Transpiration in plants:

A thermodynamic imperative

Carmen N. Hernández and Karo Michaelian, Circuito de la Investigación Científica, Ciudad Universitaria, Instituto de Física, México.

Abstract

In this article we determine the importance of transpiration in plants at three different levels of organization: the plant itself, the ecosystem, and the biosphere, all in terms of entropy production due to transpiration.

We propose that transpiration is a thermodynamic imperative rather than a physiological burden for the plant. Plants have not replaced their prevalent metabolism C3 with those of less loss of water, C4 or CAM. We argue that the fact that plants retain higher rates of transpiration along evolution could be explained using thermodynamic criteria.

Nature Precedings : doi:10.1038/npre.2010.5463.1 : Posted 30 Dec 2010

Introduction

The purpose of life is to increase the global entropy production of the Earth in its interaction with its solar environment, for which, life must be stable and sustainable. The integrated entropy production over 3,800 millions years of life on Earth is greater than the entropy production of exploiting all the atomic bombs in the Earth at the same time ending with all possible life.

If such a thermodynamic vision is correct and life exists to increase entropy, then it is important to understand how this goal is achieved and what are the implications.

Phototrophic organisms, as plants, are the base of the trophic chain, however they also have a strong interaction with the abiotic world, e.g., by regulating the water cycle and the temperature of Earth's surface. An integral overview of the role they play and how they interact with their environment is needed, so we can visualized how the human activity or global warming could affect them and vice versa, or how they are related with the evolution of the Biosphere, therefore general criteria are needed to establish this importance.

Assuming that the goal is to increase global entropy production, then we would be able to establish the importance of phototrophic organisms *ei*ther as entropy producers *per se* or as catalysts that allow the increasing of global entropy production of the Biosphere.

We decided to work with a plant, assuming that the most important contribution is due to transpiration.

Transpiration is the evaporation of water through the stomata, cuticle and lenticels of a plant. The most important being transpiration stomata. Biologists argue that transpiration in the stoma only occurs as a consequence of the necessity of the plant to obtain carbon from their environment in order to allow photosynthesis. The carbon is in gas phase in the atmosphere as $CO_{2.}$ When the plant captures it, through the open stoma, some water vapor escapes. By transpiring great amounts of water the plant is at risk of dehydrating and even death. So, from this perspective transpiration is considered a disadvantage because it represents a constant risk of death by dehydration and doesn't offer any important selective advantages. A plant can grow in an environment with 100% relative humidity, where the transpiration is negligible, so it is not vital to the development of plant either (Salisbury, 1985).

However, some advantages can be related with transpiration; because the movement of water implies that a great amount of nutrients are brought to the plant. Also, when the plant transpires heat is lost, and in the process the leaves are brought to an optimal temperature for photosynthesis.

Our view is different, transpiration in plants is a primary processes (not a disadvantage) that contributes to the entropy production, which seems to be the goal of life. This work is a continuation of efforts towards describing biological processes in terms of thermodynamics, in particular, in understanding entropy budgets in a plant and ecosystem (Kurata,2004)(Aoki, 1987)(Tesar,2007)(Kleidon, 2009). Kleidon has analyzed the importance of transpiration as part of the hydrological water cycle, and the importance of transpiration as one of the entropy budgets at the Earth's surface. Computer simulations show that a land covered with vegetation can evaporate twice than a desert land. Aoki(1987) and Tesar(2007) have analyzed the entropy budgets of a lake and a watershed respectively taking into account transpiration.

Our efforts are designed to extend the study of transpiration beyond their contribution in the water cycle, we want to establish the importance of transpiration as a factor that contributes to the entropy production on plants and ecosystems.

Aoki and Kleidon have both considered the entropy production related with the internal processes of the plant, such as transpiration, photosynthesis, respiration and the internal transport of water and nutrients against gravitational forces. They have established that transpiration is the most important of these processes. To our knowledge, no comparison has been made of the importance of transpiration with some absolute measure, for example, the total entropy production posible for a plant.

We need at least an aproximated value of the total entropy production that a plant can reach. As a first aproximation we assume that the plant is close to a stationary state, where the negative external flux of entropy coming from the sun equals the internal entropy production. In this manner we can compare the entropy production due to tranpiration with the maximun value that entropy production can reach, and determine the percentage that can be associated with transpiration; then establishing the absolute importance of transpiration in plants as a process that keeps the plant near a stationary state.

