G_p) and the rate that can be realized by the available carbohydrates (G_a): $Min(G_p, G_a)$.

The potential rate of grain growth (G_p) is the product of the number of grains (N_g) and the potential growth rate of the individual grains (P). In maize, the number of kernels is mainly related to the current flux of assimilates around silking (Edmeades & Daynard, 1979), and in wheat to the net photosynthesis per unit degree-day in the period from ear initiation to anthesis (Rawson & Bagga, 1979). However, in both crops, kernel number can often be estimated satisfactorily on the basis of the amount of biomass at anthesis (Stapper & Arkin, 1980; Spiertz & van Keulen, 1980).

The potential rate of dry matter accumulation of individual kernels is a function of their development stage (Figure 48) and usually increases with temperature. The exponential increase in the growth rate during the lag phase is approximated here by a linear increase from zero when 1/3 of the lag phase has elapsed, to the maximum value at the end of this phase (Figure 48). An estimate of the
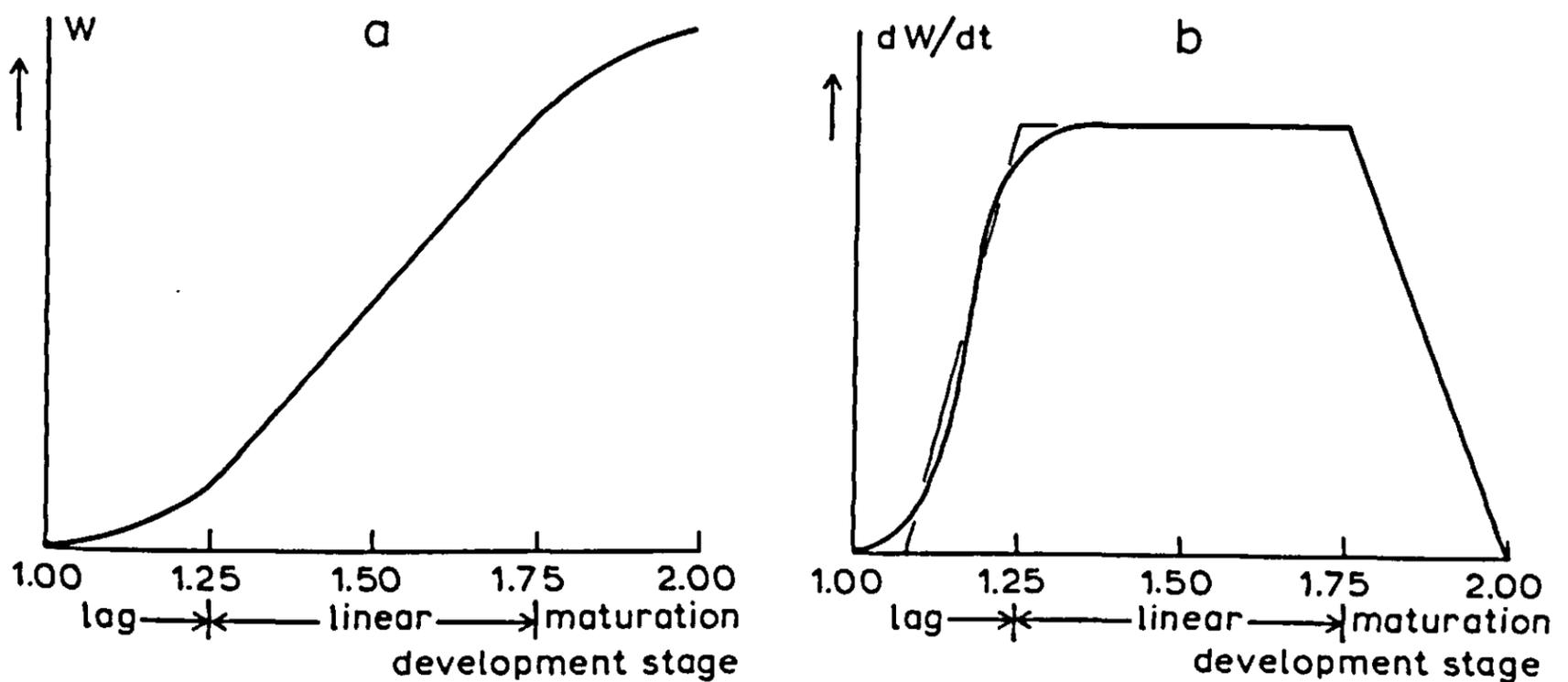
Figure 48. Schematic representation of cumulative weight (W) and growth rate (dW/dt) of individual grains as a function of development stage (1 = flowering, 2 = ripeness). The broken line represents the simplification used in the model.

Figure 49. Procedure to be included in the model SUCROS87 to account for sink-source relationships in grain growth. In the source-limited version of the model SUCROS87 (Figure 46), the statements used to calculate GPHOT, ASRQ, FST, GST, GSO, and WSO and FSTTB must be omitted. Parameters given are for spring wheat and maize.

```
* Weight of grains (kg/ha)
  WSO  = INTGRL(0.,GGR)
* Actual growth rate of the grains (kgDM/ha/d)
  GGR  = AMIN1(GGRP,GGRA)

* Potential growth rate of the grains (kgDM/ha/d)
  GGRP = NGRAIN * 0.01 * PGRI * GRTMP * GRDVS
* No. of grains / m2 as a function of above-ground biomass at anthesis
  NGRAIN = INTGRL(0.,  (NGA + NGB * TADRW) *   ...
                  INSW(DVS-1.,0.,1.) * INSW(-NGRAIN,0.,1.))
  PARAM NGA = 0., NGB = 2.0
* Potential growth rate of individual grains (mg/kernel/d) at 16 °C
  PGRI = PKRWT / ((F2 + 0.5*(0.67*F1+F3)) * GFD16)
* Potential kernel weight (mgDM/kernel)
  PARAM PKRWT = 45.
* Relative duration of lag, linear and maturation phase, resp.
  PARAM F1 = 0.11, F2 = 0.61, F3 = 0.28
* Grain fill duration (days at 16 °C), derived from DVRR
  PARAM GFD16 = 56.8
* Influence of temperature and development stage on PGRI
  GRTMP = AFGEN(GRTMPT,DAVTMP)
  GRDVS = AFGEN(GRDVST,DVS)
FUNCTION GRTMPT = 0,0., 8,0., 10,0.37, 16,1.00, 20,1.22, 25,1.37, ...
