MEMO : EN/INPA/DH-11
SUBJECT: MORE, A MODEL FOR MACROPHYTES
TO : PPA-ELETRONORTE
FROM : JOHANNES SMITS
DATE : 23 MARCH 1987

1. INTRODUCTION

SUPPORTED BY A LITERATURE STUDY A MODEL WAS DEVELOPED FOR THE GROWTH OF FLOATING MACROPHYTES ON RESERVOIRS. IT IS CALLED MORE, AN ACRONYM FOR 'MACROPHYTES OCCUPATION OF RESERVOIRS'. MORE HAS TO BE CONSIDERED A FIRST STEP TOWARDS THE SIMULATION OF THE BEHAVIOR OF FLOATING MACROPHYTES. IT CALCULATES PLANT BIOMASS DENSITY (CARBON, DRY AND WET WEIGHT), TOTAL WET WEIGHT AND PERCENTAGE RESERVOIR COVER AS A FUNCTION OF TIME AND SPACE (THREE SEGMENTS). MORE HAS BEEN PROGRAMMED IN FORTRAN, IS FULLY OPERATIONAL AT THE MOMENT AND CAN BE USED FOR THE ANALYSIS OF MACROPHYTE BEHAVIOR. APPLICATION OF MORE TO A REAL CASE HAS TO BE POSTPONED UNTIL THE PROCESS PARAMETERS HAVE BEEN QUANTIFIED WITH SUFFICIENT ACCURACY AND A CALIBRATION HAS BEEN CARRIED OUT.

SOME ASPECTS OF MACROPHYTE GROWTH HAVE BEEN LEFT OUT OF THE FIRST DEVELOPMENT STEP. SINCE MORE DEALS WITH ONLY ONE MACROPHYTE SPECIES AT THE SAME TIME, INTER-SPECIES COMPETITION HAS BEEN IGNORED. HOWEVER, THE MODEL IS ABLE TO CALCULATE THE DEVELOPMENT OF DIFFERENT SPECIES IF THE INPUT PARAMETERS ARE ADJUSTED ACCORDINGLY.
GENERATIVE REPRODUCTION HAS NOT BEEN CONSIDERED BECAUSE IT SEEMS TO BE OF MINOR IMPORTANCE IN RESERVOIRS (COMPARED WITH VEGETATIVE REPRODUCTION) AND ALSO BECAUSE THE PROCESSES INVOLVED ARE EXTREMELY COMPLEX.
THE OCCURRENCE OF SEVERAL PHASES OF GROWTH (SHOOT, ADULT PLANT, FLOWERING PLANT, ETC.) HAVE NOT BEEN TAKEN INTO ACCOUNT BECAUSE IT DOES NOT SEEM TO HAVE MAYOR EFFECTS ON THE BIOMASS PRODUCTION RATE, AT LEAST NOT DURING THE GROWTH SEASON. ITS RELATION TO AGING SHOULD BE AN IMPORTANT ITEM FOR FURTHER MODEL DEVELOPMENT.
THE EFFECT OF INTERNAL NUTRIENTS ON PRODUCTION HAS BEEN SKIPPED BECAUSE THE NUTRIENT LEVELS IN RESERVOIR ARE USUALLY LOW ENOUGH TO LIMIT 'LUXURY' UPTAKE TO A LARGE EXTENT.
BESIDES THESE ASPECTS FUTURE EXTENSIONS MAY CONCERN INTERRELATIONS BETWEEN GROWTH LIMITING FACTORS (TEMPERATURE, LIGHT AND NUTRIENTS), DISTINCTION BETWEEN ABOVE- AND UNDER-WATER BIOMASS, AND LENGTH OF THE PHOTO-PERIOD IN RELATION TO PRODUCTION.

A COMPLICATION IS CREATED BY HORIZONTAL AND VERTICAL INHOMOGENEITY WITH RESPECT TO THE DISSOLVED NUTRIENT CONCENTRATIONS, WHICH RESULTS IN VARYING NUTRIENT AVAILABILITY

IN THE HORIZONTAL PLANE. IT IS THOUGHT THAT THIS COMPLICATION SHOULD BE ADEQUATELY DEALT WITH IN THE WATER QUALITY MODEL TO BE COUPLED TO MORE IN THE FUTURE. DISSOLVED NUTRIENT CONCENTRATIONS ARE CONSIDERED NON-VARIANT WITH RESPECT TO SPACE IN ITS PRESENT VERSION.