The amount of entropy production due to transpiration also counts for the total entropy production that the Biosphere should produce to keep a stationary state. We can compare the total entropy production per square meter of the Biosphere, assuming that it is in a stationary state(Aoki, 1983), with the entropy production per square meter due to transpiration of green vegetation.

In ecosystems the entropy production can be taken as a fisrt coefficeint that discribes their dynamics in a thermodynamic framework.

Supposing that the plant is close to a stationary state, we assume that the plant does not grow and that the external conditions are constant, these assumptions are only achievable if the plant does not grow and we are in a tropical or subtropical zones, where the amount of solar radiation is almost constant.

The present work defines the system as the plant and transpiration is consider as an internal process that produces entropy. All the radiation fluxes flowing in and out the plant contribute to the external flux of entropy (Ulanowicz, 1987). These fluxes can be estimated as the solar radiation that passes through the atmosphere and is absorbed by the plant minus the radiation emitted by the plant. The emitted radiation can be determined from the black body spectrum of the plant modulated by its efficacy of emission.

Thermodynamic framework for population dynamics

Within ecosystems in a previous article Michaelian (2005) proposed a framework for describing the population dynamics of an ecosystem based on non-equilibrium thermodynamic theory. This framework is restricted to ecosystems with constant boundary conditions, where "constant" implies with respect to the natural relaxation time of the organisms involved.

In this model the entropy production is proposed to be a many body expansion of form:

$$\left(\frac{d_i S}{dt}\right) = \sum_{\gamma} p_{\gamma} \left[\Gamma_{\gamma}^{i} + \sum_{\gamma'}^{n} p_{\gamma'} \Gamma_{\gamma\gamma'} + \sum_{\gamma'\gamma''}^{n} p_{\gamma'} p_{\gamma''} \Gamma_{\gamma\gamma'\gamma''} + O(4) \right] > 0 \quad , \quad (1)$$

where p_{γ} represents the population of specie γ, and the parameters needed to describe the dynamics (Γ's) are the average rates of entropy production per capita of one specie due to the interaction with an individual of another specie or of the same specie.

For example, for a plant the first coefficient Γ_{γ}^{i} is related to its one-body processes such as metabolism, transpiration, photosynthesis, and internal transport or water and nutrients. Since 95% of the free energy arriving at the leaf surface from the sun is used in transpiration (Gates,1966), the one-body entropy production parameter Γ^{i} for the plant can be approximately equated with the measured entropy production due to transpiration.

It has been established empirically that a system with constant boundary conditions will arrive at a stationary state where the total change of entropy of the system is zero; in which case the entropy production $\frac{d_i S}{dt}$ will be matched by an external flow of entropy $\frac{d_e S}{dt}$ (Prigogine, 1968)

$$\frac{dS}{dt}=\frac{d_i S}{dt}+\frac{d_e S}{dt}=0 \quad . \tag{2}$$

For an irreversible process the entropy production is always positive and becomes equal to zero in equilibrium.

$$\frac{d_i S}{dt}\geq 0 \tag{3}$$

We can rewrite the entropy production for an open system as the sum of thermodynamics fluxes *J* multiplied by generalized forces *X. T*he coupling between different irreversible processes is established by principle; macroscopic results have greater elements of symmetry than their causes(Prigogine, 1967)

$$\frac{d_i S}{dt}=\sum_{\gamma} J_{\gamma} X_{\gamma} \tag{4}$$

Since the entropy production at the stationary state must be positive equation (2) implies that the external flux must be negative,

$$\frac{d_e S}{dt}\leqslant 0 \quad . \tag{5}$$

If we applied this result to the population dynamics frame work and write the external flux of entropy as:

$$\frac{d_e S}{dt}=\sum_{\gamma}^{n} p_{\gamma} \Gamma_{\gamma}^{e}<0 \tag{6}$$

Where $\Gamma_{\gamma}^{e}{}'s$ represents the average per capita external flux of entropy due to get through species γ.

The inequality establish in (6), implies that at least one specie must introduce negative entropy into the ecosystem. A flux of negative entropy is thus necessary for an ecosystem to reach more complex and stationary state.

