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Modelling physical processes in higher plants using leaf replicas for space applications

Modélisation de processus physiques de plantes supérieures à l'aide de répliques de feuilles pour des applications spatiales

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Abstract. In the future, higher plant cultivation will be a key component of Bioregenerative Life-Support Systems. This will require a deep understanding of phenomena that play an important role at the core of plant metabolism and of their interaction with the environment. Plants are complex organisms that must be studied with the use of leaf replicas. This enables the study of physical phenomena at the leaf surface, without biochemical or biological interactions nor genetic variability. To assess the influence of gravity, it is a necessary step to develop precise mechanistic models of plant behaviour in space. This review article presents the state-of-the-art of leaf replicas and concomitant phenomena, with a space gaze.

Résumé. À l'avenir, la culture de plantes supérieures sera un élément clé des systèmes de support de vie biorégénératifs. Cela nécessitera une compréhension approfondie des phénomènes qui jouent un rôle important au cœur du métabolisme des plantes et de leur interaction avec l'environnement. Les plantes sont des organismes complexes qui doivent être étudiés à l'aide de répliques de feuilles. Ceci permet l'étude des phénomènes physiques à la surface des feuilles, sans interactions biochimiques ou biologiques, ni variabilité génétique. Pour évaluer l'influence de la gravité, il est nécessaire de développer des modèles mécanistes précis du comportement des plantes dans l'espace. Cet article de synthèse présente l'état de l'art des répliques foliaires et des phénomènes concomitants, pour une application spatiale.

Keywords. Leaf replica, Transpiration, Energy balance, Life-support systems, Heat exchange, Biophysical phenomenon, Mechanistic modelling.

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Mots-clés. Réplique foliaire, Transpiration, Bilan énergétique, Systèmes de support de vie, Échange de chaleur, Phénomène biophysique, Modélisation mécaniste.

1. Introduction

The four pillars of life-support systems (LSS) are the provision of air, water, and food, as well as waste treatment [1, 2]. For long-duration space exploration missions, it will be necessary to recycle as much resources as possible and to grow food *in situ* [3]. Plants allow the supply of fresh vitamins and nutrients which will be lacking after many months in space [4, 5]. They also enable the recycling of oxygen and carbon into fresh nutrients and water sanitation through photosynthesis [6]. Moreover, it is well accepted that they contribute to the crew well-being [7].

Plants have grown in low Earth orbit [8, 9] for decades, but many challenges still remain before it will be possible to grow them sustainably for food production [10–13]. Since plants are reactive biological organisms, the elementary processes that govern their growth and development need to be thoroughly understood before they can reliably be grown on a larger scale in space and integrated within a bioregenerative LSS (BLSS) [12, 14]. This can be achieved with a mechanistic, multi-layer, and multi-scale (in space and time) approach to allow the development of knowledge-based models, which are prerequisites for implementing predictive models and run simulations out of the standard parametric range (e.g., in reduced gravity). For example, buoyancy-driven gas exchange at the leaf surface is altered in microgravity [15–18] and since it drives biomass and oxygen production [19], its understanding is crucial for plant growth in space.

Gas and heat exchange is largely dependent on leaf and plant canopy boundary layer thickness, which is a physical phenomenon linked to convective properties of the growth environment [17, 18, 20–22], which can be modelled independently of biological processes [23, 24]. It is influenced by airflow movements, which depend on forced and free convection—a result of buoyancy forces which therefore depends on gravity [17, 18]. Gas and heat exchange also depends on the plant stomata size and density, which are dependent on plant species and their growth environment [25–27].

The fact that plants present a genetic variability and are reactive systems [23,28,29] makes hard to study a given phenomenon independently from the others, in a controlled way. Therefore, leaf replicas have been developed and used to study strictly physical processes without influence of plant biological processes, particularly in the context of heat and mass exchange [21, 22, 30–45]. Most of the studied leaf replicas are made of metal and/or felt sheets and can incorporate pores to simulate stomata or resistors to study heat exchange. Their design depends on the hypotheses and research questions of the study.

The objective of this review is to provide an overview of the state-of-the-art of existing leaf replicas and their use to answer various questions pertaining to heat exchange and water transport across plants. A focus will be on the specific context of developing mechanistic models of plant gas exchange for applications in BLSS.

2. Challenges in using real plants

The high sensitivity of plants to their environment and their genetic variability makes it challenging to study their biophysical processes in spaceflight conditions, where volume and experiment opportunities are limited.

2.1. *Plants are reactive systems*

Plants need light (energy), water, carbon and nutrients and if these parameters are too far from optimal conditions, abiotic stress can appear [46]. Another source of stress can be the rapid changes in environmental physical parameters, such as temperature, light, or relative air humidity. The stress associated with these factors occurs within seconds to minutes of the parameter change and affects the metabolic processes of the plant which in consequence can lead to reduced yield [47].

