Plant Transpiration — Have Plants Evolved a Wasteful Use of a Scarce Resource?

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INTRODUCTION

Although plants have characteristics that promote water retention under stress situations, their general water budget appears to be far in excess of actual plant requirements.

For instance, a growing plant transpires ten times as much water as is required for new cell vacuolation, and one hundred times the amount of water required for CO_2 fixation.[1] The amount of water transpired on a hot day may be several times the plant's fresh weight and of the total water absorbed by plants, up to 98% can be transpired.[1,2]

These anomalous factors are considered in relation to the transpirational process, such as the driving mechanism, xylem resistance, the role of stomata in the CO_2/H_2O compromise, water use efficiency, and means through which plants cope with stress and high leaf temperatures.

THE DRIVING MECHANISM

Transpiration involves the movement of water through plants from the soil through the root system via the xylem to both the internal leaf parenchyma and the leaf atmosphere, and its ultimate evaporation via the stomatal pores to the external atmosphere.

This theory of water movement is based on the apparent metastable state of water in the xylem elements. The water, through common molecular cohesion and adhesion to xylem cell walls, exists as a single unit of high tensile strength, which can be pulled upwards via a gradient in the internal plant water potential and external atmospheric water potential. That is, the sap moves upwards because of a decrease in water potential from the soil to the atmosphere.

The driving force of the process is the low (more negative) atmospheric water potential, that drops dramatically with a slight reduction in atmospheric humidity, and solar energy, which provides the latent heat for evaporation of the water.[3] From this thermodynamic perspective there is more than adequate energy available to ensure water flow.

For example, at 98% relative humidity the water potential of air (-27.5 bars) is low enough to move water up a plant to a height of 281 metres.[3] Everington[4] questions the validity of the adhesion-cohesion theory beause cavitation, or breaks in the water column, does occur naturally in the xylem. However, cavitation does not necessarily impede water flow as there is a complex of interconnections between xylem vessels.[5] The sum effect of these links, despite vertical cavitation, still maintains enough connections to facilitate a unit pull through the whole plant.

The tensions developed in trees are very high during periods of rapid transpiration. For example, field measurements by the writer of cut stems of *Erythrophleum chlorostachys* at Nabarlek (in western Arnhem Land, Northern Territory, Australia) in the dry season of the wet-dry tropics showed xylem tensions of 36 bars (35.5 atmospheres). Higher tensions can be measured in arid land vegetation.

Given that the water potential hypothesis is valid, the process it explains is highly efficient, regardless of the consequences, at moving relatively large volumes of water through plants, except in the case of where high relative humidities lessen the atmospheric pull on water from the soil via the plant, to the point that root pressure can actually take over and force water upwards through the plant.

An aspect of plant growth where the transpiration system appears inefficient is the situation of plants growing in an atmosphere of very low relative humidity. Daubenmire[6] points out that the xylem are "relatively inefficient in supplying water to meet the demands of transpiration, even at times when growth is plentiful." This aspect of transpiration would explain leaf wilting during high

temperatures despite adequate availability of soil moisture, that is, the loss of water from the leaf parenchyma reduces cell turgidity as xylem flow cannot keep up with leaf water loss, before stomatal closure. When drying soil causes absorption to lag behind transpiration, permanent wilting and death by dehydration occurs. Kramer[7] says that "probably more plants are injured or killed by excessive transpiration than by any other cause."

In view of the stress that the transpiration mechanism can place on plants and the current day demand on the xylem, plants could be perceived as existing under a temporal heat and humidity regime that imposes a present day high stress existence on the majority of plant types. In an earlier regime of higher humidity, plants would not have had to transpire as much. Root pressure would have played a more important part in the absorption of water into and through plants. Perhaps we are observing what Sutcliffe[2] refers to as "the necessary evil" of transpiration at a time in Earth history where plants are required to cope on a global scale with an abnormal current regime of lower humidities and widely oscillating temperatures. Leaving aside the problem of CO_2 intake at this stage, it is noted that Salisbury and Ross say that "many plants can be grown through their life cycles in an atmosphere of 100% relative humidity where transpiration is greatly reduced ..." and "many plants grow better in an atmosphere of high relative humidity".[3]

STOMATA

The behaviour of stomata in transpiring plants is crucial as the "effective control of water transport must ultimately be exercised in the gas phase by the stomata".[8] Most of the CO_2 required by plants enters the leaf atmosphere via stomata by diffusion and "1/2 to 6/7's of the H_2O precipitated on land returns to the atmosphere by evapotranspiration", mainly via stomata.[9] Lengthy periods of opening of the stomata are essential for CO_2 intake and subsequent photosynthesis due to low atmospheric levels of CO_2. The presence of an internal leaf atmosphere is necessary for CO_2 diffusion into the mesophyll cells as movement of CO_2 via other means, such as diffusion through transpired water, would be 10^{-4} times less than for diffusion through an atmosphere. The area of stomata is a low proportion of total leaf area, and experiments done by Brown and Escombe (in Rutter[1]) show that diffusion of CO_2 is adequate through fine pores. One of their results, that demonstrated the practical physics of fine orifice diffusion, showed that for a 1% perforated screen area across a tube, the rate of inward diffusion was 40% of that obtained for a fully open tube.