                  30,1.48, 35,1.48
FUNCTION GRDVST = 0.,0., 1.07,0., 1.11,1., 1.72,1., 2.0,0., 2.5,0.

* Growth rate of the grains that can be sustained by available assimilates
  GGRA = WRES /ASRQSO /TC
* Time constant (d) for translocation of carbohydrate reserves
  PARAM TC = 2.
```

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```
* Weight of reserves (kgCH20/ha)
    WRES = INTGRL(0., GRES - DRES)
* Growth rate of reserves (kgCH20/ha/d)
    GRES = FRES * (1.-FLV) * GSH
    FRES = AFGEN(FRESTB,DVS)
FUNCTION FRESTB = 0.,.05, .60,.05, .70,.15, .80,.30, .90,.40,   ...
    1.0,.60, 1.1,.85, 1.2,1.00, 2.5,1.00
* Rate of depletion of reserves (kgCH20/ha/d)
    DRES = GGR * ASRQSO
* Growth rate of stems (kgDM/ha/d) including carbohydrate reserves
    GST = (1.-FLV) * GSH  -  DRES

    ASRQ=FSH*(1.46*FLV + (1.-FLV)*(1.51*(1.-FRES)+1.00*FRES))+1.44*FRT
    GPHOT = DTGA * 30./44. * RDFRL
* Reduction factor for gross assim. due to accumulation of CH20 reserves
    RDFRL = LIMIT(0.,1.,(RESLMX-RESL)/(RESLMX-0.75*RESLMX))
* Carbohydrate reserve level (kg CH20 / kg DM)
    RESL = WRES / (WST + NOT(WST))
    PARAM RESLMX = 0.40


* Main references to the parameters for spring wheat:
* NGA,NGB: Spiertz & van Keulen (1980)
* F1,F2,F3: van Keulen & Seligman (1987); GRDVS: calculated from F1,F2,F3
* GRTMP: van Keulen & Seligman (1987; based on Sofield et al.,1977)
* FRESTB: modified after van Keulen & Seligman (1987)
* RESLMX: Spiertz (1977)


***               PARAMETERS FOR MAIZE               ***
    NGA = -50. * NPL
    NGB = 0.5
    PARAM PKRWT = 300., GFD16 = 70.8
    PARAM F1    = 0.20, F2 = 0.55, F3 = 0.25
FUNCTION GRDVST = 0.,0., 1.13,0., 1.20,1., 1.75,1., 2.0,0., 2.5,0.
FUNCTION GRTMPT = 0,0., 10.,0., 16.,1.0, 34.,4.0
FUNCTION FRESTB = 0.,.05, .60,.05, .70,.15, .80,.20, 1.00,.40,   ...
                  1.2,1.00, 2.5,1.00

    PARAM RESLMX = 0.40


* Main references to the parameters for maize:
* NGA,NGB: Stapper & Arkin (1980)
* F1,F2,F3: Stapper & Arkin (1980); GRDVS: calculated from F1,F2,F3
* GRTMPT: Stapper & Arkin (1980); linear temp. response with Tbase=10 °C.
*    U.S. grain maize cultivars Tbase=10 °C (Stapper & Arkin,1980)
*    NW European silage maize cultivars Tbase=6 °C (Bloc et al.,1983) ->
*    HU=730 °C d, GFD16=73.0, GRTMPT(6,0, 16,1, 36,3)
* GGRA: experimental data suggest that, at least in silage maize, a time
*    constant (TC) of 5 to 7 days performs better than that of 2 days
*    used by van Keulen & Seligman (1987) in wheat
* RESLMX: Deinum & Knoppers (1979)
```

average potential growth rate may be obtained from the kernel dry weight under potential conditions (W_p) and the duration of grain fill (D_g):

$$\bar{P} = W_p/((0.5 \cdot 0.67 f_1 + f_2 + 0.5 f_3) D_g)$$

Equation 72

in which $\bar{P}$ is the average rate of grain fill for the linear phase (mg kernel^{-1} time^{-1}), f_1, f_2 and f_3 refer to the relative duration of the lag phase, the linear phase

and maturation phase, respectively. Typical values for f_1, f_2 and f_3 are 0.25, 0.50 and 0.25, respectively. $\bar{P}$ refers to the storage capacity of the grains and is dependent on the environmental conditions during the period of cell division (Reddy & Daynard, 1983). When the duration of grain fill (D_g) is expressed in °C d, a linear relationship between rate of grain fill and temperature is assumed, which is applicable for maize (Figure 49; Stapper & Arkin, 1980). For wheat, a non-linear relationship is used (Figure 49; van Keulen & Seligman, 1987).

The foregoing defines the capacity of the sink. The size of the carbohydrate source is calculated from the current CO_2 assimilation (Figure 46) complemented by the pool of reserve carbohydrates, which is obtained as the integral of the rates of replenishment and depletion of the reserves. During the pre-anthesis period, some of the primary assimilates are allocated to this reserve pool according to fixed keys (van Keulen & Seligman, 1987). After grain set, the changes in the reserve pool are treated more mechanistically. All current assimilates, not used for structural growth of leaves, stems or inflorescence frame, contribute to the reserves. Dividing the amount of reserves that can be mobilized each day by the carbohydrate requirement per unit grain weight, gives the rate of grain growth that could be sustained by the available carbohydrates (G_a). The storage capacity of the plant for carbohydrate reserves is limited, and leaf photosynthesis is reduced as the maximum capacity is approached (Barnett & Pearce, 1983). In the model, therefore, a maximum content of reserves in the stem is defined and the rate of canopy photosynthesis is reduced when this content is approached (Figure 49).

The actual growth rate of the grains takes either the value of the source-determined growth rate (G_a) or that of the sink-determined growth rate (G_p), whichever is the lowest. This actual growth rate also determines the rate of depletion of the reserves.

Leaf area The area of green leaves is the major determinant for light absorption and photosynthesis of the crop. Under optimum conditions, light intensity and temperature are the environmental factors influencing the rate of leaf area expansion. Light intensity determines the rate of photosynthesis and hence the supply of assimilates to the leaves. Temperature affects the rates of cell division and extension.

During the early stages of crop growth, temperature is the overriding factor. The rate of leaf appearance and final leaf size are constrained by temperature through its effect on cell division and extension, rather than by the supply of assimilates.

