•••••ABSTRACT

Water uptake and root growth are important components of mechanistic crop growth models. We developed a method to simulate water uptake and root growth based on the partitioning of carbon between the shoot and root. A relationship between leaf water potential and potential transpiration rate is generated for each period of the day. Water uptake rate is calculated as a function of water potential gradient between the leaf and soil, hydraulic conductivity, root length and root resistance to water flow. The water uptake rate is compared to the potential transpiration rate and leaf water potential is compared to the thresholds for turgor loss in the potential evapotranspiration rate vs leaf water potential relationship. As the soil dries and the potential transpiration rate increases, the leaf water potential decreases which causes a loss of leaf turgor and diverts additional carbon to the roots to grow new roots with higher conductance. This allows the plant to meet a higher transpiration demand with less of a change in leaf water potential. As programmed in GLYCIM the method has an advantage only under levels of moderate water stress. It is also sensitive to the water holding capacity of the soil and is more advantageous when the soil water holding capacity is high.

*INTRODUCTION*

One of the most important environmental variables that affects plant growth and yield is soil water. The availability of soil water is largely determined by the growth characteristics of the plant root system and the availability of water in the soil. The availability of soil water to the plant varies over time and location in the soil profile and can even depend on atmospheric conditions (i.e., ET). Plants need to respond to rapidly changing soil hydraulic and atmospheric conditions, as a result, plant roots are highly dynamic and adaptable. Many studies have shown that plants respond to water stress by increasing root growth at the expense of shoot growth resulting in higher root:shoot rations when stressed. It would be useful to have a model to mimic this strategy as a method to simulate plant response to moisture stress. One way of simulating this process is to vary the allocation of carbon to the roots as a function of moisture stress. This method is used in the soybean model **GLYCIM** and in the **2DSOIL**, a modular simulator of plant and root processes. Here we describe the model of root growth and water uptake and show how the model behaves under different water availabilities. We can use such models to look for gaps in our knowledge and as a framework to guide further experimentation and interpret results.

OBJECTIVE

• Present a method of modeling root growth in response to water stress based on trading carbon for water

THEORY

THE ROOT GROWTH MODEL

**Procedural Outline of Root Growth:**

* There is a potential growth rate for optimum conditions
* The potential rate is modified by soil conditions to provide an actual rate
* Roots are grown at the actual rate using available carbon.

**Root growth depends on the following soil variables:**

1. Soil mechanical resistance (a function of soil matric potential and bulk density)
2. Soil temperature
3. Soil oxygen status

**Important Steps**

* A root growth reduction factor in the range 0 to 1.0 is assigned to each cell based on the favorability of the most limiting factor of the three variables given above. The soil cells are then sorted according to the growth reduction factor.
* Root growth begins in the cells with the highest favorabilities and continues with that order

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* Carbon is allocated to each cell in the order of favorability to grow roots at the rate determined by multiplying potential growth by the most limiting factor.
* Carbon is allocated to each cell in turn until:
  1. The pool is exhausted or
  2. all cells with roots have been given carbon
* Left-over carbon goes to a root-carbon pool to be made available for root growth at a later time. At night some root-carbon may be transferred to the shoot-carbon pool according to a pre-defined proportion.
* During periods of moisture stress when the plant has lost turgor, the root growth rates are increased by a factor of 1.5 to allow the roots to use more of the available carbon
* After periods of moisture stress when the plant is recovering from loss of turgor, the growth rates are increased by a factor of 2.0 while the leaf water potentials are recovering.

CARBON PARTITIONING

* Carbon for root growth is allocated from photosynthate using a partition coefficient which is a function of vegetative stage. The coefficient varies from near 1.0 when the plant emerges to 0.1 at the first reproductive stage.
* This figure shows the range of carbon partitioning as a function of moisture stress.



* Carbon allocated for root growth but not used also goes to the root carbon pool. At the end of each day a portion of this carbon is moved to the shoot carbon pool according to the relative shoot and root weights.

CALCULATION OF LEAF WATER POTENTIALS AND TURGOR PRESSURES.

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* The threshold leaf turgor pressure (PT) required for shoot growth adjusts dynamically with leaf turgor pressure (P) as a function of time.:

Here 0.2 MPa is the threshold value below which the leaf can no longer adjust. Time is measured from dawn.