According to [48] active suppression of growth is part of the plant survival strategies in response to adverse environments. The exact mechanisms, however, remain unknown, making it hard to take stress factors into consideration while modelling the growth or while computing for example the energy balance or transpiration rate.

Another factor which can affect the accuracy of the modelling is the plant morphology description. As it was highlighted in [49], the size and density of stomata can vary not only within the same plant species but also within the same plant if the environment conditions slightly vary. For example, small light or wind gradient can result in different stomatal densities between the leaves of a single plant. Moreover, the opening and closing of stomata is closely related to the time of day and to weather conditions [25, 50].

According to the plant needs, leaves can also modify the magnitude of absorbed solar radiation—incident, reflected, and transmitted—by orientating the leaves towards or against the sun and the wind [51]. As a consequence, untangling the biological and physical parameters is not simple.

2.2. *Sample size*

The estimation precision of the energy components or mass exchange between the environment and plants can also be affected by the variability of the collected samples, the variability of the process and the heterogeneity of environmental conditions. It was proven that light gradients across a growth chamber can cause significant differences in structure and physiology of the leaves [52]. These results highlight the fact that sample size may significantly affect the accuracy of ecophysiological trait estimates. To receive meaningful results, the sample size should be adjusted to the required confidence level and margin of error, as well as to the expected variation between individual results [53]. Taking all those factors into consideration, finding the optimal plant size sample is a challenge in spaceflight conditions where mass and volume are limited. Moreover, sample size might be limited by external factors like time, funding, or human capital.

One of the examples of a limited space and time are studies done in microgravity conditions—parabolic flights or outer space studies. Parabolic flight is one of the main sources of data on heat and mass exchange and boundary layer in microgravity, mainly because of its relatively low cost and availability, compared to studies in low Earth orbit. Additionally, most of the systems which were tested in space did not have the possibility to measure all of the previously mentioned parameters and phenomena on plants or leaf replicas because of the lack of humidity and/or temperature control [54]. In parabolic flight studies, the periodic evolution of the gravity level induces extra stresses to the plants. As described in the previous section, the influence of these stresses is not yet fully detailed and understood, and this might introduce confounded factors to the measurements.

Leaf replicas have been introduced in order to study physical processes occurring at the leaf level in steady and transient states, without the bias caused by environmental stress factors or genetic variability occurring on limited sample size. The collected data can be used for primary validation of predictive models describing these processes without biochemical interaction.

A model, which can accurately simulate physical processes, can later be extended or scaled to the whole canopy level [51].

3. Leaf replicas used in recent literature

Different types of replicas have been used to study physical processes within plants. Depending on the purpose, we identified three groups of replicas:

- Simple replicas made of one material (dry and wet),
- Complex replicas with simulated stomata,
- Replicas with internal heating.

The major topics analysed with replicas concerned the energy balance and transpiration rate and the boundary layer conductance. The symbols and notations, used later in this section, to present how leaf replicas can simplify the equations, are summarized in Table 1.

3.1. *Energy balance*

3.1.1. *Description of the biophysical phenomena*

The temperature of the environment is one of the major factors affecting almost all plant processes like photosynthesis, respiration, biosynthesis, membrane transport, transpiration and the volatilization of specific compounds [51]. Consequently, it is crucial to precisely understand its role in all processes.

Leaves absorb most of the short-wave radiation emitted by the sun (E_{photons}), from which small fractions are reflected, transmitted, or used in metabolic processes. As a result, plants developed mechanisms to dissipate the induced heat, to avoid getting overheated, so that these heat loss mechanisms are crucial for their survival. Heat is also given off as a side effect of photosynthesis through transpiration. The main components of plant energy balance are [55]:

- Emitting long-wave infrared radiation (E_{ray}),
- Convection heat transfer (E_{conv}),
- Latent heat transfer (E_{lat}).

All of the energy balance components are presented on the Figure 1.

During metabolic processes plants also produce some energy and during photosynthesis a certain amount of energy is consumed, however the amount of heat involved during these processes is relatively small compared to the processes mentioned above and is usually neglected in the calculations [51]. At steady state the conservation of energy implies that the sum of all these energy components is equal to zero, but even a small change in one of the components of the energy balance will cause a change in the leaf temperature. Mechanistic approaches to plant energy balance models have been described in [20, 24]. In general, the energy balance can be described using the following equation:

$$\frac{\mathrm{d}T_{\text{leaf}}}{\mathrm{d}t} = \frac{E_{\text{photons}} - E_{\text{ray}} - E_{\text{conv}} - E_{\text{lat}}}{Cp_{\text{leaf}}} \tag{3.1.1}$$

where Cp_{leaf}—the leaf specific heat capacity in J·K^{-1}.

For discrete light spectrum (like the ones in use on ISS), the amount of energy absorbed by the plants can be calculated using the equations described in [24]:

$$E_{\text{photons}} = I^{\max} N_A hc \sum_{i=\lambda_{\min}}^{\lambda_{\max}} \frac{\gamma_i}{\lambda_i} \tag{3.1.2}$$

Table 1. Summary of the symbols and notations.