In these early stages, leaf area increases more or less exponentially over time. In the model, the leaf area index (ha leaf ha^{-1} ground) of the crop is calculated by multiplying the leaf area per plant by the planting density. The leaf area per plant (L, m^2 $plant^{-1}$) is described by the exponential function:

$$L_t = L_0 \cdot e^{R_L \cdot t}$$

Equation 73a

so that the daily increase in leaf area is:

$$L_{t+\Delta t} - L_t = L_0 \cdot e^{R_L \cdot (t + \Delta t)} - L_0 \cdot e^{R_L \cdot t} = L_t(e^{R_L \cdot \Delta t} - 1) \qquad \text{Equation 73b}$$

in which L_0 is the leaf area at emergence, R_L the relative growth rate of leaf area (d^{-1}), t the time after emergence (d), and Δt the integration interval (d). Note that in calculating the increase in leaf area over the discrete time interval Δt, a difference equation is used rather than a differential equation (see Answer to Exercise 52 in Section 4.2).

The relative growth rate is defined as a function of temperature. For the relatively wide range of temperatures where R_L responds more or less linearly to temperature (van Dobben, 1962; Causton & Venus, 1981; Hunt, 1982), R_L can be defined per degree-day rather than per day (Figure 46). Some unpublished field data have shown that the exponential model should be restricted to the situation where the development stage $D < 0.3$ and LAI < 0.75.

In the later development stages, leaf area expansion is increasingly restricted by assimilate supply. Branching and tillering generate an increasing number of sites per plant, where leaf initiation can take place and mutual shading of plants further reduces the assimilate supply per growing point. For these later stages, the model calculates the growth of leaf area by multiplying the simulated increase in leaf weight by the specific leaf area $(m^2\ g^{-1})$ of new leaves.

Various ways of expanding this simple approach can be envisaged. Relative growth rate can be defined as a function of temperature, irradiance and development stage. The specific area of new leaves can be defined in relation to temperature and irradiance (Acock et al., 1978; Sheehy et al., 1980; Ng & Loomis, 1984). In a more mechanistic approach, leaf area growth can be simulated from leaf appearance rate and rate and duration of expansion of individual leaves; all in relation to environmental factors (Stapper & Arkin, 1980; Jones & Hesketh, 1980).

To account for leaf senescence, a constant relative death rate of leaves is defined, starting from a certain point in the crop's development and affected by temperature. Leaf death rate (ha ha^{-1} d^{-1}) is calculated from the area of green leaves (ha ha^{-1}) and this relative death rate (d^{-1}) by a difference equation similar to Equation 73b used for the daily increase in leaf area. The net growth rate of green leaves is obtained by subtracting the death rate from the leaf area growth rate. In a more comprehensive approach, various leaf classes can be defined according to their time of appearance. For each class, leaf age is followed in time and when a certain age is reached, the class is aborted (Section 2.2; Johnson & Thornley, 1983).

In addition to this developmental ageing, leaf senescence also occurs due to shading at high LAI. A relative death rate due to self-shading is therefore defined that increases linearly from zero at a certain, critial LAI, to its maximum value at twice this LAI. Typical values for the maximum relative death rate and the critical LAI are 0.03 d^{-1} and 4 ha ha^{-1}, respectively.

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In some crops, organs other than leaves contribute significantly to crop assimilation (e.g. the ears in wheat). In such situations, the CO_2 assimilation of these organs must be taken into account in the model.

4.1.4   Crop species and site characteristics

The crop species, or cultivar, is characterized by a set of parameters and functions. Estimation of their numerical values from experimental data is discussed in this Subsection in some detail.

Distribution and absorption of light in the canopy The radiation flux incident on a leaf is partly absorbed and partly scattered. Scattering consists of reflection and transmission. Species differ in the optical properties of their leaves (Gausman & Allen, 1973). In the model, a value of 0.20 is used for the scattering coefficient of individual leaves for PAR ('light').

The light distribution within the canopy is characterized by the extinction coefficient (k in Equation 62). As a reference, we consider the situation where the leaves show a spherical angle distribution (i.e. as if they were placed on the surface area of a sphere), and are distributed randomly within the canopy volume. Assuming the above scattering coefficient of 0.20, the theoretical value of the extinction coefficient for the diffuse radiation flux is 0.72 (Goudriaan, 1977).

Actual values, however, can deviate substantially from this theoretical value. Crops with more erect leaves have lower k values, whereas crops with more prostrate leaves show higher values of k. In the model, a spherical leaf angle distribution is assumed. Alternative distributions can easily be implemented using the procedure described by Goudriaan (1988). A clustered distribution of leaves increases mutual shading, resulting in reduced light absorption and hence a lower value for k. However, especially in dicotyledons, new leaves are formed, preferably in gaps within the canopy, thus increasing the value of k. In the model, an actual value for the extinction coefficient for diffuse radiation is used. The ratio between this actual value and the above theoretical value is used as a cluster factor. The various extinction coefficients and the fraction sunlit leaf area are multiplied by this factor.

Light absorption by organs other than leaves results in a calculated extinction coefficient that is too high, if the measured extinction is related to leaf area only. If light absorption and assimilation by these organs are important, as for ears and panicles in cereals, these processes should be accounted for explicitly in the model; e.g. by treating them as competing assimilators (Appendix 7). This is also necessary for other factors, such as foliar diseases, that affect the photosynthetic capacity of the leaves and are distributed non-uniformly over canopy depth.

Typical values of k are 0.4 to 0.7 for monocotyledons and 0.65 to 1.1 for broadleaved dicotyledons (Monteith, 1969). The extinction coefficient can be estimated from measurements of PAR above and below a canopy with a known LAI (Equation 62), making sure that PAR is measured rather than total global

radiation. The extinction coefficient for total radiation is about 2/3 that of PAR. The extinction coefficient is best measured under a uniform overcast sky; then all radiation is diffuse so that the extinction coefficient is not affected by solar elevation.

Photosynthesis-light response of individual leaves The response of leaf photosynthesis to light intensity is characterized by its slope at low light intensity (ε) and its maximum rate at light saturation (A_m) (Equation 64). With respect to the photosynthetic pathway, three groups of species can be identified: C_3 and C_4 species and CAM plants. Lists of C_4 species have been published by Downton (1975) and Raghavendra & Das (1978).