* Any change in leaf water potential during the day is partially balanced by a change in leaf osmotic potential. This allows us to calculate the critical levels of leaf water potential given in Figure 1. In the model, temporal increments of leaf water potential and turgor pressure are proportional:
* Here, and subsequently, *ψL* is leaf water potential and *PL* is leaf turgor pressure. The superscript 0 indicates the beginning of the time interval. The parameter *fπ* adjusts the leaf water potential for osmoregulation.
* The threshold value of the leaf water potential *ψLT* that prevents all shoot expansion is:
* The leaf water potential at 2 bars of turgor pressure *ψL,2* is:
* The leaf water potential at zero turgor *ψL,0* is:

* During the day, LWP never rises above its dawn value and can never be above -0.2 MPa
* The final leaf water potential in any time step is calculated to satisfy the necessary water uptake rate.



Water uptake rates are calculated for the points B, C, D, and E in Figure 1 using the following threshold leaf water potentials:

* ψ0L, The threshold leaf water potential during the previous time step where shoot growth stops.
* ψL,T, The threshold leaf water potential for the current time step.
* ψ L,2 The leaf water potential at 0.2 MPa leaf turgor pressure
* ψ L,0 The leaf water potential at 0 leaf turgor pressure

These estimated water uptake rates (U) are compared to the atmospherically determined rate (potential transpiration, TP).

PROGRAM OPERATION

The method operates by comparing the potential transpiration rates (TP) to the uptake rates at threshold values of leaf water potential (U(ψ)) and determining the level of moisture stress.

* TP<U (ψ0L) The plant can take up water without having to reduce its leaf water potential beyond the turgor loss threshold value for the last time step and with roots grown without additional carbon. This is the non-stressed condition. The leaf water potential is then adjusted to meet the potential transpiration demand.
* TP<U(ψL,T) and TP >U(ψ0L) The plant cannot take up water without lowering its leaf water potential beyond the turgor loss threshold value from the previous time step. However, it does not have to lower its leaf water potential beyond the threshold value determined for this time step. This will result on a partial loss of turgor. The plant will divert some carbon from shoot growth to provide for additional root growth. The amount of carbon diverted depends on the leaf turgor pressure and whether or not it has decreased since the last time step. If the turgor pressure is less than 0.5 MPa and falling and the shoot growth time ratio is less than 1.0 some proportion of additional carbon is diverted toward root growth. In this case the stomates also begin to close. The closure of the stomates is proportional to the water uptake calculated at the threshold leaf water potential ψL.T divided by the potential transpiration rate:

The leaf water potential is then adjusted to meet the potential transpiration rate using additional roots. During this time the shoot growth time is reduced by some fraction (Shoot Growth Time ratio) that is determined from the turgor pressure and leaf water potential and how they change over time.

* TP<U(ψ L,2) and TP>U(ψL,T) The leaf water potential must fall below the threshold value for turgor. Shoot growth ceases completely. If the turgor pressure is less that 0.5 MPa but greater than 0.2 MPa a fraction of additional carbon is diverted toward root growth. If the turgor pressure is less than 0.2 MPa then all carbon is diverted toward root growth.
* TP>U(ψ L,2) Here the plant loses turgor and there is no growth. The stomates are assumed to be 90% closed. The plant can adjust its leaf water potential to take up water by making some osmotic adjustments.
* When leaf turgor pressure begins to increase again after it has fallen below 0.2 MPa the shoot growth time ratio can increase to a value greater than 1.0 to allow the plant to make up growth lost during stress

CALCULATION OF WATER UPTAKE

Water uptake is calculated as:

Here:

U(ψL) i = Water uptake rate in cell *i*

ψ s,i = Soil matric potential in cell *i*

ψL = Leaf water potential corresponding to the points A, B, C, or D in figure 1.

R = Resistences in the root, radial ( r) and vascular (v), and resistance in soil (s)

Rs is a function of the radius water must travel to reach the root (calculated from soil matric potential), and the average soil hydraulic conductivity in the cell. The root resistences vary with mature and young roots.

Water is taken out of each cell in the same order as their favorability for growth.

* We have made several modifications to the root growth and water uptake code relative to the code currently used in GLYCIM. We plan to test the model with these changes these at a later stage. These modifications are:
  1. Increase of the potential growth rate of roots during and after water stress
  2. Distributing water uptake among all the cells with roots that take up water. Initially, actual uptake was often satisfied before the program iterated among all the soil cells.
  3. Defining stomatal closure based on available water uptake rate rather than on available water in the soil and leaf water potential.

SIMULATIONS

The simulations demonstrate the model's behavior in terms of carbon partitioning, root growth, water uptake and plant water stress. We compare simulations with and without extra partitioning of carbon during moisture stress. The model is implemented in GLYCIM. We consider these scenarios:

Frequent irrigations, 2.5 cm each, every three days to replace water lost by evapotranspiration (shallow wetting).