The greatest source of negative entropy available to any ecosystem is related to the solar radiation, and the autotrophic organisms are the ones that introduce this negative entropy into the ecosystem. This fact makes the autotrophic organisms the base of the trophic chain, however, this is not the only role that the autotrophic organisms play in the ecosystem dynamics, and thats what we want to emphasize. In a thermodynamic framework the role of autotrophic organisms as entropy producers is more important than their role as introducer of negative entropy to the ecosystem.

A further criterion will be necessary to model the population dynamics of ecosystems the evolution criteria of Prigogine(1967). This criterion establishes that for a system with constant boundary conditions, the change in the entropy production *P* due to changes in the generalized forces *X* is less than or equal to zero,

$$\frac{d_X P}{dt} \leq 0 \quad . \tag{7}$$

For the population dynamic model that was proposed, the evolution criteria of Prigogine becomes indispensable as the relation that determines the change in time of the populations. If we recognize that the generalized forces are the population p_γ and the fluxes are the terms in brackets, then;

$$\frac{d_X P}{dt} = \sum_\gamma \frac{dp_\gamma}{dt}\left[\Gamma^i_\gamma + \sum_{\gamma'} p_{\gamma'} \Gamma_{\gamma\gamma'} + \sum_{\gamma'\gamma''} p_{\gamma'} p_{\gamma''} \Gamma_{\gamma\gamma'\gamma''} + O(4)\right] \leq 0 \quad . \tag{8}$$

External Flux of entropy

In the case of a plant the greatest contribution to the external flux of entropy is related with the incident and outgoing radiation. As Ulanowicz (1987) proposes, we treat the radiation as a gas of photons and calculate the external flux of entropy as:

$$\frac{d_e S}{dt} = \frac{1}{T}\frac{de_{plant}}{dt} = \frac{k}{hc}\left\{ \int_{\lambda_1 = 0.3\mu m}^{\lambda_2 = 50\mu m} \left(e_{out}(\lambda) - e_{in}(\lambda) \right) \lambda d\lambda \right\} dt \tag{9}$$

where $e_{out}(\lambda)$ represents the spectrum emitted by the plant, and $e_{in}(\lambda)$ represents the absorbed spectrum.

The light that reaches the plant is the combination of the solar spectrum and the infrared radiation of the environment. For the short wave radiation between $0.3\,\mu m$ and $3.0\,\mu m$ we use the experimental data taken by Kindel(2001) in Hawaii, since both Mexico City and Hawaii are in the same latitude. Then we renormalized for our experimental conditions in therms of three parameters: cloudiness, hight and air mas.

For the long wave emitted by the environment we consider two contributions. First we assumed the spectrum of a black body with the corresponding temperature of the soil, and second we consider the infrared emission of the atmosphere . The complete spectrum is then multiplied by the absorption spectrum of the plant to give $e_{in}(\lambda)$.

For the emitted spectrum of the plant $e_{out}(\lambda)$, we assumed that the plant radiates as a blackbody at the temperature of the leaves. This was multiplied by the emissivity in function of λ .

The spectra used in the integral of equation (9), are given in figure (1).