At a leaf temperature of 20°C, both C_3 and C_4 species have an *initial light use efficiency* (ε) of approximately 12.5 μg CO_2 J^{-1} absorbed PAR or 0.45 kg CO_2 ha^{-1} leaf h^{-1} (J m^{-2} s^{-1})$^{-1}$ (Ehleringer & Pearcy, 1983). In C_3 species, ε decreases with increasing temperature due to accelerated photorespiration. This temperature effect is relatively small: ε changes by about 1% with each change of 1°C in temperature (Farquhar et al., 1980; Ehleringer, 1978; Leverenz & Oquist, 1987). In C_4 species, ε is not affected by temperature because photorespiration is suppressed in the C_4 pathway.

Among both C_3 and C_4 species, there is hardly any variation in ε (Ehleringer & Pearcy, 1983). However, when ε is expressed per unit of incident PAR, instead of per unit of absorbed PAR, apparent differences may be due to differences in the absorption coefficient of the leaves (Hunt et al., 1985). Yellowing of leaves results in increased reflection and transmission and, therefore, in an apparent decrease of ε.

A large variation shows up in measured values of the *gross assimilation rate of leaves at light saturation* (A_m). The main sources of variation are differences in measurement conditions of temperature and ambient CO_2 concentration, differences in physiological and anatomical properties of the leaves as a result of differences in leaf age and pre-treatment, and variation among species and cultivars.

The influence of temperature on the rate of leaf photosynthesis is described in the model by multiplying the value of A_m by a temperature-dependent factor. The relationship between temperature and A_m is based on Versteeg & van Keulen (1986), where various reaction types are distinguished according to crop species and habitat (Figure 50).

The photosynthetic capacity of the leaves is affected by the preceding conditions of radiation and temperature to which they were exposed: leaves adapt their photosynthetic capacity to the environment. Therefore, A_m shows a seasonal course, which correlates with the time course of radiation and temperature (Parsons & Robson, 1981; Hodanova, 1981). This adaptation may be mimicked by using a seven-day running average of the value of A_m which has been adjusted for the environmental conditions (Schapendonk & Gaastra, 1984; Acock et al., 1978). A consequence of this adaptation is that the photosynthetic characteristics

A_m

$(kg\ CO_2\ ha^{-1}\ (leaf)\ h^{-1})$

90

80

70

60

50

40

30

20

10

0

4   3

2

1

5   10   15   20   25   30   35   40   45
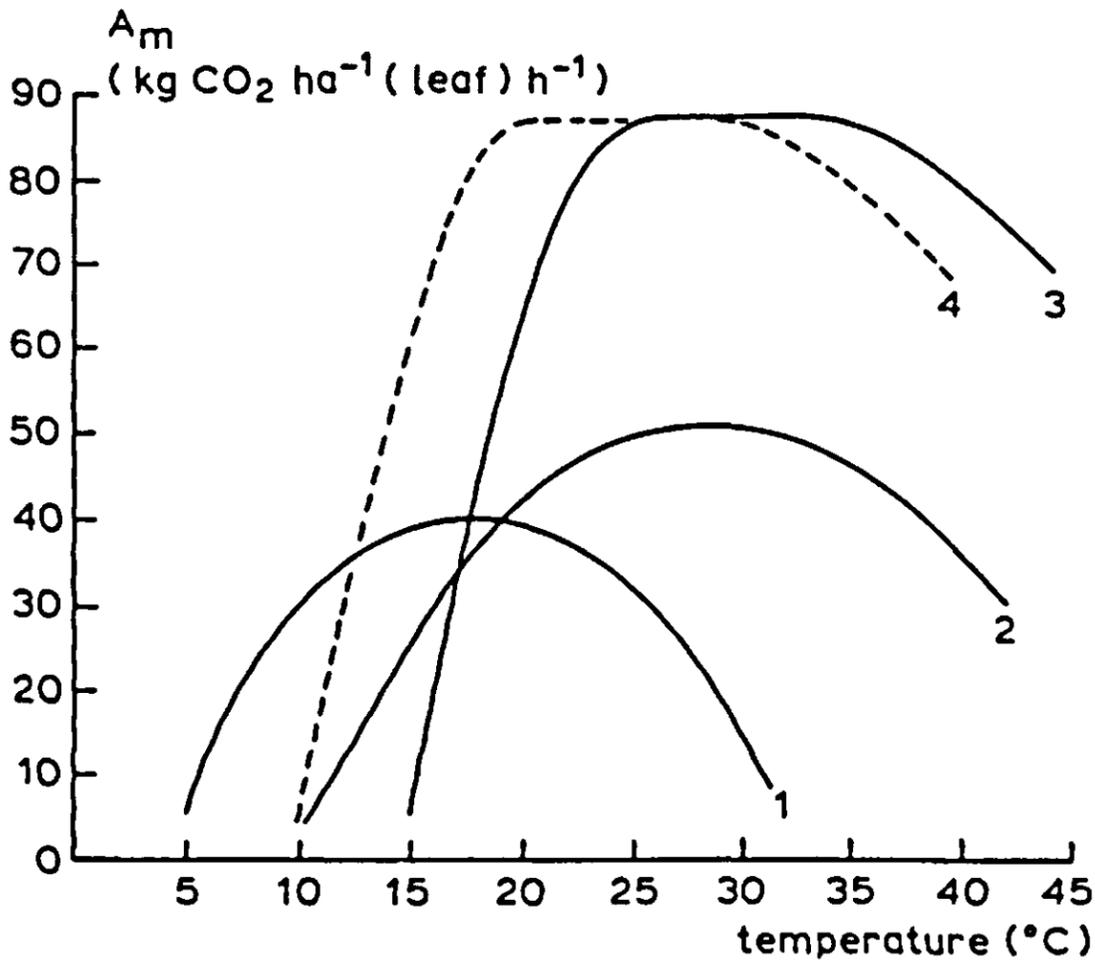
temperature (°C)

Figure 50. Average relationship between maximum assimilation rate of single leaves at light saturation (A_m) and temperature for (1) C_3 crops from temperate climates, (2) C_3 crops from warm climates, (3) thermophile C_4 crops, and (4) cultivars of C_4 crops adapted to temperate climates. (Source: Versteeg & van Keulen, 1986).

of leaves of plants grown in climate rooms, are not representative of those for plants grown in the field.

The photosynthetic capacity of a leaf is also affected by its age: A_m reaches a maximum shortly after full expansion of the leaf, followed by a gradual decline with ageing (Rawson et al., 1983; Dwyer & Stewart, 1986). Differences in photosynthetic capacity of the leaves are closely related to their nitrogen content, whether these variations are due to age, growing conditions or fertilizer application (van Keulen & Seligman, 1987). Leaves lower in the canopy have a lower photosynthetic capacity because they are older, have adapted to lower radiation levels (Acock et al., 1978; Williams, 1985) and also have lower nitrogen concentrations. The value of A_m used in the model, refers to the photosynthetic capacity of full-grown leaves at the top of the canopy, as these leaves absorb most of the radiation. Effects of canopy senescence are introduced by a multiplication factor which is a function of development stage.

