# Appendix A
# A Note on Transpiration

**David Seckler**[1]
*International Water Management Institute, Colorado, USA*

> Crop losses to water shortage may exceed those from all other causes combined.
>
> (Kramer, 1980)

> Always the beautiful answer
> Who asks a more beautiful question
>
> (e.e. cummings)

## Introduction

This note is the product of a dialogue in the International Water Management Institute (IWMI) over the simple question: 'Why do plants need so much water for transpiration?' 'Transpiration consists of the vaporization of liquid water contained in plant tissues and the vapor removal to the atmosphere' (Allen *et al.*, 1998).[2] Between 200 and 1000 kg of transpired water is lost to the atmosphere in the production of only 1 kg of plant biomass. And this is just for biomass; the amount of transpiration per unit

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[1] It should be emphasized that this note is written by an economist, not a plant scientist or similar expert. I hope that what is sacrificed in terms of expertise may be partly compensated for by a somewhat different perspective on the issues and the need to write it in simple language more accessible to other interested laypersons. Fortunately, previous drafts of this note have been closely reviewed, corrected and contributed to by two real experts in the field: Richard G. Allen of Idaho State University and Terry Howell of the Agriculture Research Service of the US Department of Agriculture (USDA). I am enormously grateful for the time they devoted to this task and our interesting and enjoyable correspondence. I have also benefited from criticisms of a previous draft by Bruce Bugee of Utah State University and a constructive review of the final draft by Parviz Soltanpur of Colorado State University. Of course, all remaining errors, whether of commission or omission, remain my responsibility.

I have also benefited a great deal by discussions with Andrew Keller of Keller–Bliesner Engineering, Logan, Utah, concerning both this note and a companion paper to this one, which he has written: *'Note on crop yield to water relationships'*. We are grateful to the International Water Management Institute for supporting both of these notes, as part of a research programme in water productivity.

[2] This is the reference work on the subject and should be studied by anyone interested in the use of water in agriculture – which constitutes most of the developed water resources used in the world.

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of grain or other fruits is at least twice this amount. Clearly, this is an important question for an institution like IWMI, which is dedicated to more productive water use: 'More crop per drop'.[3]

One result of this study is that it is now easier to understand why the dialogue in IWMI never reached a satisfactory conclusion. While some of the central features of transpiration are clearly understood and command broad agreement among experts, other important aspects remain hazy and controversial. The problem, in other words, is that in some respects this 'beautiful question' has several 'beautiful answers', some of which are contradictory. This has made the present note exceptionally difficult and interesting to write. To accommodate this problem, extensive quotations and references are used in the text and footnotes, and I have used the personal pronoun to distinguish my own thoughts from those of authorities in the few cases where I thought they might be worth mentioning.

## The Process of Transpiration

The *Columbia Electronic Encyclopedia* provides a lucid overview of the process of transpiration.[4]

> Transpiration, in botany, is the loss of water by evaporation in terrestrial plants. Some evaporation occurs directly through the exposed walls of surface cells, but the greatest amount takes place through the stomata, or intercellular spaces (on the leaves). Transpiration functions to effect the ascent of sap from the roots to the leaves (thus supplying the food-manufacturing cells with water needed for photosynthesis) and to provide the moisture necessary for the diffusion of carbon dioxide ($CO_2$) into and oxygen ($O_2$) out of these cells. The rate of transpiration is almost always far greater than the above functions would seem to warrant; in most plants 200–1000 lb. (or kg) of water are transpired for each pound (or kg) of solid material added to the plant. Various factors influence the transpiration rate. Photosynthesis, induced by light, has the effect of increasing the water pressure in the guard cells that border each stoma and that, in expanding, pull apart to widen the stomal aperture and thereby increase water loss. Low humidity promotes the diffusion of water vapour from the air passages inside the leaf into the outside air. A lack of water in the soil cuts down the water supply to the cells, thus lowering the water pressure and thereby limiting expansion of the guard cells. Therefore, the rate of transpiration is highest on a bright, dry day and lowest at night or in drought conditions. Morphological factors, such as reduced leaf surfaces, a heavy cuticle layer on the leaves, low numbers of stomata, and stomata recessed below the other epidermal cells, also lower the rate; plants, such as conifers and cacti, conserve water in these ways. Plants also lose some water by guttation, a process whereby water is exuded directly through pores called hydathodes. The reaction of a plant to excessive water loss is wilting and, eventually, death.