THIS MEMO OFFERS A GLOBAL PICTURE OF THE FORMULATIONS OF THE PRESENT VERSION OF MORE. THE JUSTIFICATION AND ELUCIDATION OF THE FORMULATIONS HAVE BEEN KEPT CONDENSED, TAKING INTO ACCOUNT THAT THE PRESENT TEXT ONLY HAS THE STATUS OF A MEMO. MORE ELABORATED COMMENTS, INCLUDING ALL RELEVANT INFORMATION AND DATA FROM THE AVAILABLE LITURATURE, WILL BE ADDED IN A FINAL REPORT. HOWEVER, ALL LITERATURE USED HAS BEEN COMPILED IN A LIST OF REFERENCES, ADDED TO THIS MEMO.

2. THE BASICS

THE CLASSIC GROWTH EQUATION FOR PRIMARY PRODUCERS CONTAINS THE RATES OF GROSS PRODUCTION AND LOSSES, MULTIPLIED WITH THE BIOMASS DENSITY. IT HAS BEEN USED FOR PHYTOPLANKTON AND MACROPHYTES (6,7,11) AND CAN BE FORMULATED AS FOLLOWS:

$$DCB/DT = (PG - R - M - L).CB \qquad (2.1)$$

IN WHICH,
CB = BIOMASS DENSITY (G/M2)
PG = GROSS PRIMARY PRODUCTION RATE CONSTANT (1/D)
R = RESPIRATION RATE CONSTANT (1/D)
M = MORTALITY RATE CONSTANT (1/D)
L = LOSS RATE CONSTANT (1/D)
T = TIME (D)

THE MORTALITY COMPRISES ONLY NATURAL MORTALITY. THE LOSS RATE MAY INCLUDE SUCH PROCESSES AS DESTRUCTION CAUSED BY WAVES OR WATER LEVEL CHANGE, HARVESTING AND CHEMICAL ABATEMENT. THE GROSS PRODUCTION IS A FUNCTION OF A NUMBER OF LIMITING FACTORS, USUALLY DESCRIBED AS:

$$PG = PGMAX.F(T).F(N).F(I).F(PH).F(CB) \qquad (2.2)$$

IN WHICH,
PGMAX = MAXIMUM GROWTH RATE FOR UNLIMITED CONDITIONS (1/D)
T = TEMPERATURE (OC)
N = DISSOLVED NUTRIENT CONCENTRATION (MG/L)
I = INSOLATION (W/M2)
PH = HYDROGEN POTENTIAL (1/D)

ALL LIMITING FUNCTIONS MAY VARY FROM 0 TO 1 AND AMPLIFY EACH OTHER IN THIS CONCEPT.

THE MODEL HAS AN OPTION WITH RESPECT TO THE OCCURRENCE OF A DISTINCT GROWING SEASON, A VERY SIMPLE ALGORITM TO TAKE THE

AGING OF THE MACROPHYTES INTO ACCOUNT. THIS OPTION INVOLVES THE CHOICE OF THE GROWING SEASON BY SUPPLYING THE FIRST WEEK AND THE FINAL WEEK TO MORE. PG IS SET EQUAL TO ZERO DURING THE PERIODS BETWEEN GROWING SEASONS.

UNTILL SOFAR WE DID NOT TAKE SPACIAL DIFFERENCES AND HORIZONTAL MASS TRANSPORT INTO ACCOUNT. HOWEVER, IT IS OBVIOUS FROM MANY OBSERVATIONS THAT FLOATING MACROPHYTES THRIVE IN THE MORE QUIESCENT REGIONS OF A RESERVOIR (1,8,19,21,26). THEY NEED PROTECTION AGAINST THE WIND, WHICH MAY CAUSE SUBSTANTIAL DAMAGE BY MEANS OF WAVES INDUCTION. SUCH PROTECTION CAN BE DELIVERED BY EMERGENT DEAD VEGETATION, DENDRITIC SHORE-LINES, SHORE VEGETATION AND BORDERING HILLS. FOR THIS REASON MORE CONSIDERS THREE LONGITUDINAL RESERVOIR SEGMENTS: THE CENTRAL BODY WITH OPEN WATER AND TWO SIDE-SEGMENTS WITH SHELTER AGAINST WIND. EXCHANGE OF MACROPHYTES BETWEEN THE SEGMENTS IS A FUNCTION OF WINDSPEED, WIND ORIENTATION AND ADVECTIVE FLOW. EQUATION 2.1 CAN BE EXTENDED FOR EACH SEGMENT TO:

$$DCB/DT = (PG - R - M - L - TO).CB + TI \qquad (2.3)$$

IN WHICH,
TO = RATE OF MASS TRANSPORT OUT OF THE SEGMENT (1/D)
TI = RATE OF MASS TRANSPORT TO THE SEGMENT (G/(M2.D)