Despite small stomatal openings and the external boundary layer resistance, water vapour moves rapidly out of the leaf sub-stomatal atmosphere due to the rapidity of diffusion through these small pores and the atmospheric water potential gradient. Thus plants, via their stomata, continually balance their need for CO_2 and their need to retain water for maintaining cell turgor. Although stomatal closure will reduce water loss, plant metabolic processes will also be hindered.

The means through which stomatal reaction operates is by two feedback loops. Control of water stress and CO_2 requirements are mediated by the movement of abscisic acid, potassium and water in or out of the guard cells (after Raschke,[9] Salisbury and Ross[3]). Raschke says that plants have "evolved the stomatal feedback system for the reconciliation of the two opposing priorities."[9]

However, stomatal opening would be reduced and water loss lessened if there was a higher availability of atmospheric CO_2 to increase diffusion rates into plant leaves. An environmental regime of higher atmospheric CO_2 plus a high humidity would provide optimum conditions for prolonged stomatal opening and a low level of transpiration, thus reducing the apparent dramatic turnover of water in plants, with an accompanying increase in plant water use efficiency.

The spectacular fixation of carbon in massive flood coal deposits and limestones in a previous Earth time phase is evidence that high atmospheric CO_2 levels have occurred during the existence of land plants. It is well known that plants are more productive when grown under high CO_2 levels. For example, experiments by Morison and Gifford[10] have shown that "with good nutrient, water and light supply, a doubling of carbon dioxide concentration increased the dry weight of young well spaced plants of 16 species by an average of 65%, though this ranged from 26 to 132%." Water use efficiency was also enhanced under these conditions.

It is proposed that stomatal oscillations associated with high transpiration rates and water budgets in current land plants are an anachronism and are a product of environmental change, namely, that plants have been propelled from an optimal environment of high humidities and high atmospheric CO_2 to a current stressful environment of low humidities and low atmospheric CO_2.

COPING WITH STRESS

Some plants have in their design metabolic mechanisms and structural features which assist them in coping with the problem of the CO_2/H_2O compromise in environments of high water stress.

Certain tropical monocots and desert plants can reduce water loss through high efficiency photosynthesis. Bjorkman and Berry,[11] when comparing Californian desert plants with a four-carbon pathway (e.g. *Atriplex* vosea) to a three-carbon species (e.g. *Atriplex patula),* calculated that the C4 plant would transpire only a fifth as much water as the G3 species when both plants were photosynthesising at the same rate. The C4 plants in such cases can maintain smaller stomatal openings than the C3 plants and hence lose less water vapour, for the ability of the C4 plants to maintain photosynthesis at a low intercellular concentration of CO_2 accelerates the diffusion of CO_2 into leaves at rates well above those of the G3 plants.

However, the overall water use efficiency (WUE) of the two contrasting photosynthetic groups is not great. For example, Fischer and Turner[12] quote WUE values for desert shrubs of 1.4 grams of dry matter produced per 1000 grams H_2O for the C4 species *Atriplex canescens* compared to a mean value of 0.7g/1000g H_2O for G3 species such as Larrea tridentata. These are not significant differences relative to the volume of H_2O passing through the plants. Container experiments suggest that there are not large differences in WUE between plants of the same life form within the C3 and C4 groups.[12] In respect of crop studies of productivity and yield of plant species with differing photosynthetic metabolisms, Gifford[13] concludes that at the level of crop growth rate there is no apparent difference between best examples of the two groups when grown in their own preferred natural environments. Four carbon plants will transpire quite rapidly given adequate soil moisture. If the concentration of CO_2 is increased then the rate of photosynthesis in C3 plants can equal that in C4 plants.

Wodell[14] considers adaptive features of xerophytic plants which can contribute to reduction of water loss, uptake increase, water storage and efficient water translocation. Transpiration can be avoided or modified by evasion, leaf shedding, sunken stomata, thick cuticles, low surface/volume stem and leaf ratios, day stomatal closure (Crassulacean acid metabolism or C.A.M. succulents) or as in the case of bryophytes and lichens, through cell shrinkage.