An important product of the process of photosynthesis is carbohydrate. The building blocks of carbohydrate are: (i) hydrogen, which plants acquire by breaking down water molecules; and (ii) carbon, which is acquired by breaking down molecules of $CO_2$. Water is obtained from the soil, through the plant roots. $CO_2$ is obtained from the atmosphere, through the stomata. The waste product of photosynthesis, $O_2$, is dispelled from the plant through the stomata into the air, where it is happily recycled by animals.

As noted above, the stomata are surrounded by guard cells, which may be pictured as doughnut-shaped bladders of water, with the pore of the stoma being the hole of the doughnut. Photosynthesis increases the water pressure in the guard cells (known as the turgor pressure), causing them to expand and thereby opening the stomata. This

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[3] I would like to take this opportunity to set the record straight on this much-used slogan of IWMI's. It was invented by Chris Perry of IWMI around 1995. And of course it is subject to the usual constraints for environmental quality, equity, gender, etc.

[4] *The Columbia Electronic Encyclopedia*, 6th edn. (Encyclopedia. com), 'Transpiration'. This excellent source is freely available on the Internet. Here as elsewhere statements in brackets are mine.

enables the plant to absorb $CO_2$ and expel $O_2$. But, when the stomata are open, water vapour in the leaf is exposed to the atmospheric forces of evaporation. When soil water is plentiful, this does not normally present a problem for the plant: it simply absorbs sufficient amounts of water from the soil through the roots to compensate for the water losses of transpiration. But, if soil water is scarce, the plant could die of dehydration. The aptly named guard cells protect the plant against this fate, at least temporarily. With a relative shortage of soil water, the guard cells lose turgor pressure and the stomata close. While this protects the plant from dehydration, by reducing transpiration, it also reduces the intake of $CO_2$, the rate of photosynthesis and, hence, plant growth.

There is a high – indeed, almost perfect – correlation between the rate of transpiration and the rate of plant growth. However, 'correlation is not causation'. The question is whether this high correlation implies a causative role of transpiration in plant growth. The basic process of transpiration outlined above does not necessarily imply such a role. The exchange of gases with and the loss of water vapour to the atmosphere vary together because both processes are driven by atmospheric conditions and are conducted through and governed by the stomata. In this view, absorption of $CO_2$ is the central element of the process and transpiration is merely a consequence of the process. As Condon *et al.* (2002) put it, transpiration 'is the required unit of exchange for the acquisition of $CO_2$ by plants'.

There is no question that this view of transpiration is correct, so far as it goes; but is this all there is to it? Does transpiration provide beneficial functions for plant growth, at least to some degree and under some conditions? The answer to this question determines at least the theoretical potential for saving water in crop production by reducing transpiration (neglecting, for now, the question of whether this can be done in practical ways). This question of the beneficial functions of transpiration is the focus of the rest of this discussion.

## Two Beneficial Functions of Transpiration[5]

Two possibly beneficial functions of transpiration are frequently mentioned in the literature.

First, transpiration helps to cool plants in extremely high temperatures. While this is true, most plants (unlike many animals) spend most of their time within their comparatively wide range of temperature tolerance. One authority says, 'leaves in the sun rarely are seriously overheated even when transpiration is reduced by wilting' (Kramer and Boyer, 1995). This is partly because there is almost always some moisture evaporating from the leaf. However, temperature can seriously affect plant growth beyond the limits of their tolerance. And the effects of temperature differ substantially among plants.[6]

Secondly, transpiration helps in the movement of sap, nutrients and moisture from the roots to the leaves (as stated in the above citation from the *Columbia Electronic Encyclopedia*). Since this second function seems to be controversial, it warrants a more extended discussion.

> Sap ascends (upward through the plant) at a rate of from 1 foot to 4 feet (30–122 cm) per hour; in the case of redwood it rises easily to a height of almost 400 ft. (120 m). The exact mechanisms behind this enormous lifting force are not certain, although several principles are thought to be involved. Chief among them is the pull of transpiration; as water evaporates from the leaf cells, they draw in liquid osmotically from the xylem tubes to replace it.

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[5] Another excellent Internet source for this and the preceding section is *Kimball's Biology Pages*, based on a biology textbook by John W. Kimball. See 'Transpiration' and the associated hypertext.

[6] An excellent review of the possible effects of temperature and $CO_2$ changes on plant growth, associated with global warming, is found in H. Wayne Polley, Implications of atmospheric and climatic change for crop yield and water use efficiency, *Crop Science* 42, 131–140 (2002).