THE SURFACE AREAS OF THE SEGMENTS ARE CALCULATED AS A FRACTION OF THE TOTAL SURFACE AREA. THE FRACTIONS ARE SUPPLIED TO THE MODEL AS INPUT PARAMETERS, THE QUANTIFICATION OF WHICH HAS TO BE BASED ON THE PRESENCE OF THE FOUR WINDSPEED REDUCING FACTORS MENTIONED ABOVE. THE TOTAL AREA IS CALCULATED WITH THE SAME GEOMETRICAL FORMULA AS IS BEING USED IN THE MODELS STRATIF AND OXY:

$$AT = AMAX.(1-G.(1-H/HMAX))^{E} \qquad (2.4)$$

IN WHICH,
AT = TOTAL SURFACE AREA (M2)
AMAX = MAXIMAL SURFACE AREA AT MAXIMAL DEPTH (M2)
H = DEPTH (M)
HMAX = MAXIMAL DEPTH (M)
G = COEFFICIENT
E = COEFFICIENT

THE LIMITING FACTORS, LOSS RATES AND TRANSPORT RATES MENTIONED ABOVE ARE ELABORATED IN THE FOLLOWING SECTIONS.

3. THE PRODUCTION LIMITING FACTORS

3.1 TEMPERATURE

INFORMATION WITH RESPECT TO THE TEMPERATURE DEPENDENCE OF GROWTH AND PRIMARY PRODUCTION CAN BE FOUND IN REFERENCES 1,5,6,7,11, 15,30,32,36,37 AND 39. SEVERAL FUNCTIONS HAVE BEEN USED IN THE PAST TO DESCRIBE THE TEMPERATURE DEPENDENCE. MOST OF THEM ARE SIMPLE EXPONENTIAL RELATIONS AND ONLY CONSIDER THE SUBOPTIMAL TEMPERATURE RANGE. THIS IS NOT REALISTIC IN THE CASE OF MACROPHYTES GROWING IN (SUB-)TROPICAL AREAS. THE TEMPERATURE IS HIGHER THAN THE OPTIMAL TEMPERATURE DURING A SUBSTANTIAL PART OF THE TIME. ALTERNATIVES, WHICH TAKE AN OPTIMUM INTO ACCOUNT, ARE PARABOLIC FUNCTIONS, S-FUNCTIONS OR BELL-SHAPE FUNCTIONS. THE CHOSEN FUNCTIONS BELONG TO THE LATTER CATHEGORY:

$$F(T) = EXP(-TCO1*(TOPT-T)^2) \qquad FOR\ T<TOPT \qquad (3.1)$$

$$F(T) = EXP(-TCO2*(TOPT-T)^2) \qquad FOR\ T>TOPT$$

IN WHICH,
TCO1 = COEFFICIENT 1
TCO2 = COEFFICIENT 2
TOPT = OPTIMUM TEMPERATURE (OC)

ON THE ONE HAND THESE FUNCTIONS HAVE THE ADVANTAGES OF SIMPLICITY AND CORRECT SHAPE, ON THE OTHER THEY LACK FLEXIBILITY WITH RESPECT TO THE WIDTH OF THE OPTIMUM. THE TEMPERATURE IN THESE FORMULA SHOULD BE CORRECTED FOR THE FACT THAT PLANTS ON TOP OF A WATER SURFACE USUALLY EXPERIENCE A HIGHER TEMPERATURE THAN THE ATMOSPHERIC OR WATER TEMPERATURE (37).