Name	Symbol	Unit
Light velocity	c	$m \cdot s^{-1}$
Molar air specific heat capacity at constant pressure	C_p	$J \cdot mol^{-1} \cdot K^{-1}$
Liquid water specific heat capacity at constant pressure	Cp_{H_2O}	$J \cdot kg^{-1} \cdot K^{-1}$
Specific heat capacity of humid air	C_s	$J \cdot kg^{-1} \cdot K^{-1}$
Specific heat capacity of i component	C_p^i	$J \cdot K^{-1}$
Diffusion coefficient for water	D_{H_2O}	$m^2 \cdot s^{-1}$
Heat diffusion coefficient	D_t	$m^2 \cdot s^{-1}$
Convection energy	E_{conv}	W
Latent energy	E_{lat}	W
Short-wave radiation energy	$E_{photons}$	W
Net longwave energy	E_{ray}	W
Gravitational acceleration	g	$m \cdot s^{-2}$
Leaf conductance for water vapour	G^{H_2O}	$mol \cdot m^{-2} \cdot s^{-1}$
Boundary layer conductance for water	$g_{BL}^{H_2O}$	$mol \cdot m^{-2} \cdot s^{-1}$
Stomatal conductance for water	$g_s^{H_2O}$	$mol \cdot m^{-2} \cdot s^{-1}$
Boundary layer conductance for heat transfer	g_{BL}^{heat}	$m \cdot s^{-1}$
Planck constant	h	$J \cdot s$
Height of plant chamber	H	m
Maximum light absorption rate	I^{max}	$mol \cdot s^{-1}$
Incident shortwave radiation	I_s	$W \cdot m^{-2}$
Heat capacity	k	$J \cdot m^{-2} \cdot K^{-1}$
Heat transfer coefficient	k_t	$m \cdot s^{-1}$
Leaf characteristic length	L	m
Leaf area	LA	m^2
Water mass in the leaf	m_{H_2O}	kg
Avogadro number	N_A	mol^{-1}
Atmospheric pressure of the bulk air	P_{bulk}	Pa
Water partial pressure in bulk air	$p_{bulk}^{H_2O}$	Pa
Water partial pressure at the leaf surface	$p_{leaf}^{H_2O}$	Pa
Ideal gas constant	R	$J \cdot mol^{-1} \cdot K^{-1}$
Temperature	T	K
Bulk air temperature	T_{bulk}	K
Bulk air velocity	V_{bulk}	$m \cdot s^{-1}$
Forced convection velocity	V_{forced}	$m \cdot s^{-1}$
Free convection velocity	V_{free}	$m \cdot s^{-1}$
Short wave absorbance	α	-
Percentage of the wavelength	γ_i	-
Boundary layer thickness	δ	m
Emissivity	ε	-
Incident photon wavelength	λ_i	m
Air density	ρ	$kg \cdot m^{-3}$
Water vapor molar density	ρ_{mol,H_2O}	$mol \cdot m^{-3}$
Stefan–Boltzmann constant	σ	$W \cdot m^{-2} \cdot K^{-4}$
Water transpiration rate	φ_{H_2O}	$mol \cdot s^{-1}$
Water latent heat of vaporisation	Λ_{mol}	$J \cdot mol^{-1}$
Subscript i refers to leaf, replica, black replica, white replica, dry replica, wet replica, heated replica respectively	i_{leaf}, i_{rep}, i_{black}, i_{white}, i_{dry}, i_{wet}, i_{heated}	-

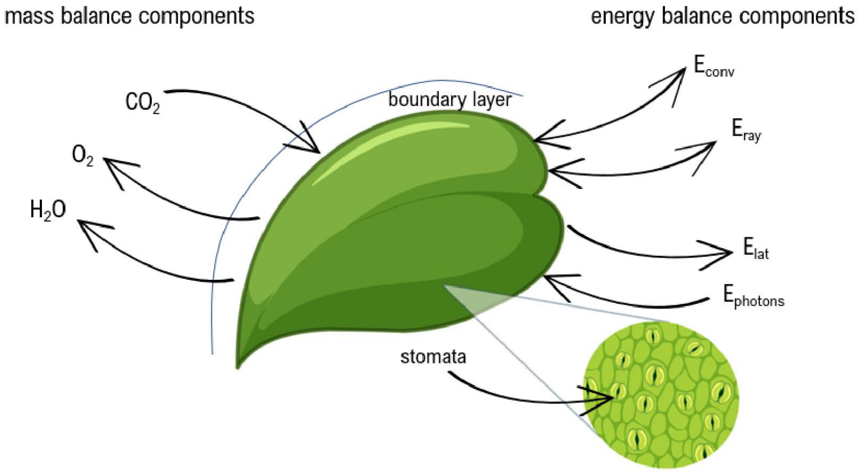

Figure 1. Leaf energy balance components.

where $I^{\max}$—maximum light absorption rate, N_A—Avogadro number, h—Planck constant, c—light velocity, $\lambda_{\min/\max}$—respectively the lowest and highest wavelengths of the light source, γ_i—percentage of the wavelength λ_i.