Non-structural carbohydrate contents in leaves increase when the rate of conversion of assimilates into structural biomass is lower than the rate of assimilation. Such an increase in reserve content reduces the rate of photosynthesis. This feedback mechanism occurs at low night temperatures, under nutrient or water stress, and when sink size is small. The latter occurs in development phases where growth of stems and leaves is limited and the storage organs have not attained their potential growth capacity.

The photosynthetic capacity of leaves varies with crop species and cultivar. The coefficient of variation in A_m among genotypes within a species is of the order of 5–10% (Spitters & Kramer, 1986). Species can be grouped according to C_3 and C_4 types. Characteristic values range from 15–50 kg CO_2 ha^{-1} leaf h^{-1} for C_3 species and from 40–90 kg CO_2 ha^{-1} h^{-1} for C_4 species. Species from ruderal habitats show higher values than species from shaded habitats. In the model, estimates of ε and A_m must be used, which are found by fitting the exponential function (Equation 64) to data of gross photosynthesis of individual leaves. Such estimates may deviate from the measured values of photosynthetic efficiency at low light and photosynthesis at light saturation. If no firmly based value of A_m is available, a value of 40 kg CO_2 ha^{-1} h^{-1} for C_3 species and 70 kg CO_2 ha^{-1} h^{-1} for C_4 species is, in general, a reasonable estimate.

Maintenance respiration Respiration is usually measured as CO_2 evolution in the absence of light energy. This dark respiration can be partitioned into growth and maintenance respiration; estimation procedures being reviewed by Amthor (1984). Typical values for the maintenance coefficients of leaves, stems, roots and storage organs were given in Equation 69. As mentioned previously, these coefficients are affected by temperature, nitrogen content and mineral content of the plant tissue, and by the metabolic activity of the crop.

Measured rates of dark respiration of full-grown leaves, showed a large variation among species and among cultivars (M.J. de Kock, CABO, Wageningen, unpubl.).

The maintenance coefficients applied in the model are not based on conclusive evidence. This introduces a significant uncertainty in simulating the rate of crop growth, especially when the standing biomass is large compared to the current rate of photosynthesis, as at the end of the growth period.

Growth respiration The assimilate requirements to produce structural biomass are a function of the chemical composition of the biomass only. Assimilate requirements for the various groups of constituents are given in Table 13. Typical values for leaves, stems and roots are derived from their chemical composition, which is relatively constant. Storage organs of different species vary considerably in composition as indicated by Sinclair & de Wit (1975) and Penning de Vries et al. (1983).

Chemical analysis of plant material according to the specified groups of constituents is cumbersome. Elaborating on the approach of McDermitt & Loomis (1981), Vertregt & Penning de Vries (1987) developed a simpler, but still accurate method to determine the efficiency of the conversion processes. The assimilate requirement for the synthesis of plant biomass is calculated from its carbon and ash content by the empirical equation:

$$Q = (5.39\,C + 0.80\,ash - 1.191)\cdot 1.0526 \qquad \text{Equation 74}$$

in which Q is the carbohydrate requirement (kg CH_2O kg^{-1} DM), C the carbon

content ($kg\,C\,kg^{-1}$ DM), and ash the ash content after ashing at 550°C (kg ash kg^{-1} DM). The factor 1.0526 represents the transport costs which are assumed to be 2/38 molecules of glucose for each molecule transported.

Phenological development The rate of phenological development is mainly determined by temperature. The temperature response can be evaluated in field experiments planted at intervals, or in climate rooms where the plants are grown at various temperatures. Dates of the major phenological events (e.g. emergence and anthesis) are observed. The development rate, being the inverse of the time between two phenological events, is plotted against average temperature. The resulting relationship is, in general, linear over a wide range of temperatures. For this range, the temperature response can be characterized by slope and intercept of the linear regression (Equation 71). The intercept with the temperature axis is the base temperature (T_b), below which the development rate is zero. The inverse of the slope represents the temperature sum (ΣT in °C d) required to complete the development phase.

Species originating from temperate regions show a base temperature of 0°C–3°C, while species of sub-tropical and tropical origins have a base temperature of 9°C–14°C (Angus et al., 1981). Within a species, cultivars may vary substantially in their temperature requirements. The temperature sum, therefore, must be characterized for each cultivar or group of cultivars (maturity classes).

Pattern of dry matter distribution In the model, the total daily dry matter increment is distributed over the various plant organs, according to key values dependent on the phenological development stage only. These key values can be estimated from experiments in which the crop is harvested at regular intervals during its growing period. At each harvest, the total dry weight is separated into the various plant organs. For each harvest interval, the growth in dry weight of a certain organ is expressed as a fraction of the total dry weight increment over that interval. These fractions are plotted against the average development stage or temperature sum for each harvest interval, and the dry matter distribution pattern is inferred. The fractions obtained show a substantial error variation, because each value is calculated on the basis of four dry weights, each having its own error.

As the distribution functions refer to total growth, the data must be adjusted to allow for weight loss due to fallen leaves. Redistribution of dry matter later in the growth period must also be taken into account. Growth of storage organs occurs partly from the translocation of carbohydrate reserves mainly from stems, and nitrogenous compounds mainly from leaves.

Leaf area. For the early growth stages, leaf area expansion is described by an exponential function, whereas for the later stages it is calculated by multiplying the simulated leaf weight increment by the specific leaf area of the new leaves.

Specific leaf area can be obtained from the same experiments used to derive the

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pattern of dry matter distribution. Specific leaf area (SLA, ha leaves kg^{-1} leaves) of new leaves is estimated for each harvest interval by dividing the increase in LAI over the harvest interval by the increase in dry weight of green leaves. SLA is expressed as a function of development stage.