> Because of the great cohesiveness of water molecules, the resulting tension affects the entire continuous column of water down to the root tips, which in turn absorb more water from the soil.[7]

Also:

> The rise of water in plants depends chiefly on the attraction of water molecules for each other. In large masses of water this attraction is not obvious, but in long, slender tubes it is readily demonstrable, becoming stronger as the tube becomes slenderer. A column of water in a tube as slender as a plant vessel strongly resists being broken, and a pull at the top is transmitted throughout the column. Thus the water can be pulled upward, like a rope through a pipe … This explanation of the rise of water in plants is called the *theory of cohesion*.[8]

Kimball (see note 5) reports experimental evidence on the astonishing pulling force of transpiration. A 150-foot-tall rattan plant was cut at the base, the stem placed in a sealed container of water. The plant continued to draw water from the container and 'the resulting vacuum becomes so great that the remaining water begins to boil spontaneously'. He also notes that coastal mangrove trees use this vacuum effect to desalt sea water through a membrane in their roots. The vacuum required for this task is around 500–800 lb. per square inch!

However, while transpiration-pull (as Kimball describes it) may be needed for very tall plants – like redwoods or rattan, where the pumping head is high – some scientists believe that root pressure and, possibly, other forces are able to perform this function for most (possibly shorter) plants. Kimball ('Root Pressure') directly addresses this theory and rejects it on the grounds that some plants have no root pressure, sometimes root pressure is negative and transpiration and root pressure are not well correlated.

In a previous draft of this note, I suggested a possible way to resolve this controversy through the following (mental or actual) experiment. Assume that the relative humidity (RH) of the ambient atmosphere of a plant is 100% and there are no other stresses on the plant. No transpiration would occur and yet the stomata would be open to receive $CO_2$ and expel $O_2$. How well would the plant do under these conditions? One of the reviewers reported that such an experiment was actually done in plant growth chambers, where all these factors are controlled: 'they grew cotton at various relative humidities and water and soil salinities. The 100% RH (relative humidity) treatments (little transpiration demand) did not bloom and set bolls well' (Terry Howell, personal communication).[9] Thus, assuming that there were no temperature or other stresses in this experiment, it appears that transpiration does perform some beneficial function in plant growth.

However, another reviewer of a draft of this note in which this experiment was reported said that 'only 1 to 2% of the transpiration is needed to move nutrients from the roots and for the water needed in photosynthesis'. And: 'Plants grow fine in 99% humidity assuming disease is prevented by other means' (Bruce Bugbee, personal communcation). It should be noted that the difference between the 100% RH in the experiment and the 99% RH in the reviewer's comments could provide the 1–2% of water needed for these purposes.[10] Even so, if this is the only beneficial function of transpiration, it does not represent enough water loss to worry about.

The discussion up to this point may be summarized by saying that, with the exception of the small amounts discussed above and the possible transport function in very tall plants, the consensus opinion of most

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[7] The *Columbia Electronic Encyclopedia*, *op. cit*. 'Sap.'

[8] Daniel I. Arnon, *Encyclopedia Americana*, 'Plants.'

[9] As Richard G. Allen notes, this effect was probably caused by nutrient deficiency due to insufficient transpiration – as discussed in the section on 'The Third Function of Transpiration,' below.

[10] I am grateful to Andrew Keller for pointing this out.

experts is that transpiration is apparently just a 'necessary evil'. It is evil because of the tremendous loss of water to the atmosphere; it is necessary because of the need to keep stomata open to absorb $CO_2$. And that is all there is to it.

### My Reservations

In my opinion, the above consensus creates a question that is even larger than that of transpiration itself. Given the crucial importance of water to plant survival and reproduction, how could plants evolve to be such wasteful users of such a scarce resource? One of the impressive features of the evolutionary record is how organisms adapt and evolve to make efficient use of resources in their specific environments. It is true that plants evolved in an aqueous environment, where water was not originally a constraint, and it is true that they have the formidable task of extracting very low densities of $CO_2$ out of the atmosphere, thus exposing themselves to evaporation losses.[11] However, while these are good reasons for this apparent waste of water, I do not find them compelling.[12] In fact, at one point, I thought that transpiration might represent a strong challenge to aspects of the theory of evolution itself.

This evolutionary question has driven a search for other possible functions of transpiration – a third function lurking in the background, so to speak, as in the film, *The Third Man*. As it turns out, there is indeed a third function of transpiration, which is well documented, is essential to plant growth and can account for most of the water used in transpiration. This is the function of transpiration in moving solutions of nutrients, not through the plant, but from the soil to the roots of the plant. That this important function is usually neglected in discussions of the functions of transpiration is perhaps accounted for by the fact that it occurs outside the plant itself, in the interface of the plant and its soil environment.