Irrigations of 5.0 cm every 10 days to fill the profile (deep wetting).

Irrigations of 5.0 cm every 15 days.

The soil (Table 1) is a Dundee Loam from Bolivar Co., MS. (fine-silty, mixed, thermic Aeric Ochraqualf). (The maximum depth used was 100 cm.

Table 1. Characteristics for Dundee Silt Loam.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Depth | Bulk  Density | Sand | Silt | Clay | θ33 | θWP |
| cm | Mg m-3 | kg kg-1 | | | m3 m-3 | |
| 0-16 | 1.224 | 31.0 | 42.7 | 26.3 | 0.289 | 0.229 |
| 16-40 | 1.354 | 35.5 | 42.1 | 22.4 | 0.289 | 0.246 |
| 40-100 | 1.299 | 42.5 | 38.9 | 18.6 | 0.290 | 0.243 |

Data provided by Dr. Frank Whisler, Mississippi State University)

RESULTS

**Results of simulations for soybean growth and yield using three levels of water stress and two methods of carbon partitioning**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Water  stress | Partition  Method | Shoot  mass | Root  mass | Shoot/  Root | Grain  yield | Leaf  area |
|  |  | g | g |  | kg ha-1 | cm2 |
| low (a) | Extra | 93.5 | 16.1 | 5.8 | 7276 | 6286 |
|  | Min | 93.8 | 16.0 | 5.9 | 7276 | 6279 |
| med (b) | Extra | 78.7 | 10.6 | 7.4 | 6397 | 5653 |
|  | Min | 80.7 | 8.8 | 9.2 | 6571 | 5505 |
| high (c) | Extra | 54.3 | 4.3 | 12.6 | 5343 | 3848 |
|  | Min | 52.9 | 3.6 | 14.9 | 5176 | 3568 |
|  |  |  |  |  |  |  |

There is little difference for the two methods of partitioning carbon for the frequent irrigations, *a*. Figure 2 shows little difference in leaf water potential between the two methods. There is also little difference in root growth (Figure 3)

For irrigation method *b* there is more moisture stress. There is more root growth and slightly less shoot growth where additional carbon has been partitioned for root growth based on water stress. The differences on leaf water potential in figure 2 shows more negative leaf water potentials in the minimum carbon allocation method. The total leaf areas and yield, however are not very different.

For irrigation method c, there shoot and root weights are further reduced for both methods but the difference is not large compared to the differences for method *b*. The differences in leaf water potential shown in figure 2 are also large with more negative values in the minimum allocation method. Yield, leaf area, root mass and shoot mass are somewhat higher for the case where additional carbon is made available for root growth.

Figure 3 shows higher root densities deeper in the profile for the plants that received additional carbon for root growth.

DISCUSSION AND CONCLUSIONS

* Plants subject to moderate water stress show increased root:shoot ratios over non-stressed plants. In simulations where additional carbon is allocated, the root:shoot ratios are also higher for the less irrigated simulations. The increased root growth is reflected in higher leaf water potentials in simulations where additional carbon is made available for root growth during stress. The overall effect on yield in these simulations is small, however.
* Where there are frequent irrigations root growth is greater near the surface as opposed to the simulations with less frequent irrigations. There is a smaller difference in root distributions for the two methods of allocating carbon when water is not limiting.
* Model simulations show that at times there is more carbon available for root growth then the actual root growth rates can support, is this realistic?
* Research has shown that plants often take several days to recover from severe moisture stress and sometimes the recovery is only partial. The model does not take this into account.
* Comparisons with the two versions (with and without additional carbon) revealed that unless the potential growth rates of the roots are increased when additional carbon is available the additional carbon has little advantage for root growth. This is because a portion of the unused carbon it transferred to the shoot pool to be used for above ground growth.
* The advantage of increased root growth will also be greater in soils with larger water holding capacities.
* The model described here is an analogy for a biological system and is still incomplete. Under the conditions tested, however, it does give reasonably realistic results for root/shoot ratios. However, we did not see the expected differences in plant size with moisture stress. This may be due to the lack of code that deals with leaf and stem morphology under moisture stress. Knowledge in this area is still not complete

**GLYCIM**

Acock, B., and A. Trent. 1991. The soybean simulator, GLYCIM: Documentation for the modular version 91. Agric. Exp. Stn., Univ. of Idaho, Moscow, ID.

**2DSOIL**

Timlin, D.J., B. Acock, and M. Th. van Genuchten (ed). 1996. 2DSOIL, A Modular Simulator of Soil and Root Processes. USDA/ARS, Remote Sensing and Modeling Lab, Beltsville, MD and Soil Salinity Lab, Riverside, CA.