For continuous light spectrum (like the sun), the absorbed energy can be described as:

$$E_{\text{photons}} = \int_{\lambda_{\min}}^{\lambda_{\max}} \frac{I \cdot N_A hc}{\lambda} \, \mathrm{d}\lambda. \tag{3.1.3}$$

By assuming the plant canopy and the surroundings have similar emissivity, and according to the Stefan–Boltzmann law, the net radiation energy for the leaf can be calculated using following equation:

$$E_{\text{ray}} = \varepsilon\sigma(T_{\text{leaf}}^4 - T_{\text{bulk}}^4)LA \tag{3.1.4}$$

where ε—emissivity coefficient value usually between 0.94 and 0.99 for plants, σ—Stefan–Boltzmann constant, T_{leaf}—leaf temperature, T_{bulk}—bulk air temperature and LA—leaf area.

Although heat exchanged via transpiration is one of the main components of the energy balance, subsequent leaf cooling is a consequence of the stomatal opening required to sustain photosynthesis and leading to water evaporation through them, rather than a mechanism to control leaf temperature. Without latent energy loss however, the leaf temperature could rapidly rise to lethal level [56].

The latent heat flux can be calculated using the following equation:

$$E_{\text{lat}} = \Lambda_{\text{mol}}\varphi_{\text{H}_2\text{O}} \tag{3.1.5}$$

where Λ_{mol}—water latent heat of vaporisation and $\varphi_{\text{H}_2\text{O}}$—water transpiration rate.

Another component of plant heat balance is the convective heat transfer which is related to the air flow around the leaf. Heat and mass diffuse through the leaf boundary layers and are modelled by the boundary layer conductance [52]. It can be described with the following equation [24]:

$$E_{\text{conv}} = C_p k_t \frac{P_{\text{bulk}}}{RT_{\text{bulk}}}(T_{\text{leaf}} - T_{\text{bulk}})LA \tag{3.1.6}$$

where C_p—molar air specific heat capacity at constant pressure, P_{bulk}—atmospheric pressure of the bulk air, T_{leaf}—leaf surface temperature, LA—leaf area, k_t—heat transfer coefficient defined as a function of heat boundary layer thickness and heat diffusion coefficient:

$$k_t = \frac{D_t}{\delta} \tag{3.1.7}$$

where δ—boundary layer thickness D_t—heat diffusion coefficient.

Because of the phenomena described in this article appear in a gas phase—the Prandtl and Schmidt numbers are close to unity, the heat and mass boundary layers described here later, are assumed to be equal and named δ hereafter.

The boundary layer thickness can be calculated using following equation:

$$\delta = \frac{2}{\xi}\sqrt{\frac{\upsilon L}{V_{\text{bulk}}}} \tag{3.1.8}$$

where ξ—empirical coefficient, usually varying between 1–1.33, υ—air kinetic viscosity, L—leaf characteristic length, V_{bulk}—bulk air velocity.

Where bulk air velocity is defined in the following way:

$$V_{\text{bulk}} = V_{\text{free}} + V_{\text{forced}} \tag{3.1.9}$$

where V_{free}—free convection velocity, V_{forced}—forced convection velocity.

Free convection velocity is a function of gravity:

$$V_{\text{free}} = \sqrt{2gH\frac{\Delta\rho}{\rho}} \tag{3.1.10}$$

where g—gravitational acceleration, H—height of the chamber $\Delta\rho$—density gradient between the surface of the leaf and bulk air ρ—air density. Detailed description of this model can be found in [24].

For studies conducted in microgravity, the lack of natural convection must be considered, as it significantly affects the energy balance components [56]. The studies in microgravity will allow to understand this phenomenon and test the accuracy of the model.

3.1.2. *Associated replicas*

To study the energy balance of a leaf, many researchers used dry replicas (Table 2). The idea was to use a dry reference surface with properties (radiative and aerodynamic) similar to a real leaf and to place it in the same environment as a real plant or other replicas in order to assess the net energy flux due to light energy exchanges [31, 32]. The source of the energy provided to the replica was an external light source [32–34] or internal heating by using resistors [35, 36]. The use of dry replicas eliminates the latent heat term from the energy balance equations and thus enables their simplification; it also allows to remove from the equation most of the effects of the surrounding environment like for example long wave radiation.

Dry replicas were used to estimate the convective heat transfer in normal conditions—for different airflows [32,38], leaf temperatures [35,36], or gravity conditions [32,33] without secondary effects of the stress on other energy balance components.