For the early, exponential stage (Equation 73), the relative growth rate of leaf area is defined as a function of temperature. The temperature response can be derived from field experiments planted at intervals. Over the range of temperatures where the relative growth rate increases more or less linearly with temperature, the logarithm of leaf area per plant is a linear function of the accumulated temperature after emergence:

$$\ln L_t = \ln L_0 + R'_L \Sigma T_t \qquad\qquad \text{Equation 75}$$

in which L_0 is the extrapolated leaf area at emergence (m^2 plant^{-1}), R'_L the relative growth rate of leaf area (°C^{-1} d^{-1}), and ΣT the temperature accumulated above the base temperature (°C d). L_0 and R'_L are estimated from intercept and slope of the linear regression of ln L on accumulated temperature. In the case of non-linear temperature relationships, the relative growth rate (d^{-1}) can be defined as an empirical function of temperature.

The relative death rate of leaves can be estimated from the slope of the linear regression of the logarithm of the green leaf area index on time in days or degree-days. This is true for crops where leaf expansion and leaf senescence are separated in time, such as those with a determinate growth habit like cereals. When new leaf formation and senescence proceed concurrently, as in indeterminate species, calculating the relative death rate must take account of leaf growth. Apart from the development-related senescence, leaf senescence is accelerated by most stress conditions, and functioning of the foliage may be terminated by killing frosts.

Initialization The model is initialized with the LAI at crop emergence. This initial value is obtained by multiplying the extrapolated leaf area per plant at emergence (L_0 in Equation 75) by the plant density. Date of emergence, if not given, can often be well predicted from the date of planting and from a fixed temperature sum required for emergence (Subsection 4.2.3; Tamm, 1933; Bierhuizen & Wagenvoort, 1974; Angus et al., 1981).

Site characteristics The site is defined by its latitude (negative values for the Southern hemisphere) and by daily values of global radiation and average temperature. Weather data measured at a nearby meteorological station are generally sufficient. If no records of global radiation are available, daily global radiation can be estimated from relative sunshine duration (Frère & Popov, 1979). If no daily values of the weather characteristics are available, but only weekly or monthly averages, these averages can be used. However, due to the non-linear relations in the model, such as the response of assimilation to absorbed radiation, use of average values may lead to biased results. If this is the case, it

may be advisable to allow for the variation between days by generating daily values from the average data (Geng et al., 1985a, b).

4.1.5 Applying the model

SUCROS87 simulates the daily potential rate of crop growth, i.e. the growth rate under ample supply of water and nutrients in a pest, disease and weed free environment under the prevailing weather conditions. Extensions can be made to account for the effects of water and nutrient deficiencies (Section 4.2; van Keulen, 1982b; Stroosnijder, 1982; van Keulen & Wolf, 1986) and for the presence of weeds, diseases and pests (Sections 4.2.6, 4.2.7, 4.3 and 4.4).

To run the model, crop species and site must be characterized. The site is defined by its latitude and by data from standard meteorological stations for daily weather. Crop species and cultivar are characterized by a set of tables and parameters. In Figure 51, typical values are given for various crop species. The model is formulated in terms of the basic growth processes and is, therefore, widely applicable. Nevertheless, the species characteristics are to some extent dependent on environment and cultivar. To improve the accuracy of the model predictions, it may therefore be necessary to adjust the parameters on the basis of field experiments carried out in the target environment. An example of the performance of the model illustrated for potatoes is given in Figure 52.

Crop growth is often described by an empirical model, consisting of a regression equation (e.g. a logistic function). Sometimes, environmental variables, such as radiation and rainfall, are incorporated in the regression. These models can generate accurate yield predictions, especially when the regression parameters are estimated on the basis of extensive sets of experimental data. The predictions are restricted to the same environment on which the regression is based. These empirical, descriptive models, however, give little insight into the causes of the observed variation in yields.

SUCROS87 is a mechanistic model that explains crop growth on the basis of the underlying processes, such as photosynthesis and respiration, and how these processes are influenced by environmental conditions. The predictive ability of mechanistic models does not always live up to expectation. It should be realized, however, that each parameter estimate and process formulation has its own inaccuracy, and that these errors accumulate in the prediction of final yield. However, yield prediction is a secondary aim of these models. Their primary aim is to improve insight into the studied system by integrating the present knowledge quantitatively in terms of a simulation model. By studying the behaviour of the model, better insight into the real system is gained.

Figure 51. Parameters and functions to characterize winter wheat, maize, potato and sugar beet, respectively. These sets were implemented in the SUCROS87 model (Figure 46) and validated against the results of experiments conducted in the Netherlands under favourable growing conditions. Estimates of parameters and functions are, if not recorded elsewhere, mainly based on Dutch field experiments (Spitters et al., unpubl. data).

```
***                        WINTER WHEAT                        ***
* Initial leaf area (cm2/plant) and relative leaf growth rate (cm2/(cm2 °C d))
PARAM LAO = 6.5, RGRL = 0.0070, TBASE = 0.
* spring growth starts at 200 °C d after 1 Jan. (TIMER TIME=1.)
* in subroutine GLA:
        IF (TSUM.LT.200.)  GLA = 0.
        IF ((TSUM.GE.200.).AND.(LAI.LE.0.)) GLA = NPL * LAO * 1.E-4
TSUM = INTGRL(0., AMAX1(0., DAVTMP-0.))
PARAM SLA = 0.0020
FUNCTION AMTMPT = 0.,0.01, 8.,0.01, 10.,0.4, 15.,0.9, 25.,1.0, 35.,0.

* Pre-anthesis and post-anthesis development rate as a function of temp.(1/d)
FUNCTION DVRVT = -10.,0., 0.,0., 30.,0.0239
FUNCTION DVRRT = -10.,0., 0.,0., 30.,0.0330
* simplified relationship DVRV based on 1254 °C d from 1 Jan. to anthesis
* For a subroutine to calculate DVR of winter wheat in relation to
*    vernalization, photoperiodicity and temperature see Weir et al.(1984)
*    and Reinink et al.(1986)

* Relative death rate of leaves (1/d) as a function of temperature and DVS
RDRDV = AFGEN(RDRT,DAVTMP) * AFGEN(RDRDST,DVS)
* Relative death rate of leaves (1/d) as a function of temperature
FUNCTION RDRT   = 0.,.03, 10.,.03, 15.,.04, 30.,.09
* Multiplication factor for RDRDV as a function of DVS
FUNCTION RDRDST = 0.,0., 0.59,0., 0.60,0.085, 0.89,0.085, ...
                  0.90,0.5, 1.09,0.5, 1.10,1.0, 2.5,1.0
* Other parameters and functions are identical to those given for spring wheat

* Main references:
* LAO, RGRL, SLA, DVRV, RDRDST: estimated from a collection of
*    winter wheat data given by Groot (1987)
* AMTMPT: function accounts for reduction in leaf photosynthesis due to
*    increased contents of non-structural carbohydrates at low spring
*    temperatures (Groot, 1987)
* RDRT: van Keulen & de Milliano (1984)


***                          MAIZE                            ***
PARAM NPL = 11.11, DAYEM = 135.
