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Free-Energy Transfer in Plants

Abstract. *Free-energy transfer was used to study water transport through the soil-plant system. Resistances to free-energy transfer are proportional to resistances to water transfer. Under certain conditions, the proportionality factor is 1. For a sunflower plant in moist soil, plant resistance to free-energy transfer was 30 times the soil resistance, and root-stem-leaf resistances were in a ratio of about 2 : 1 : 1, respectively. However, root and leaf resistances were equal when considered for a unit pathlength.*

The movement of water in living organisms has two distinct aspects: water entry into single cells and water transport among arrays of cells. Little is known about the second aspect, particularly with regard to transport through whole plants.

The liquid pathway from the soil through the plant is composed of a set of resistances in series. Studies have been devoted to water movement through the soil (*1*), root (*2, 3*), and the vascular system and leaf (*3, 4*), but comparative data for the entire pathway are unavailable. I now describe a way of measuring resistance, which is based on the transfer of free energy through the plant, and this concept is used to compare resistances in various portions of the soil-plant transport system.

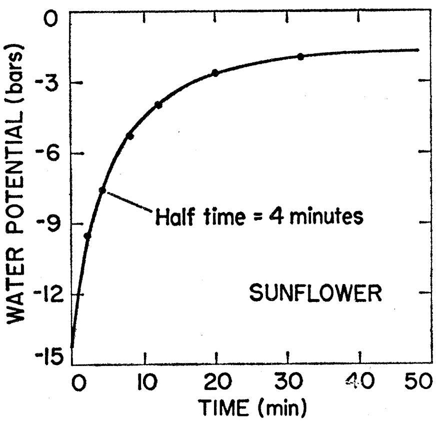

Fig. 1. Predicted (●) and observed (———) water potentials of a sunflower leaf recovering from a water deficit. Resistance to the transfer of free energy is determined from the half-time for recovery.

I have reported simultaneous recovery curves for water uptake and water potential in nontranspiring leaves recovering from water deficits (*5*). Most leaves had different and apparently unique kinetics of water uptake with time; however, the kinetics of changes in water potential appeared similar. Because a simple phenomenon seemed to govern changes in water potential, I have studied the water potential data, with the hope that the results could be applied to the flow of water through the plant.

The rise in water potential that occurs as a leaf recovers from a water deficit represents a transfer of Gibbs free energy to the leaf. Knowing the volume of water in the leaf and the change in potential with time permits an estimate of this transfer. Changes in potential at constant temperature are related to the energy dissipation (dS/dt) of irreversible thermodynamic processes by:

$$V(d\psi/dt) = dG/dt = -T(dS/dt) \quad (1)$$

where V is the average volume of water in the leaf (cm^3), ψ is the water potential of the leaf (bars), t is the time (seconds), G is the Gibbs free energy of water in the leaf (bar cm^3; 1 bar cm^3 = 10^6 erg), T is the Kelvin temperature, and S is the entropy (bar cm^3 deg^{-1}). The mathematical treatments of energy dissipation in heat and diffusive transfers are similar, and the diffusion of deuterated water follows these laws in some tissues (*6*). Thus, similar principles may be applicable to the free-energy transfer observed in leaves, particularly in view of the proportionality between changes in water potential and energy dissipation (Eq. 1).

Leaves are usually thin, largely two-dimensional arrays of reasonably homogeneous cells. They may be idealized to two infinite plane sheets of cells, one above a plane representing the vascular system and one below this plane. Since the vascular plane is generally located midway between the upper and lower epidermis, the pathlength (l, cm) for free-energy transfer to either epidermis would be half the leaf thickness. According to these boundary conditions, a leaf with a low and initially uniform water potential should follow the heat or diffusive transfer equation for a plane sheet (*7*) and should permit calculation of the resistance to free-energy transfer (r):

$$r = t_{1/2}/0.195l \quad (2)$$

where $t_{1/2}$ is the half-time for recovery (seconds).

To determine whether leaves behave as plane sheets during free-energy transfer, the appropriate transfer equation (*7*) was used to predict leaf-water potentials at various times during recovery from water deficits. Water potential was measured by sealing the blade of a slightly wilted sunflower leaf in a thermocouple psychrometer that estimates potentials of intact leaves (*5*). After the first measurement, the petiole of the leaf was cut under degassed water, and leaf water potential was followed during the subsequent water uptake. There was excellent agreement between the observed water potentials and those predicted from the transfer equation (Fig. 1). The same results were obtained with leaves of soybean, garden bean, papaya, abutilon, cottonwood, sugar maple, and tomato, as well as sunflower. Thus, free-energy transfer through planar leaves approxi-