The shapes of the leaf replicas were usually mimicking the shape of real leaves tested in parallel, such as those of barley wheat, strawberry or sweet potato [31, 32, 36]. Dry replicas were made from copper [32], brass sheet [35], Perspex [36] or aluminium sheet [31, 34]. Scientists were searching for materials with optical properties close to the ones of real leaves [32, 35, 36].

Vialet-Chabrand and Lawson however have highlighted in [31] that the reference materials did not have exactly the same optical and thermal properties as real leaves, and this may introduce a bias in estimating the heat balance parameters. The authors suggested to directly include

Table 2. Summary of the energy balance studies done with replicas.

Studied phenomena	Type of replica	Reference	Tested parameters	Used sensors	Environment
Energy balance	Dry replica	[31]	Day/night transition	IR camera, thermocouples, light sensor	Controlled
	Pair of dry/wet replica	[32]	Wind speed, irradiance	Thermocouples	Controlled
		[33]	Gravity, wind speed	IR camera	Controlled
		[34]	Wind speed	Thermocouples, anemometer, scale	Controlled
	Heated replica/non heated replica	[35]	Wind speed	Thermocouples, anemometer	Controlled
		[36]	Wind speed, wind angle	IR camera, thermocouples, radiometer	Controlled
	Replica with stomata	[30]	Wind speed, humidity, irradiance, pores density	IR camera, thermocouples, heat flux sensor	Controlled
		[31]	Day/night transition	IR camera, thermocouples, light sensor	Controlled

differences in thermal and optical properties in the energy balance equations and predict the leaf thermal kinetics from a reference material instead of mimicking leaf properties [35]:

$$\frac{\mathrm{d}T^{\mathrm{leaf}}}{\mathrm{d}t} = \frac{Cp^{\mathrm{rep}}\frac{\mathrm{d}T^{\mathrm{rep}}}{\mathrm{d}t} - (E^{\mathrm{leaf}}_{\mathrm{photons}} - E^{\mathrm{rep}}_{\mathrm{photons}}) + (E^{\mathrm{leaf}}_{\mathrm{ray}} - E^{\mathrm{rep}}_{\mathrm{ray}}) + (E^{\mathrm{leaf}}_{\mathrm{conv}} - E^{\mathrm{rep}}_{\mathrm{conv}}) + E^{\mathrm{leaf}}_{\mathrm{lat}}}{Cp^{\mathrm{leaf}}} \tag{3.1.11}$$

The terms are as explained above. The superscript leaf is of the real leaf, the subscript rep for replica.

Another approach to simplify energy balance is by using dry and wet replicas with similar thermal capacity. Measuring the temperature difference between them in the same environmental conditions enables the computation of the latent heat flux from the wet replica. Indeed:

$$Cp^{\mathrm{rep}}\left(\frac{\mathrm{d}T^{\mathrm{dry}}}{\mathrm{d}t} - \frac{\mathrm{d}T^{\mathrm{wet}}}{\mathrm{d}t}\right) = (E^{\mathrm{dry}}_{\mathrm{photons}} - E^{\mathrm{wet}}_{\mathrm{photons}}) - (E^{\mathrm{dry}}_{\mathrm{ray}} - E^{\mathrm{wet}}_{\mathrm{ray}}) - (E^{\mathrm{dry}}_{\mathrm{conv}} - E^{\mathrm{wet}}_{\mathrm{conv}}) - (E^{\mathrm{dry}}_{\mathrm{lat}} - E^{\mathrm{wet}}_{\mathrm{lat}}) \tag{3.1.12}$$

The terms are as explained above. The superscript dry is of the dry replica, the subscript wet for wet replica.

Since the short-wave incoming radiation energy, the long-wave energy and the convection energy are the same for both replicas, the equation can be derived only with the modelling of the latent energy flux:

$$Cp^{\text{rep}}\left(\frac{\mathrm{d}T^{\text{dry}}}{\mathrm{d}t}-\frac{\mathrm{d}T^{\text{wet}}}{\mathrm{d}t}\right)=E_{\text{lat}}^{\text{wet}} \tag{3.1.13}$$

By using replica with stomata together with dry replica it is possible to calculate the latent energy flux of the leaves with the specified size of stomata by applying Equation (3.1.13).

Heated replicas combained with not heated ones were used to calculate the convection energy. If the replica did not have an external source of energy (other than the heater in one of them) and if the temperature of the not heated one is equal to the temperature of the environment the Equation (3.1.12) can be simplified to:

$$Cp\frac{\mathrm{d}T^{\text{heated}}}{\mathrm{d}t}=-E_{\text{conv}}^{\text{heated}} \tag{3.1.14}$$

The terms are as explained above. The superscript heated is of the heated replica.