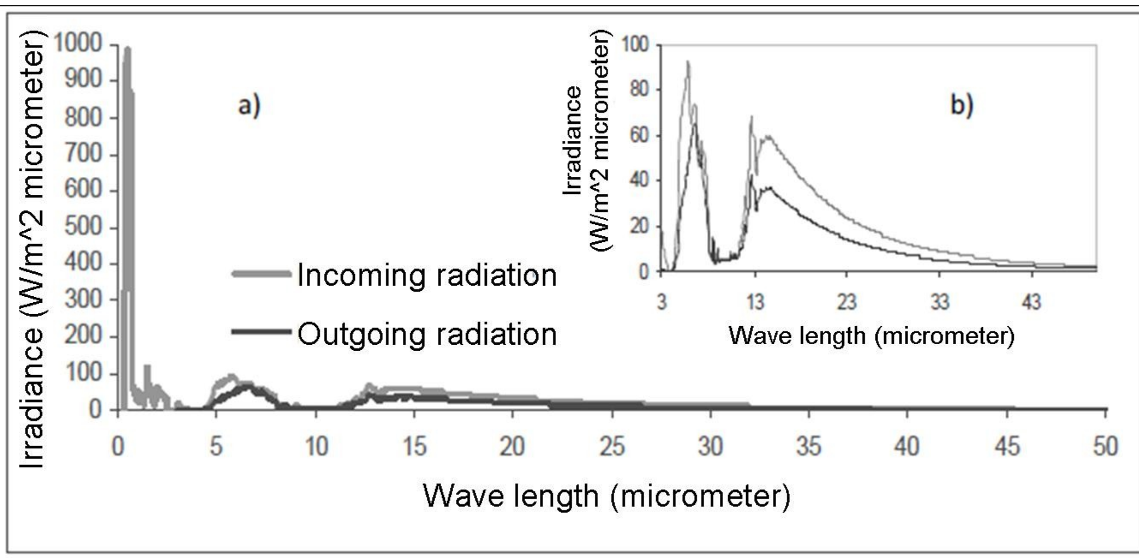

Figure 1. Spectrum emitted and absorbed by the plant in all the range of interest, from 3.0 to 50.0μm.

Nature Precedings : doi:10.1038/npre.2010.5463.1 : Posted 30 Dec 2010

Figure 1.a)The full range of the incoming and outgoing spectrum for the plant. b) Zoom to the IR range.

The lower integration limit is associated to the shortest wave length that can passes through the atmosphere, and, for the upper limit, we assume that the infrared absorption and emissions at wavelengths above 50 μm are weak, so longer wavelengths can be neglected.

The numerical value of the integral in equation (9) is related with the parameter Γ^e shown in equation (6). This value is important for two reasons; to compare with the total amount of negative entropy that passes through the Earth (Aoki,1983) , and as a reference to establish the thermodynamic importance of transpiration in the plant at stationary state.

Internal entropy production

The entropy production of a plant can be associated with transpiration, photosynthesis, metabolic processes and interactive processes with other organisms. In the transpiration process, the water changes from liquid to vapor inside the leaves and reaches the atmosphere through the stoma. It is possible to model the process of transpiration as a chemical reaction of different initial and final states,

$$H_2O_{liquid\ inside\ the\ plant} \rightarrow H_2O_{gas\ in\ the\ atmosphere} \quad .$$

The entropy production for this change of phase can be given in terms of equation (4) (Prigogine, 1968),

$$\frac{d_i S}{dt} = \sum_i X_i J_i = \frac{A}{T} \vee = \left(\frac{-1}{T} \sum_\gamma \nu_\gamma \mu_\gamma\right) \frac{d\xi}{dt} \tag{10}$$

where A is the affinity, $\vee = \frac{d\xi}{dt}$ is the rate of the reaction, ξ is the extent of the reaction and T the temperature. The affinity of a chemical reaction can be defined as: $A = -\sum_\gamma \nu_\gamma \mu_\gamma$, where μ_γ is the chemical potential of constituent γ and ν_γ the stoichiometrical coefficients of the constituent in the reaction,

$$\frac{d_i S}{dt} = \left(\frac{\mu_{liquido}}{T_{líquido}} - \frac{\mu_{vapor}}{T_{vapor}} \right) \frac{dn_{vapor}}{dt} \qquad (11)$$

where dn_{vapor} are the number of moles of water transpired in time dt.

The chemical potential is related to the molar entropy (Callen, 1960)

$$\mu = -T \left(\frac{\partial S}{\partial n} \right)_{E,V} = -Ts \quad , \qquad (12)$$

where n is the number of moles, and s the molar entropy. Equation (11) then becomes, for a time interval Δt

$$\frac{d_i S}{dt} = (s_{vapor} - s_{liquid}) \frac{\Delta n_{vapor}}{\Delta t} - R \ln\left(\frac{\% RH}{100} \right) \frac{\Delta n_{vapor}}{\Delta t} \qquad (13)$$

where RH is the relative humidity, *s* is the molar entropy, R is the gas constant. All the parameter in relation (13) can be measured, the molar entropy was looked up in a web page:

http://www.efunda.com/Materials/water/steamtable_sat.cfm

Here molar entropy is given as a function of temperature or saturation pressure. We use the temperature of the leave for the molar entropy of the water in the liquid phase and the air temperature for the molar entropy of the water as vapor.