### The Third Function of Transpiration[13]

Soil nutrients are dissolved in water and absorbed from this solution by the roots. Some of the nutrients are acquired by root interception from the soils immediately adjacent to the roots, but these soils typically do not have a sufficient amount of nutrients to meet plant needs. Nutrients are supplied to the roots from more distant soils by two different processes. One is by diffusion of nutrients (ions) through soil water to the roots, as

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[11] Bugbee (B. Bugbee, personal communication) notes that because of the low concentration of $CO_2$, relative to $O_2$, in the atmosphere, it is '700 times' easier for animals to take oxygen in without losing water than for plants to take $CO_2$ in without losing water. Therefore, it is not correct to think of plants as inefficient water users. This is an excellent point; however, it would also be interesting to compare the different requirements of animals and plants for these two factors.

[12] For example, letting my imagination run, I wondered if plants could not use their remarkable ability to create semipermeable membranes to create one in the stomata that would let $CO_2$ in, let $O_2$ out and keep $H_2O$ in. I asked a research chemist, Terry Krafft, about this and he said that it should not be difficult to create such a membrane. In fact, at a convention he saw a fish living happily in a sealed polymer bowl of this nature. But I forgot to ask him how they fed the fish! Given the ingenuity of plants and their enormous variety, I would not be astounded if someone actually found a dry-area plant with something like this membrane.

[13] The discussion of this subject is partly from Kramer and Boyer (1995, pp. 286–290). Strangely, even these authors appear to dismiss this bulk-flow function in a discussion of the alleged benefits of transpiration earlier in their book (p. 203). One gets the impression that the benefits section was written before the later one and they forgot to change it – which is perfectly understandable by anyone who has written a book. Much of the research summarized in this source is from Stanley A. Barber and his collaborators, referenced in connection with Table A.2, below.

determined by concentration gradients in the solutions. The other is by bulk flow of nutrient-carrying solutions to the roots. Transpiration plays a vital role in bulk flow by continually evacuating the water from spent solutions surrounding the roots, thereby generating convective flow of new solutions, carrying additional nutrients, to the roots. Since the solutions are fairly dilute, large amounts of water must be evacuated to generate these flows. Table A.1 provides a quantitative view of these effects.

Table A.1 shows that, when transpiration is at a moderate level of 500 times plant biomass, the soil solution is more than sufficient to supply calcium (Ca) and magnesium (Mg), but is considerably below the requirements for potassium (K) and phosphorus (P). In the latter case:

> If the inorganic ions are absorbed at a relatively greater rate than bulk flow can provide, as with phosphate and potassium, the concentration in the soil solution will decrease next to the root. In response, ions are released from the soil particles and tend to buffer the concentration. Nevertheless, there is a lowering at the root surface and ions will tend to move into the depletion zone by diffusion in addition to bulk flow.
>
> (Kramer and Boyer, 1995, p. 288)

Thus, transpiration, through bulk flow, is the first factor in providing nutrients to the roots, but, if this is insufficient, diffusion provides a localized and potentially limited supplementary supply of nutrients. These effects are partly governed by different diffusibilities among the nutrients. In addition, it was found that transpiration 'had little effect on uptake (of ions) by roots in low external solution concentrations, but had a significant effect when the external concentrations were high' (Kramer and Boyer, 1995, p. 289).[14] This seems to imply that the effect of transpiration is higher when soil moisture is lower. It was also found that the transpiration effect was strongest when plants were growing most rapidly.

Another authority stresses the importance of mass flow in the reproductive stage of plant growth:

> An important proportion of water-stress induced crop failure occurs when the stress coincides with flowering. In many instances, this is the result of reduced transport of critical nutrients to the developing reproductive structure. The most significant nutrients in this regard are boron, copper and calcium each of which is delivered to the grain solely in the transpiration stream. In the absence of these nutrients, reproductive growth is permanently impaired.[15]

He goes on to note that these problems can be alleviated by appropriate nutrient-management practices.

**Table A.1.** Supply of elements to maize roots by bulk flow caused by transpiration (from Kramer and Boyer, 1995).

| Element | Plant dry matter (%) | Required concentration[a] | Actual concentration[b] |
|---|---|---|---|
| Ca | 0.22 | 0.11 | 0.83 |
| Mg | 0.18 | 0.15 | 1.15 |
| K | 2.0 | 1.02 | 0.10 |
| P | 0.20 | 0.13 | 0.002 |

[a]Concentration of soil solution needed if transpiration is 500× (plant) dry matter (mM).
[b]Concentration of soil solution in 145 maize soils (mM).