PARAM LAO = 6.69, RGRL = 0.0294, TBASE = 10.
* Exponential growth ends at DVS=0.3 or when LAI>0.75
PARAM AMX = 70., EFF = 0.45
FUNCTION AMDVST = 0.,1.0, 1.3,1.0, 1.6,0.5, 2.0,0.25, 2.5,0.25
FUNCTION AMTMPT = -10,.01, 9,.05, 16,.80, 18,.94, 20,1., 30,1., 40,.75
PARAM KDF = 0.65, SCP = 0.20
PARAM MAINSO = 0.01, ASRQSO = 1.49
FUNCTION DVRVT = 0.,0., 10.,0., 30.,0.0471
FUNCTION DVRRT = 0.,0., 10.,0., 30.,0.0471
* emergence to silking 425 °C d (Tbase=10 °C) or 730 °C d (Tbase=6 °C)
* silking to maturity  425 °C d (Tbase=10 °C) or 730 °C d (Tbase=6 °C)
* fractional allocation to shoots (FSH), leaf blades (FLV),
```

* stems + leaf sheaths (FST), cobs (excl.grains) (FCOB)
FUNCTION FSHTB = 0.0,0.60, 0.1,0.63, 0.2,0.66, 0.3,0.69, 0.4,0.73, ...
    0.5,0.77, 0.6,0.81, 0.7,0.85, 0.8,0.90, 0.9,0.94, 1.0,1.0, 2.5,1.0
FUNCTION FLVTB = 0.,.70, .25,.70, .80,.15, .95,0., 2.5,0.
FUNCTION FSTTB = 0.,.30, .25,.30, .80,.85, .95,.45, 1.1,0., 2.5,0.
FUNCTION FCOBTB = 0.,0., .80,0., .95,.55, 1.1,1.0, 1.2,0., 2.5,0.
FUNCTION SLAT   = 0.,0.0040, 0.7,0.0010, 2.5,0.0010
* SLA as a function of DVS
RDR   = INSW(DVS-1.0,0.,AMAX1(RDRDV,RDRSH,RDRLT,0.001))
RDRDV = RDRSL * (DAVTMP - 8.)
RDRSL = INSW (DVS-1.35, 0.0005, 0.0030)
RDRLT = INSW (DVS-1.25, 0., LIMIT(0.,1.,(6.-DAVTMP)/6.))
* RDR according to concept of Jones & Kiniry (1986): death due to
* ontogenetic development (RDRDV), self-shading (RDRSH) and low, chilling
* temperatures (RDRLT). RDRSL callibrated on Dutch field data.

* Main references:
* AMDVST: inferred from measurements of crop photosynthesis by
*   W.Louwerse (unpubl.)
* AMTMPT: Versteeg & van Keulen (1986)
* FSHTB: Foth (1962)
* FLVTB,FSTTB: Dutch field data with cv. LG11; Hanway (1962,1963)
* DVRV: Dutch field data with the early cv. LG11

***   POTATO   ***
PARAM NPL = 3.8, DAYEM = 137.
PARAM LAO = 155., RGRL = 0.012, TBASE = 2.
* Exponential growth ends at 450 °C d after emergence or when LAI>0.75
PARAM SLA = 0.0030
PARAM AMX = 30., EFF = 0.45
FUNCTION AMTMPT = -10.,0.01, 3.,0.01, 10.,0.75, 15.,1.0, 20.,1.0, ...
                   26.,0.75, 33.,0.01, 45.,0.01
PARAM KDF = 1.00, SCP = 0.20
PARAM MAINSO = 0.0045, ASRQSO = 1.28

* Fractions of dry matter growth allocated to:
* 'shoots'(FSH) = leaves(FLV) + stems (incl. stolons)(FST) + tubers(FSO)
FSH = LIMIT(0.80,1.00, 0.80 + 0.20 * (TSUME-IND)/430.)
FLV = LIMIT(0.,0.75, 0.75 - (TSUME-IND)/430.)
FSO = LIMIT(0.,1., (TSUME-IND)/430.)
IND = 1. / (0.0015 + 0.00079 * MATR)
PARAM MATR = 7.
* Maturity class (MATR) 2.5 for very late cv's to 9.5 for very early cv's
*   (cv. Bintje: MATR = 7.)
TSUME = INTGRL(0.,DTEFFT * INSW(DAY-DAYEM,0.,1.))
DTEFFT = LIMIT (0.,11.,INSW(DAVTMP-13.,DAVTMP-2.,29.-DAVTMP))
* Temperature sum (°C d) after emergence for tuber initiation and growth

* Relative death rate due to developmental ageing (1/d)
RDRDV = INSW(TSSNC, 0., AMAX1(8., DAVTMP - 2.) ...
       * EXP(-11.7+0.68*MATR) * EXP(TSSNC * (0.0068 - 0.00060*MATR)))
TSUMEM = INTGRL(0.,DTEFFL * INSW(DAY-DAYEM,0.,1.))
DTEFFL = AMAX1 (0.,DAVTMP-2.)
TSSNC = TSUMEM - 725.
* Leaf senescence starts after 725 °C d (Tbase=2 °C) after plant emergence
* and is affected by temperature and maturity class of the cultivar

* Main references:
* FSH,FLV,FSO: Spitters & Neele (1986,unpubl.), van Heemst (1986)
* RDRDV: Spitters & Neele (1986,unpubl.)

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* MAINSO:
*    0.70 (starch content) * 0. + 0.30 * 0.015 (non-sugar='stem'maintenance)
*    in line with measurements of Burton (1963,1964,1974) 48 h after harvest
* AMTMPT: Versteeg & van Keulen (1986)
* DTEFFT: inferred from Ingram & McCloud (1984)


***                        SUGAR BEET                        ***
PARAM NPL = 7.8,  DAYEM = 121.
PARAM LAO = 0.845, RGRL = 0.0156, TBASE = 3.
* Exponential growth ends at 450 °C d after emergence or when LAI>0.75
PARAM SLA = 0.0020
PARAM AMX = 45.,  EFF = 0.45
FUNCTION AMDVST = 0.,0.50, 500.,1.0, 700.,1.0, 1700.,0.80, 3000.,0.60
* DVS in °C d (Tbase=2 °C)
FUNCTION AMTMPT = -10.,0.01, 3.,0.01, 10.,0.75, 15.,1.0, 20.,1.0, ...