To measured the loss of water $\frac{\Delta n_{vapor}}{\Delta t}$ we used a simplified lismetric method by weighing the loss of water corresponding to a given isolation period Δt.

The air temperature corresponds to the monthly average, of the temperature reported every 30 minutes by the National Meteorological System (SMN, for the initials in Spanish). Unfortunately we couldn't measured the leaf temperature at the same rate, so we measure the leaf temperature in function of the air temperature reported by the National Meteorological System. We found that the leave temperature is approximately 3 degrees above the air temperature, and thats the value we use for the molar entropy in equation (13). The leaf temperature was measured with a LMD35 sensor. Also the value for the relative humidity (RH) was taken from the SMN.

We work with two different kinds of plants Laurel Rosa and Flor de mayo. Both was flowering during the data acquisition.

Results

Figure 2 displays the result. The first column (left to right) represents the entropy production associated with the transpiration process for a “Laurel Rosa”. The second column (only shown in April and May) represents the entropy production for a “Flor de Mayo”. The third column represents the external flux of negative entropy as calculated for each month using equation (9). Finally, the right most column represents the entropy production of the Earth assuming a stationary state, as calculated by Aoki(1983).

From these results, transpiration provides at least 50% of the entropy production of the plant in a stationary state. Transpiration can be associated with approximately 25% of the entropy production of the Earth assuming that it is in a stationary state.

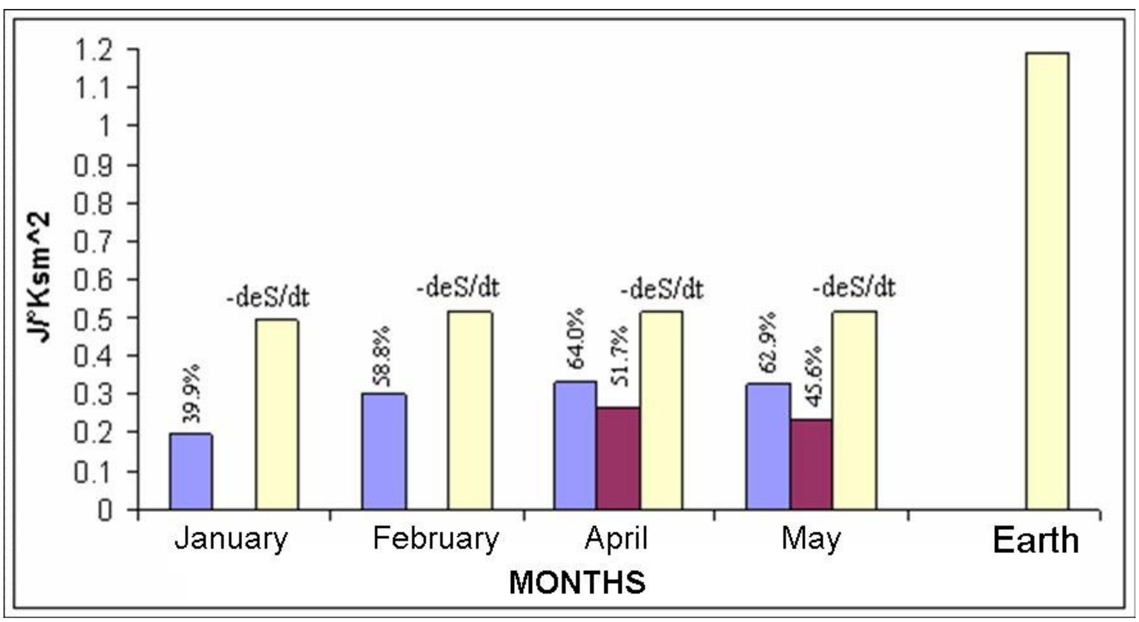

Figure 2. Entropy production of the plant due by transpiration, and the external flux of negative entropy arriving at the Earth (Aoki, 1983) and at the plant from the Sun.

For comparison all the values presented in figure 2 were normalized per unit area. In the case of plants the area is the leaf surface and for the Earth is the surface as a sphere.

This result demonstrates the importance of plants in the thermodynamic work of the biosphere: dissipating the solar photon flux.

We found that at least 50% of the entropy produccion is due to transpiration.This has implications to the process of evolution. If we assume that the purpose of life is to increase the rate of global entropy production, then the evolutionary selection must occur in the direction that the process that most contribute persist.