3.2. *Transpiration*

3.2.1. *Description of the biophysical phenomenon*

The transpiration rate ($\varphi_{\text{H}_2\text{O}}$) from the Equation (3.1.5) can be calculated using the following equation:

$$\varphi_{\text{H}_2\text{O}}=\Lambda_{\text{mol}}\frac{G^{\text{H}_2\text{O}}}{P_{\text{bulk}}}(p_{\text{leaf}}^{\text{H}_2\text{O}}-p_{\text{bulk}}^{\text{H}_2\text{O}})LA \tag{3.2.1}$$

where P_{bulk}—bulk air total pressure, $p_{\text{leaf}}^{\text{H}_2\text{O}}$—water partial pressure at the leaf surface, $p_{\text{bulk}}^{\text{H}_2\text{O}}$—water partial pressure in bulk air and LA—leaf area, $G^{\text{H}_2\text{O}}$—leaf conductance for water vapour defined as:

$$G^{\text{H}_2\text{O}}=\frac{g_{\text{BL}}^{\text{H}_2\text{O}}+g_s^{\text{H}_2\text{O}}}{g_{\text{BL}}^{\text{H}_2\text{O}}\cdot g_s^{\text{H}_2\text{O}}} \tag{3.2.2}$$

where $g_s^{\text{H}_2\text{O}}$—stomatal conductance for water and $g_{\text{BL}}^{\text{H}_2\text{O}}$—boundary layer conductance for water vapour, defined as a function of boundary layer thickness, where boundary layer thickness depends on the gravity. For the detailed equations, please refer to [24].

The leaf conductance for diffusion of water vapour depends on the stomatal and boundary layer conductance. The boundary layer conductance depends on their thicknes which depends on the gravity as it was described in Equations (3.1.8)–(3.1.10), so transpiration is another component which is strongly affected by a reduced or the absence of gravity and therefore needs to be studied.

3.2.2. *Associated replicas*

In the studies of transpiration rates, a few types of replicas have been used (see Table 3). The simplest approach was to use a wet replica together with a real leaf to determine the air water vapor resistance [22, 37].

When a wet replica was combined with a dry one, the resistance value could later be used to calculate the transpiration rate of the real leaf [34]. One of the early studies of the transpiration used two aluminium sheets, a bare one and one with a wet filter glued to it [34]. Both replicas had thermocouples sticked to the surface and were placed on a scale to measure the evaporation rate. The goal of the study was to determine the air water vapor resistance. Currently the simple wet replicas were mostly made from wet cloth or paper and placed on a supporting structure.

Table 3. Summary of the transpiration studies done with replicas.

Studied phenomena	Type of replica	Reference	Tested parameters	Used sensors	Environment
Transpiration rate	Wet replica combined with real leaf	[22]	Wind speed	IR camera, thermocouples, hygrometer	Controlled
		[37]	Gravity	IR camera, thermocouple, leaf porometer, hygrometer	Controlled
	Wet replica	[38]	Light intensity	IR camera	Controlled
	Pair of dry/wet replica	[34]	Wind speed	Thermocouples, anemometer, scale	Controlled
	Vessel with the perforated structure on the top	[39]	Pores size, pores density	Scale, humidity sensors	Controlled
		[40]	Pores size, pores density, pore geometry	Scale, anemometer, humidity sensor,	Controlled
		[41]	Pores size, pores density, leaf angle	Scale, thermocouples, anemometer, humidity sensor, pressure sensor	Controlled
	Replica with stomata	[30]	Wind speed, humidity, irradiance, pores density	IR camera, thermocouples, heat flux sensor	Controlled
		[31]	Day/night transition	IR camera, thermocouples, light sensor	Controlled

When they were compared with dry replicas it was possible to calculate the transpiration rate by applying equation:

$$\varphi_{\mathrm{H_2O}} = \frac{Cp}{\Lambda_{\mathrm{mol}}}\left(\frac{\mathrm{d}T^{\mathrm{dry}}}{\mathrm{d}t} - \frac{\mathrm{d}T^{\mathrm{wet}}}{\mathrm{d}t}\right) \tag{3.2.3}$$

The terms are as explained above.

The simple wet replica however, did not have pores, so the evaporation was not limited by them and it was similar to the evaporation from a free surface [34]. Hence, the evaporation energy from such replicas is overestimated compared to the one of a real leaf. To solve this problem another type of replica was developed. In the literature two types of replicas with artificial stomata are described. The first one consists of a petri dish or other small vessel with a micro-perforated foil, or a plate placed on it [39–41]. The main purpose of these studies was to investigate the influence of the size, the density, the shape of pores and the angle of the leaf on the evaporation rate and relate it to the influence of stomata on leaf transpiration. The replicas were put on a scale or were weighted periodically [39–41] to measure the change in weight over time. This kind of setup allowed an accurate evaluation of the rate of evaporation, but the thermal and buffer properties of this type of replica are significantly different from those of real leaves. This is due to different surface areas, materials and thicknesses, flat shapes, not flexible structures, and greater heat capacities (due to the thick water layer in the vessel with water).