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[14] Richard G. Allen seriously questions this statement; however, I have left it in as a stimulus to future research.

[15] Patrick Brown of the University of California at Davis. Communication to an e-mail discussion on water productivity, May 2002.

Further evidence on the importance of solutions and concentrations is provided by the growth of plants in liquid solutions for research and practical purposes. Luttge and Higinbotham (1979, pp. 62–65) provide information on these solutions. For macronutrients, the concentrations vary from 24 to 224 p.p.m., and are less than 2 p.p.m. for micronutrients. Even in liquid solutions, without the resistance to water flows in soils, constant stirring of the solution is required to provide oxygen and avoid nutrient depletion in the solution adjacent to the roots.

Last, and perhaps most importantly, Barber (1995, p. 91, Table 4.4)[16] provides estimates of the amounts of major soil nutrients supplied to the roots by the three sources of root interception, mass flow (as he calls it) and diffusion, as shown in Table A.2.[17]

## Conclusion

It appears that the solution to the dilemma of transpiration discussed in this note is, appropriately, a real, liquid solution. A major beneficial function of transpiration is to generate bulk flow of solutions containing soil nutrients to the plant roots. While this function is also performed by diffusion for some nutrients, Table A.2 indicates that it is indispensable for others – and the lack of any single nutrient has a large effect on plant growth. Most important from the present point of view is that the bulk-flow function can account for most of the water used by plants in transpiration.

While this conclusion is undoubtedly subject to qualification, depending on plant species, water conditions, soil fertility and fertilization practices, it appears to provide a strong answer to the original question of 'Why do plants use so much water in transpiration?' and an important counter to the 'necessary evil' argument. It is indeed perplexing that this function does not receive more attention in discussions of the functions of transpiration and that more research attention is not given to it.

Research on transpiration is, of course, particularly important in the case of rain-fed agriculture. Many ingenious methods of reducing transpiration in rain-fed agriculture have been proposed. One method is to capitalize on the different transpiration efficiencies of different kinds of plants (Terry

**Table A.2.** Relative significance of root interception, mass flow and diffusion in supplying maize with its nutrient requirements from a fertile Alfisol silt loam (kg ha$^{-1}$).

| Nutrient | Nutrient needed[a] | Root interception | Mass flow | Diffusion |
|---|---|---|---|---|
| Nitrogen | 95 | 2 | 150 | 38 |
| Phosphorus | 40 | 1 | 2 | 37 |
| Potassium | 195 | 4 | 35 | 156 |
| Calcium | 40 | 60 | 150 | 0 |
| Magnesium | 45 | 15 | 100 | 0 |
| Sulphur | 22 | 1 | 65 | 0 |

[a] Needed for 9500 kg of grain ha$^{-1}$.

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[16] This is the most interesting and readable text on the subject I have found. See especially Chapter 4.

[17] Commenting on the zero values for diffusion of the last three nutrients in this table, Richard G. Allen wonders, how do these ions get into the water stream in the first place? He also wonders, how do pineapples, which have very low transpiration rates, get over the problem of potential nutrient deficiencies? All I can say is, as usual, very good questions!

Howell, personal communication).[18] Other methods range from the use of antitranspirants[19] to breeding plants for leaf curling and for resistance to water uptake (Richards *et al.* 2002).[20] All of these research efforts should be strongly supported. The role of transpiration in the bulk flow of plant nutrients should be considered as an integral part of this research programme. Hargreaves and Merkley (1998)[21] have indeed proposed that rates of fertilization of crops should be based on rates of transpiration, in order to avoid imbalances between these two factors. Bulk flow would appear to be an especially important factor to consider in rain-fed agriculture, where soil moisture and fertility tend to be low.

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[18] For example, 'Plants are categorized as to their P [photosynthesis] mechanisms as C4 (sorghum, maize …), C3 (cotton, wheat, rice, sugarbeet), or CAM (pineapple …). The transpiration efficiency (P/T) is generally, CAM>C4>C3. C3 plants have a greater photosynthetic respiration. CAM species keep their stomates closed during the day.'

[19] Kramer and Boyer (1995, pp. 400–402) discuss the use of antitranspirants, which are chemicals that reduce transpiration rates. Unfortunately, they tend to reduce $CO_2$ absorption and plant growth even more than transpiration.

[20] This is an excellent survey of the problems and opportunities in crop breeding for this purpose.

[21] I am grateful to Andrew Keller for this reference.