Wang et. al. (2007) has shown that plant optimizes the parameters of tranpiration such that entropy production is maximized. From all the posible non-equilibrium steady states that the system can visit, the most probable states will be the ones with the greater rate of entropy produccion. This then can explain why plants have preserved their C3 metabolism over less free energy intensive C4 and CAM metabolism, even though the risk of dehydration is greater.

The most important thermodynamic process in the plant is transpiration not photosynthesis, and it is transpiration that has been positively selected over the evolutionary history of plants.

Conclusions

An absolute measure of the importance of transpiration was obtained. The transpiration provides around 50% of the total entropy production of the plant if we consider it in a stationary state, therefor, transpiration must be considered as an important thermodynamic process on Biosphere and not just as a disadvantageous and unnecessary process for the plant.

Regarding to ecosystems, it was show that the entropy production due to transpiration is the greatest contribution to the total entropy production of a plant specie, so it could be used as first approximation to the first coefficient Γ_{γ}^{i} of equation (8)

$$\Gamma^{i}_{plant} \approx \Gamma^{i}_{transpiration}$$

We have estimated the total flux of external entropy passing through the plant was negative; which means that the plant in fact is the one that introduces negative entropy to the ecosystem, as expected.

The amount of negative entropy captured by the plants is approximately 50% of all the negative entropy that arrives from the sun. But only a small fraction of this negative entropy can be used by the heterotrophic organisms, since just 1% of all the negative entropy that enter the plant is used on photosynthesis, and can be transformed into carbohydrates. The autotrophic organisms do not bring negative entropy to the ecosystem efficiently, but they are the only ones that make it. However they are really efficient on increasing the entropy production via transpiration.

Transpiration in plants produces around ¼ of the total entropy production of the Biosphere, which means that plants play an important thermodynamic role.

Finally it was proposed that transpiration process has been retained along the plant’s evolution as an enhancer of the entropy production. We found that transpiration is an important source of entropy production, then it seems that plants with C3 metabolism have reached an stationary state with a higher entropy production that plants with less transpiration (C4 and CAM). The fact that C3 metabolisms prevails, despite its disadvantages, is suggesting that the process of transpiration will be kept in plants as long as it increase the total entropy production, following a thermodynamic criteria instead of Darwin's criteria.

Acknowledgements: The authors are grateful for the financial support of DGAPPA-UNAM project IN112809 and IN118206.

Bibliography

Aoki I. “Entropy productions on the Earth and other planets of the solar system”, Journy of the Physical society of Japan Vol 52 No 3 (1983)

Carmen Noemí Hernández Candia,Thesis: “Medición experimental del coeficiente de producción de entropía de una planta por el proceso de transpiración”, 2009, UNAM.

Callen, Thermodynamics and an introduction to thermostatics, 1°edition 1960, 2° edition 1985

Gates “Spectral Distribution of solar radiation at the Earth's surface”, Science Vol 151 (1966)

G. Job and F. Herrmann “Chemical Potencial- a quantity in search of recognition”, European Journal of Physics, vol 27, number 2 (2006)

Kleidon, “Thermodynamics, Irreversibility, and optimality in land surface hydrology” Bioclimatology and Nature Hazards, Springer (2009)

Kurata K. , Goda Y., Seki H. “Development of a chamber system (ENTRON) for measuring entropy production of plants”; American Society of Agricultural Engineers, VOL: 47 (2004)

Michaelina K. “Thermodynamic stability of ecosystems”, Journal of Theoretical Biology 237 (2005)

Prigogine “Introduction to Thermodynamics of irreversible processes” (1967)

Salisbury F. “Fisiología Vegetal”, Grupo Editorial Iberoamérica, (1985)

Tesar M. “Plant tranpiration and net entropy exchange on the Earth's surface in a Czech watershade” Biologia, Bratislava, 62/5 (2007)

Ulanowicz R.E, Hannon B.M. “Life and the production od entropy” Proc. R. Soc. Lond. B 232 (1987)

Wang J., Bras R. L., Lerdau M. Salvucci G. D. “A maximum hypothesis of transpiration”, Journal of Geophysical research, Vol 112 (2007)

http://www.efunda.com/Materials/water/steamtable_sat.cfm