3.2 NUTRIENTS

INFORMATION WITH RESPECT TO THE RELATION BETWEEN GROWTH AND PRIMARY PRODUCTION AND DISSOLVED NUTRIENT (N,P) CONCENTRATIONS IS OFFERED IN REFERENCES 1,6,9,11,12,29,30,32,34 AND 35. THE INFLUENCE OF THE NUTRIENT CONCENTRATION ON THE PRODUCTION IS GENERALLY DESCRIBED WITH MICHAELIS-MENTEN KINETICS. NO ARGUMENT WAS ENCOUNTERED IN THE AVAILABLE LITERATURE TO DEVIATE FROM THIS APPROACH. THE NUTRIENT DEPENDENCE WAS THEREFORE FORMULATED AS:

$$F(N) = CN/(KS+CN) \qquad (3.2)$$

IN WHICH,
CN = DISSOLVED NUTRIENT CONCENTRATION (MG/L)
KS = HALF-SATURATION CONSTANT (MG/L)

MORE DISTINGUIHES TWO NUTRIENTS, NITROGEN (AMMONIUM AND NITRATE) AND INORGANIC PHOSPHORUS. EQUATION 3.2 IS APPLIED FOR BOTH NUTRIENTS AND THE SMALLER VALUE FOR F(N) WILL APPEAR IN EQUATION 2.2. THIS IMPLIES THAT ONLY ONE NUTRIENT IS LIMITING THE PRODUCTION. REFERENCE 35 CONTAINS THE EVIDENCE FOR THIS ASSUMPTION.

3.3 INSOLATION

REFERENCES 5,6,27 AND 36 INDICATE A LINEAR RELATIONSHIP BETWEEN PRIMARY PRODUCTION AND INSOLATION. HOWEVER, A SATURATION AT A CERTAIN SOLAR IRRADIATION MAY BE EXPECTED, AS CAN BE DERIVED FROM REFERENCES 7 AND 15. HENCE, THE FOLLOWING SIMPLE FUNCTIONS HAVE BEEN SELECTED:

$$F(I) = SI/SIS \qquad \text{FOR } SI<SIS \qquad (3.3)$$

$$F(I) = 1 \qquad \text{FOR } SI>SIS$$

IN WHICH,
SI = AV. DAILY PHOTOREACTIVE SOLAR IRRADIATION (W/M2)
SIS = SI AT SATURATION (W/M2)

3.4 HYDROGEN POTENTIAL

VERY FEW QUANTITATIVE DATA ARE AVAILABLE WITH REGARD TO THE PH DEPENDENCE OF MACROPHYTE GROWTH. NEVERTHELESS, INHIBITION BY LOW PH HAS BEEN STIPULATED SEVERAL TIMES (1,21,35 AND 39). THE DATA GIVEN IN REFERENCE 35 SUPPORT A PARABOLIC FUNCTION WITH AN OPTIMUM:

$$F(PH) = 1-PHCO.(PH-PHOPT)^2 \qquad (3.4)$$

IN WHICH,
PHCO = COEFFICIENT
PHOPT = PH FOR OPTIMAL GROWTH

3.5 BIOMASS DENSITY

THE PRODUCTION OF NEW SHOOTS STOPS, WHEN THE MACROPHYTE MAT BECOMES CROWDED. THE PLANTS CONTINUE TO INCREASE IN BIOMASS BY GROWING IN THE VERTICAL DIRECTION, AFTER WHICH A STRUGGLE FOR LIGHT AND NUTRIENTS ARISES. THE GROSS PRODUCTION DIMINISHES GRADUALLY TO A POINT WHERE IT IS COMPENSATED COMPLETELY BY RESPIRATION AND MORTALITY. THE AVAILABLE LITERATURE (6,7,11,23 AND 28) SHOWS THAT THE DENSITY LIMITATION COULD BE REPRESENTED BY A HYPERBOLIC FUNCTION:

$$F(CB) = (DCO+1)/(CB/(DCO*CBMAX)+1) - DCO \qquad (3.5)$$

IN WHICH,
DCO = COEFFICIENT
CBMAX = MAXIMAL BIOMASS DENSITY (G/M2)

4. RESPIRATION

THE RESPIRATION HAS TWO COMPONENTS, ONE RELATED TO MAINTENANCE AND ONE RELATED TO GROWTH OF THE PLANT (13). NOTWITHSTANDING, THE MODELING EFFORTS DESCRIBED IN THE AVAILABLE LITERATURE ONLY CONSIDER ONE OF THE TWO COMPONENTS (6,11). BOTH REFERENCES IGNORE THE TEMPERATURE DEPENDENCE OF RESPIRATION. SOME MORE QUANTITATIVE INFORMATION ON RESPIRATION CAN BE FOUND IN REFERENCES 9,13,25 AND 31. THE RATE OF GROWTH COMPONENT WAS DEFINED AS A CONSTANT FRACTION OF THE GROSS PRODUCTION, THE RATE OF THE MAINTENANCE COMPONENT AS A FUNCTION OF TEMPERATURE:

$$R = RC01.PG + EXP(RC02*T-RC03) \tag{4.1}$$

IN WHICH,
RC01/2/3 = COEFFICIENTS

THE TEMPERATURE FUNCTION IS SIMILAR TO THE ONE USED FOR PHYTOPLANKTON MODELING (SEE MEMO 4).