Although such xerophytic features enhance survival, the difference in transpiration efficiency or WUE for desert plants as compared to high growth agricultural species, is not great. Odum[15] points out that 4-6 grams of dry matter are produced per 1000 grams of water for desert plants as against 2 grams/1000 grams H_2O for crops. Fischer and Turner[12] say that the overall productivity of CAM

plants is low, especially when fixing carbon in the CAM mode. Desert xerophytes sacrifice growth due to transpirational controls and although they have the genetic capacity to survive arid conditions, they do not necessarily "prefer dry conditions: most will grow very well and many better in moist conditions than in dry."[14] So despite their adaptive characteristics, the water use efficiency of xerophytes in relation to growth is not really much different to that of mesophytes, hydrophytes and halophytes.

TEMPERATURE

There is a diversity of opinion between plant physiologists about how important transpiration is in reducing heat loss in leaves.

Heating results principally from the absorption of energy from the photosynthetically active wavelengths between 400 to 700 nm, of which one fifth becomes effective for photosynthesis, the remaining 80% requiring dissipation.[1,16] Too great a heat load can lead to protein denaturation (e.g. > 50 °C). Leaf temperature is lowered by heat energy being utilized to supply the latent heat of vaporization. For example, at 30°C the latent heat of vaporization is 580 cal/gram (water).[3]

Leaf temperature and transpiration rate depend on air temperature, irradiance, wind speed, leaf dimension, leaf shape and leaf diffusive resistance. Large leaves with low stomatal resistance in hot humid temperatures rely on transpiration to maintain their optimum temperature, but if transpiration in leaves is impeded by high stomatal resistance or a thick boundary layer, low wind, hairy leaf etc., then other heat-removing mechanisms have to apply for homeostasis to be maintained. Leaves can lose heat by conductive heat loss or re-radiation, or by having shapes that minimise light interception (e.g. pine needles or leaf orientation).

Rutter's[1] graphical results with wax-treated leaves show only a maximum of 4°C between sealed and open transpiring leaves. Although this minor temperature difference may be crucial in some leaves, it could be said that transpiration can contribute generally to heat loss in leaves, but for many plants other cooling factors are more important. Against this doubtful benefit of transpiration as a temperature regulator it needs to be recognised that the magnitude of transpiration is a major hazard in the ecology of most terresterial plants.

SUMMARY

1. Plant water budgets are anomalously high.

2. There is a need to explain the current high rates of transpiration imposed on plants, and the inefficiency of the xylem vessels to meet these rates.

3. Plants do perform best in an atmosphere of high relative humidity and high CO_2 content.

4. Plants are adapted to use of photosynthetically active wavelengths, yet exhibit poor adaption to present CO_2 content in the atmosphere.

5. There is evidence deducible from the sedimentary rock record that the conditions described in (3) above were once commonplace in past Earth history.

6. Specialised metabolic mechanisms and structures in certain plants allow them to tolerate a wider range of stresses than other plants, but these special attributes do not confer any outstanding ability of relative water use over that of other plants.

7. It has not been demonstrated that high transpiration rates are necessary to bring about heat loss from leaves to ensure leaf survival.

The present state of water turnover in plants is not satisfactorily accountable in terms of plant evolutionary competence. Plant physiologists are hard pressed to demonstrate that heightened transpiration is essential or of clear adaptive advantage to plants, other than as a consequence for the need for stomata to provide for CO_2 intake. It is here proposed that plants have not evolved a wasteful use of a scarce resource, but rather, high water usage is a by-product of plants being forced to grow in present-day environments of low relative humidity and low CO_2 levels for which they are not ideally suited.

This proposed transition from a former optimal environment to the stressful present-day environment could have been a recent phenomenon and could be held responsible for extinction of certain plants.

The present-day behaviour of plants can give insight to global atmospherics preceding the process that precipitated current atmospheric conditions.

PRE-FLOOD ATMOSPHERIC CONDITIONS

The biblical model of Earth history pictures a pre-deluge world surrounded by a water canopy. This water body, whether in liquid or vapour form, as Dillow[17] has calculated, was the source of rainwater during the Flood catastrophe. Other water sources included upwelling subterranean water (the 'fountains of the great deep'}.

The atmospheric conditions under the canopy as modelled by Dillow,[17] Patten[18] and Morris,[19] consist of high CO_2 and high humidity, high partial pressures, global warm temperatures, no rain (no rainbows), a heavy diurnal dew regime and a subdued evaporation rate.

The existence of these greenhouse-type conditions is independently supported through an analysis of the apparent current day anomaly of high water turn over in plants.

The collapse of the canopy in the biblical model of Earth history is a likely candidate for the environmental event that fits the thesis in this paper, that plants have been propelled from an optimal growth environment to a less ideal stressful environment.

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