In order to solve this problem Schymanski *et al.* proposed another type of replica, which includes pores that are similar to stomata in terms of size [30]. This replica consists of a capillary filter paper glued onto aluminium tape with a water supplying tube and thermocouples sandwiched between the layers. On one side of the replica, the aluminium foil had artificial stomata with defined dimensions—similar in size to real stomata. The non-transpiring side was covered with black aluminium tape. The studies were conducted in a closed chamber and the evaporation rate was measured based on the parameters of the air coming in and out of the measurements area with the humidity sensor, anemometers, and thermocouples. The replica was tested for various humidity and wind speed conditions and with several pore densities. This setup allowed to study evaporation rate together with the energy balance. The replica was mainly developed to study the energy balance at steady state. This type of replica was slightly modified later by Vialet-Chabrand and Lawson to make measurements in dynamic conditions [31]. This replica was made of an aluminium plate which was covered by black tape with known absorbance and emissivity on non-transpiring side like in the previously described replica. The transpiring side of the leaf was covered with a felt fabric enclosed in a plastic microporous sheet, where pores had a known diameter depth and density. The felt sandwiched between the aluminium layers was saturated with water, so the only factors affecting the transpiration were the size and density of the pores and the environmental conditions (fluctuating light environment, wind speed or humidity). These factors together with the angle of the leaf facing the flow were studied in detail. This replica was studied together with two dry replicas of same absorbance but different emissivity. This allowed the calculation of every component of the leaf energy balance separately by measuring the difference in the temperature between all the replicas. The whole calculation procedure is described in [31].

3.3. *Boundary layer*

The boundary layer is a representation model of the thin layer of air that develops close to a leaf in presence of an air flow and where the physical parameters like velocity, temperature, H_2O and O_2 concentrations are modified by diffusion [57].

3.3.1. *Description of the biophysical phenomenon*

The boundary layer conductance for water ($g_{BL}^{H_2O}$) can be described using the following equation:

$$g_{BL}^{H_2O} = \frac{D_{H_2O}\rho_{mol,H_2O}}{\delta} \tag{3.3.1}$$

where: D_{H_2O}—diffusion coefficient for water, ρ_{mol,H_2O}—water vapor molar density, δ—boundary layer thickness, described with the Equation (3.1.8). For more details please, refer to [24].

It was shown in [22] that increased ventilation causes a reduction in the leaf boundary layer resistance. This phenomenon is quite significant in microgravity, where there is no free convection, and the thickness of the boundary layer goes to infinity if there is no forced convection [24]. A detailed description of the model of the boundary layer with the gravity as a parameter can be found in Poulet *et al.* [24].

3.3.2. *Associated replicas*

The experiments to study the boundary layer conductance can be divided into two groups (Table 4): experiments performed in a controlled, laboratory environment [22,30,31,33,35,36,44] and experiments in a natural environment—like field, forest or a greenhouse [21,42–44].

Most of the experiments carried out in the field used a similar design for the leaf replica. They were made of highly polished brass sheets [21,42,44] or flexible Mylar1 sheet [43]. The shape and size of the replicas were adjusted to the shape and size of the average leaf of the studied plant or tree. In between the sheets or on the bottom part the heaters were glued. The heater was or isolated with enamel coating [21], or double-sided adhesive tape [42,45] or glued with double-sided adhesive tape with epoxy resin [44], Sellotape [35] or moulded into the leaf replica [36]. The thermocouples were attached to the replica to measure the mean temperature of the replica surface and the dynamic of the temperature change. In the field experiments, replicas were attached to the real plant. In some studies, the replicas were used in pairs and were alternatively heated [42,43] or one was heated and the other not [21,44]. Similar replicas have been used to calculate the boundary layer conductance in controlled environment [35, 36, 44, 45]. In these tests, the main goal was to calculate the boundary layer conductance as a function of the leaf temperature and airflow [35, 36, 44, 45] and study the corelation between the boundary layer conductance and the angle of the wind [36]. The thickness and shape of the leaf were similar to the real leaves. In the experiment described by Schymanski *et al.* [30] the replica described in Section 3.2.2 was used, to test the leaf conductance as a function of wind speed and vapour pressure in steady state.

To simulate boundary layer parameters, Vialet-Chabrand and Lawson in [31] has proposed another approach (described as well in the Section 3.2.2). Using two dry replicas at the same time with identical thermal properties but covered with a different colour (black and white to differentiate their optical properties), allows to calculate heat boundary layer conductance in the dynamic conditions by applying equation below:

$$g_{\mathrm{BL}}^{\mathrm{heat}} = \frac{k\left(\frac{\mathrm{d}T^{\mathrm{white}}}{\mathrm{d}t} - \frac{\mathrm{d}T^{\mathrm{black}}}{\mathrm{d}t}\right) + I_s(\alpha^{\mathrm{black}} - \alpha^{\mathrm{white}}) - 2\sigma(\varepsilon^{\mathrm{white}} T^{\mathrm{white}^4} - \varepsilon^{\mathrm{black}} T^{\mathrm{black}^4})}{2\rho C_s(T^{\mathrm{white}} - T^{\mathrm{black}})} \tag{3.3.2}$$

where $g_{\mathrm{BL}}^{\mathrm{heat}}$—boundary layer conductance, I_s—incident shortwave radiation, α—short wave absorbance, ρ—air density, k—heat capacity of the replica, C_s—specific heat capacity of humid air.