5. MORTALITY

THE NATURAL MORTALITY HAS TEMPERATURE AND INSOLATION RELATED COMPONENTS. THE INSOLATION COMPONENT BECOMES RELEVANT ONLY, WHEN A MACROPHYTES MAT GETS CROWDED. THE PLANTS MAINTAIN GROWTH AT THE TOPS BUT THE LOWER LEAVES START TO DIE. FOR THIS REASON THE MORTALITY WAS QUANTIFIED BY MEANS OF A BIOMASS DENSITY DEPENDENT FUNCTION IN REFERENCE 6. OTHER REFERENCES DESCRIBE MORTALITY AS AN EXPONENTIAL (7) OR EVEN AS A RECIPROCAL (11) FUNCTION OF TEMPERATURE. FOR OUR PURPOSE IT WAS CONSIDERED BENEFICIAL TO INCLUDE BOTH COMPONENTS IN THE FOLLOWING MORTALITY RATE FUNCTION:

$$M = MC01.(CB-CBMCOV)/CB + EXP(MC02.T-MC03) \tag{5.1}$$

$$MC01 = 0.0 \quad \text{FOR } CB<CBMCOV$$

IN WHICH,
MC01/2/3 = COEFFICIENTS
CBMCOV = BIOMASS DENSITY AT 100 % COVER OF WATER SURFACE

ONCE AGAIN, THE TEMPERATURE FUNCTION IS SIMILAR TO THE ONE USED FOR PHYTOPLANKTON MODELING (SEE MEMO 4).

6. LOSS PROCESSES

THE DESTRUCTION OF PLANTS BY THE ACTION OF WAVES IS MENTIONED SEVERAL TIMES IN THE LITERATURE (1,8), BUT QUANTITATIVE DATA ARE NOT AVAILABLE. HENCE, IT WAS JUDGED SENSIBLE TO APPLY A VERY SIMPLE APPROACH IN THE MODEL. THE DESTRUCTION RATE WAS RELATED TO THE RATIO OF WAVE AMPLITUDE AND PLANT HEIGHT:

$$LW = WC02.HW/HP \tag{6.1}$$

IN WHICH,
WCO2 = COEFFICIENT (1/D)
HW = WAVE AMPLITUDE (M)
HP = PLANT HEIGHT (M)

THE WAVE AMPLITUDE IS RELATED TO THE WINDSPEED AND A FEW OTHER PARAMETERS. PRESENTLY, NO INFORMATION IS AVAILABLE WITH RESPECT TO AN APPROPRIATE RELATION AND FURTHER ELABORATION WILL HAVE TO WAIT UNTIL SOME LITERATURE STUDY ON THIS SUBJECT HAS BEEN CARRIED OUT. FOR SO LONG, THE WAVE AMPLITUDE WILL BE CALCULATED WITH:

$$HW = WCO1.WRCO.W \qquad (6.2)$$

IN WHICH,
WCO1 = COEFFICIENT
WRCO = WIND REDUCTION FACTOR
W = WIND SPEED AT THE 10 M LEVEL (M/S)

COEFFICIENT WCO1 REFERS TO A LINEAR RELATION BETWEEN AMPLITUDE AND WINDSPEED. COEFFICIENT WRCO ACCOUNTS FOR THE SHELTER IN THE SIDE-SEGMENTS.

THE LOSS OF BIOMASS RESULTING FROM A DROP OF THE WATER LEVEL IS ASSUMED TO BE PROPORTIONAL TO THE DECREASE OF SURFACE AREA OF THE SIDE-SEGMENTS. THE SURFACE AREAS OF THE SIDE-SEGMENTS REMAIN THE SAME FRACTIONS OF THE TOTAL AREA, WHICH IMPLIES THAT PARTS OF THE CENTRAL SEGMENT BECOME PART OF THE SIDE-SEGMENTS LEADING TO A REDISTRIBUTION OF THE BIOMASS AMONG THE SEGMENTS. SUCH A REDISTRIBUTION OF BIOMASS IS ALSO ESTABLISHED IN THE OPPOSITE DIRECTION, WHEN THE WATER LEVEL RISES. OBVIOUSLY, NO LOSS OF BIOMASS OCCURS IN THIS CASE.