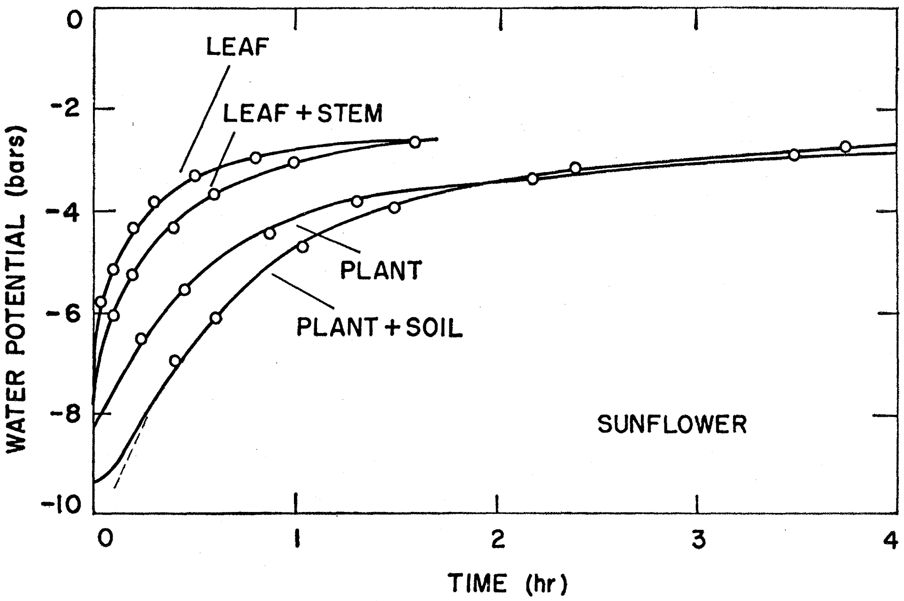

Fig. 2. Predicted (○) and observed (———) water potentials for a sunflower leaf recovering from water deficits while attached to various parts of the soil-plant flow system. Half-times are 27, 26, 12, and 6 minutes for the soil and plant, plant, leaf and stem, and leaf, respectively.

mates energy transfer through a plane sheet, and the resistance to transfer may be measured from Eq. 2. For the sunflower leaf (Fig. 1) resistance was 7.7×10^4 sec cm^{-1} and remained constant regardless of the initial water potential of the leaf.

This type of resistance may be calculated without information about water flow through the tissue or the water potential in other parts of the flow system. It is therefore well adapted to estimations of resistance in the intact plant. I calculated plant resistances by determining the resistance of the leaf and other portions of the plant, and then by determining the resistance of the leaf alone. Inasmuch as the plant flow system is composed of a set of resistances in series, they are additive, and the resistance for a particular segment can be calculated by difference.

Recovery was observed on an intact soil-grown sunflower plant with a slight water deficit. The plant was then allowed to wilt and recover several times, and progressive portions of the soil-plant system were removed between each recovery cycle. The leaf blade was not removed from the psychrometer chamber during the experiment, which took from 4 to 6 hours.

The leaf conformed to the transfer equation for a plane sheet regardless of whether it was attached to other parts of the plant (Fig. 2). The recovery time became shorter as successive portions of the transfer pathway were removed. Resistances calculated for this plant (Fig. 3) were in an approximate ratio of 2:1:1 for root to stem to leaf, with the moist soil contributing negligible resistance to the system. Relative to soil resistance, the large plant resistance dominated the soil-plant flow system under moist conditions.

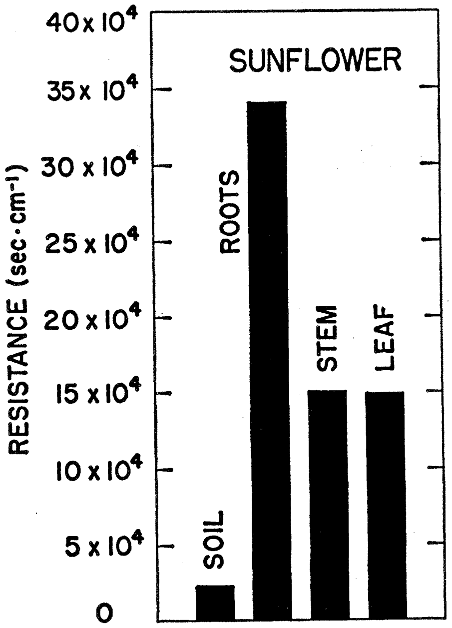

Fig. 3. Resistances to free-energy transfer in the soil-plant water transport system. The soil resistance was determined for a soil flooded briefly and then drained of excess water; root resistance was measured from the root surface to the point at which the stem emerges from the soil; stem resistance was measured from the soil surface to the petiole of the leaf used for observing recovery.

Roots are generally thought to offer the largest resistance in the flow pathway within the plant (*3, 4*). This study shows that stem and leaf resistances may also form a considerable portion of the total plant resistance. Resistances compared over a unit length of the flow path, rather than for the total segment, approximate a ratio of 1 : 0.0005 : 1 for root to stem to leaf, if one assumes that root tissues outside of the vascular system comprise the main source of root resistance. Expressed in this fashion, resistances to transfer through living tissues in the root and leaf appear quite similar. Vascular resistance is much smaller and it reflects the adaptation of the vascular system to long-distance transport.

Thus far, the analysis has been based entirely on resistances to free-energy transfer. Resistances to water transport are proportional to resistances to free-energy transfer and have a proportionality of 1 under certain conditions (*8*). Thus, the same conclusions would be expected whether transport is considered from the point of view of energy transfer or of water transfer.

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