The main goal of this experiment was to develop a procedure and model to calculate the stomatal conductance in transient regime by using replicas. A good understanding of the processes at the leaf level can pave the way to scaling up and modelling a whole canopy instead of single leaves by using mechanistic equations. The complexity of this topic is described in the next section.

4. Scaling-up gas exchange from the leaf to the canopy level with an energy balance

For the scaling-up of the physical phenomena from the leaf level to the canopy level, it is fundamental to determine among all the interactions within the plants, especially the ones that are strongly affected by the surroundings, as in most cases changing from one scale to another is not linear. For example, the prediction of canopy transpiration is different from the results which would be obtained by summing up individual leaf responses because each leaf significantly affects the surrounding environment by changing e.g., the wind speed, the irradiance, or the relative humidity. Therefore, the transpiration rate predicted for a canopy from a single leaf model would be overestimated. In addition, the change in irradiance is exponentially decreasing with

Table 4. Summary of the energy balance studies with replicas.

Studied phenomena	Type of replica	Reference	Tested parameters	Used sensors	Environment
Boundary layer conductance	Wet replica	[22]	Wind speed	IR camera, thermocouples, hygrometer	Controlled
	Pair of 2 dry replicas	[31]	Day/night transition	IR camera, thermocouples, light sensor	Controlled
	Pair of dry/wet replica	[33]	Gravity, wind speed	IR camera	Controlled
	Heated replica	[21]	Day/night transition, leaf position	IR camera, thermocouples, light sensor	Greenhouse
		[42]	Wind speed	IR camera, thermocouples, light sensor	Greenhouse
		[43]	Wind speed, time of the day	IR camera, thermocouples	Field experiment
		[44]	Wind speed	Thermocouples, humidity sensor, anemometer, scale	Field experiment, controlled
		[35]	Wind speed	Thermocouples, anemometer	Controlled
		[45]	Temperature gradient, wind speed	Thermocouples, cameras	Controlled
		[36]	Wind speed, wind angle	IR camera, thermocouples, radiometer	Controlled
	Replica with stomata	[30]	Wind speed, humidity, irradiance, pores density	IR camera, thermocouples, heat flux sensor	Controlled
		[31]	Day/night transition	IR camera, thermocouples, light sensor	Controlled

the leaf area index, and this significantly reduces the amount of light absorbed by the leaves which are not directly exposed to the sun [51].

The plant canopy generates a resistance to air movements, which in consequence reduces wind speed within the canopy and in turn lowers the boundary layer conductance of certain leaves, as compared to what would be expected based on a single leaf of similar dimension and submitted to the same environmental parameters. Transpiration also affects the local water vapour pressure around the leaf. When stomatal conductance increases, water vapour pressure around the leaves increases as well and therefore reduces transpiration (see Equation (3.2.1)). In consequence transpiration increases less than what would be expected from the increase in stomatal conductance alone [58].

A good model for scaling-up from leaf to the canopy level will be based on mechanistic processes that develop at a lower scale. Hence, it is necessary to determine mechanistic model of a single leaf behaviour under specific environmental conditions, and for that it is necessary to start with a leaf replica.

This approach will help to address the questions which still have not been completely answered, like for example: can we use a big leaf model to calculate gas exchange and energy balance of a whole plant? Or it is necessary to combine individual gas exchange of each leaf and their individual microclimate in the energy balance at the canopy level?

Answering these questions is mandatory for developing safe, reliable, and robust LSS based on plants and to reach a full control of them.

5. Conclusions—how can leaf replicas help us to fill the gap in modelling

Understanding physical processes behind stomatal conductance in space environment, linked to energy and mass balances through mechanistic models, should enable a better comprehension of plant gas exchange in greater details. To achieve this, it is crucial to quantify how the boundary layer thickness varies in changing conditions, like space, or fluctuating conditions associated to parabolic flights. Microgravity strongly affects the physical exchanges at the leaf surface, being the first step of a cascade of biological events that are a consequence of these out-of-range conditions. To achieve a detailed understanding of physical processes at the leaf surface, replicas are necessary. This will allow the development of safe and controllable life-support systems based on living organisms.

The integration of mechanistic models at the leaf level will have to be scaled at the whole canopy in order to use knowledge-based description of mass, heat and energy exchange instead of empirical models, that were not developed for closed or space environments. This is the path for the development of reliable higher plant chambers in space environments.

Conflicts of interest

Authors have no conflict of interest to declare.

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