HARVESTING IS SIMPLY FORMULATED AS A LINEAR PROCESS, THE RATE OF WHICH IS EQUAL TO A CERTAIN FRACTION OF THE DENSITY PER DAY IN EACH OF THE THREE SEGMENTS. CHEMICAL ABATEMENT COULD BE DEALT WITH IN THE SAME WAY.

7. MASS TRANSPORT

THE INFLOWING RIVER CARRIES MACROPHYTES ALONG, WHICH CAUSES A CONSTANT OR REPEATED ENTING OF THE CENTRAL SEGMENT OF THE RESERVOIR (IN OUR MODEL CONCEPT). THE ENTING RATE CAN BE FORMULATED AS FOLLOWS:

$$RENT = QI.ENT/(DRIV.A1) \qquad (7.1)$$

IN WHICH,
QI = FLOW RATE OF THE RIVER (M3/D)
ENT = BIOMASS DENSITY AT THE RIVER NEAR THE INFLOW (G/M2)
A1 = SURFACE AREA OF THE CENTRAL SEGMENT (M2)
DRIV = AVERAGE DEPTH OF THE RIVER AT THE INFLOW (M)

THE PLANTS MAY BE TRANSPORTED TO THE DAM BY (FORCED) WATER FLOW AND WIND-DRIVEN CURRENTS AND WILL ACCUMULATE AGAINST THE DAM CONSTRUCTIONS, WHERE THEY MAY PERISH BECAUSE OF THE ACTION OF WAVES AND CURRENTS OR A LACK OF LIGHT (BELOW THE CONSTRUCTIONS). THE DEAD BIOMASS SINKS AND WILL BE CARRIED AWAY BY THE OUTFLOWS THROUGH SPILLWAY AND TURBINES. THE RESULTING LOSS OF BIOMASS IS DESCRIBED WITH:

ROUT = (QO/DRES + RWPS.W.COS(WD).WIDS1)/A1 (7.2)

IN WHICH,
QO = FLOW RATE OF OUTFLOWS (M3/D)
DRES = AVERAGE DEPTH OF THE CENTRAL SEGMENT (M)
RWPS = RATIO OF WINDSPEED AND PLANT SPEED
W = WINDSPEED AT THE 10 M LEVEL (M/D)
WD = ANGLE BETWEEN THE LONGITUDINAL AXIS OF THE RESERVOIR (DIRECTED TOWARDS THE DAM) AND THE WIND DIRECTION
WIDS1 = WIDTH OF THE CENTRAL SEGMENT NEAR THE DAM (M)

THE TRANSPORT BETWEEN THE SEGMENTS HAS ONLY A WIND-DRIVEN COMPONENT, EQUAL TO:

RTR = WRCO.RWPS.W.SIN(WD).LENS1)/A1 (7.3)

IN WHICH,
WRCO = WINDSPEED REDUCTION COEFFICIENT
LENS1 = LENGTH OF THE CENTRAL SEGMENT (M)

THE WINDSPEED REDUCTION COEFFICIENT IS RELATED TO THE FOUR WIND REDUCING FACTORS MENTIONED ABOVE AND IS DIFFERENT FOR EACH SEGMENT. THE DIRECTION OF THE TRANSPORT FULLY DEPENDS ON THE WIND DIRECTION. THE MODEL TRANSPORTS BIOMASS FROM SIDE-SEGMENT 3 TO SIDE-SEGMENT 2 (VIA CENTRAL SEGMENT 1) WHEN THE ANGLE BETWEEN LONGITUDINAL AXIS AND WIND IS POSITIVE. BIOMASS GOES FROM SEGMENT 2 TO SEGMENT 3 IF THE ANGLE IS NEGATIVE.

IN ORDER TO ELUCIDATE THE RELATION OF THESE TRANSPORT TERMS WITH THOSE IN EQUATION 2.3 IT MUST BE STRESSED, THAT RENT IS EQUAL TO TI AND THAT THE SUM OF ROUT (ZERO FOR THE SIDE-SEGMENTS) AND RTR IS EQUAL TO TO.

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