                  26.,0.75, 33.,0.01, 45.,0.01
PARAM KDF = 0.69, SCP = 0.20
PARAM MAINSO = 0.003, ASRQSO = 1.29


* Fractions of dry matter growth allocated to the various plant organs
* as a function of temperature sum after emergence (Tbase=2 °C)
TSUM2 = INTGRL( 0., LIMIT(0.,19.,DAVTMP-2.) * INSW(DAY-DAYEM,0.,1.))
* shoots (leaves + crown):
FUNCTION FSHTB = 0.,0.8, 400.,0.7, 900.,0.52, 901.,0.22, 3000.,0.22
* the data suggest for TSUM2 > 900 °C d FSH=0.20 to 0.25
* (for N rates as standard in practice) to 0.35 (for a continuous N-supply)
* leaf laminae:
FUNCTION FLVTB = 0.,0.85, 370.,0.85, 665.,0.48, 820.,0.23, 3000.,0.23
* petioles + midribs:
FUNCTION FSTTB = 0.,0.10, 370.,0.10, 665.,0.43, 820.,0.67, 3000.,0.67
* crown:
FUNCTION FCRTB = 0.,0.05, 370.,0.05, 665.,0.09, 820.,0.10, 3000.,0.10
* fibrous roots (as a fraction of below-ground growth):
FUNCTION FRTTB = 0.,1.,400.,1.,500.,0.5,1000.,0.1,2000.,0.03,3000.,0.03


* Relative death rate of leaves in relation to temperature sum (1/°C/d)
RDRDV = AFGEN(RDRT,TSUM2) * LIMIT(0.,19.,DAVTMP-2.)
FUNCTION RDRT = 0,0., 600,0., 1000,.00022, 1500,.00050, 2500,.00075


* Main references:
* KDF: Tanaka (1983)
* AMTMPT: Versteeg & van Keulen (1986)
* ASRQSO:
*    0.80 (sugar content) * 0. + 0.20 * 0.015 (non-sugar='stem'maintenance)
*    The value of 0.003 corresponds with respiration measurements one or two
*    days after harvest by Koster et al., Vanstallen, Vanstallen & Vigoureux,
*    Devillers, Wyse (all: Inst. Int. Rech. Betteravieres, 1980)
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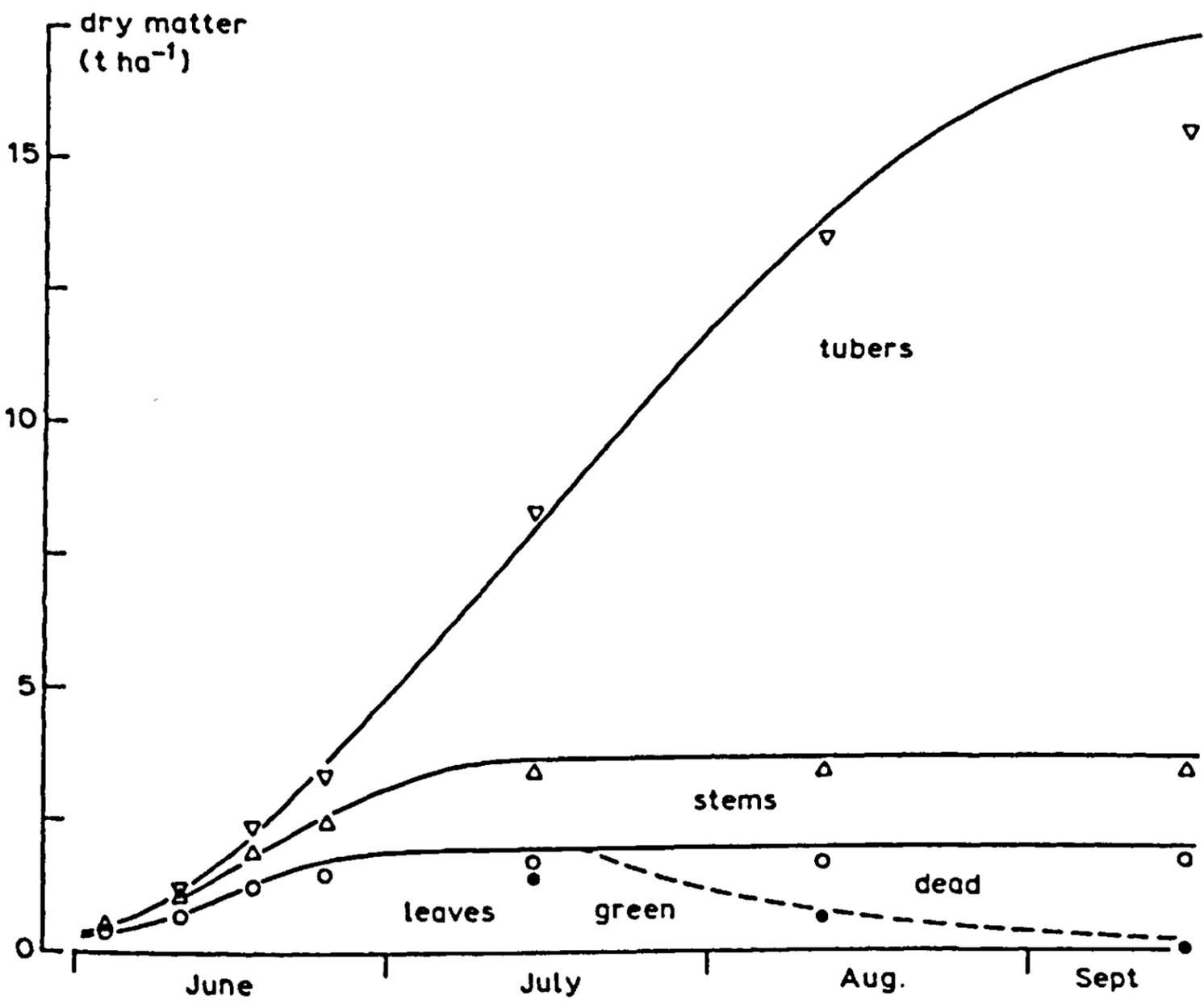
Figure 52. Cumulative organ dry weights as simulated with the SUCROS87 model version for potato. Data points refer to an experiment with cultivar Bintje in 1985 at Flevopolder, the Netherlands.