



Article Conversion of Thermal Energy to Gas Flow Kinetic Energy in the Bionic Leaf Stomata

Tomas Ūksas *, Povilas Algimantas Sirvydas, Simona Paulikienė 回 and Rasa Čingienė

Faculty of Engineering, Agriculture Academy, Vytautas Magnus University, Studentų Str. 11, Kaunas District, LT-52261 Kaunas, Lithuania; algimantas.sirvydas@vdu.lt (P.A.S.); simona.paulikiene1@vdu.lt (S.P.); rasa.cingiene@vdu.lt (R.Č.)

* Correspondence: tomas.uksas@vdu.lt

Abstract: In the technical field, the potential energy of gas under pressure is converted into mechanical kinetic energy by means of special complex channels. Leaf stomata perform a similar function in plant leaves. The shape of leaf stomata channels is much more sophisticated compared to gas flow transformation channels in energy production facilities. There is a biological prototype of a heat engine in the leaf, where leaf stomata convert thermal energy into mechanical kinetic energy of the flow with a change in leaf temperature. The paper presents experimental research on thermal energy conversion into mechanical kinetic energy of the flow in plant leaf stomata. The values of biological heat engine in a plant leaf and the associated processes are minute. The operation of the biological heat engine in a plant leaf was proven by indirect experimental measurements. After applying a light source flux to a plant leaf and inducing a temperature change in the tissues of the plant leaf, the rotational movements of a freely hanging plant leaf about the suspension axis were studied. When studying the dependence of plant leaf rotation movements on the area of the plant leaf, it was found that at a 150 W light source, the angle of rotation increased as the area of the plant leaf increased. For a plant leaf with an area of 52.5 ± 1.9 cm², the angle of rotation reached 165° ; $29.1 \pm 1.1 \text{ cm}^2$ — 143° ; $16.0 \pm 0.8 \text{ cm}^2$ — 92° ; and $9.2 \pm 0.6 \text{ cm}^2$ — 44° . The angular speed of plant leaf rotation was from 0.070–0.262 rad/s. The influence of light sources on the rotation angle of the plant leaf was studied; when illuminating the active leaf area of 25.0 ± 1.0 cm² of the plant with a 40 W power light source, after 11 s, the rotation angle reached 31°, 60 W—97°, 100 W—131° and 150 W—134°. The effect of light sources (from 40 to 150 W) on the angular rotation speed of the plant leaf varies at 0.049–0.213 rad/s, respectively.

Keywords: bionic leaf stomata; conversions thermal energy; leaf gas exchange system

1. Introduction

In the technical field, the potential energy of gas under pressure is converted into mechanical kinetic energy by means of special complex channels. Leaf stomata perform a similar function in plant leaves. The historical development of plants spans across a long period of time; therefore, plants have fully adapted to their natural habitat conditions [1]. The anatomical structure of plant organs has maximally adapted to the biological processes inside the plant and physical factors of the habitat [2]. Temperature pulsations during daylight hours [3] trigger the operation of the heat engine in the leaf stomata [1]. Stomata protective cells have complex and robust membrane transport and control mechanisms [4] where a heat motor acts in a derivative system of a plant leaf petal system. In the biological prototype of the plant leaf heat engine, the leaf stomata play an important role.

For bionic purposes, plant leaf models are used to analyze the principles of vital activity in the leaf [5–7]. Models are used to analyze the thermal effect of natural leaf transpiration [6]. In bionic applications, the results of the studies of heat and mass exchange in a plant leaf were applied to develop agriculture irrigation technologies [5]. The



Citation: Ūksas, T.; Sirvydas, P.A.; Paulikienė, S.; Čingienė, R. Conversion of Thermal Energy to Gas Flow Kinetic Energy in the Bionic Leaf Stomata. *Agronomy* **2022**, *12*, 1742. https://doi.org/10.3390/ agronomy12081742

Academic Editor: Mario Cunha

Received: 7 June 2022 Accepted: 20 July 2022 Published: 23 July 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). patterns of plant-juice flow along the microchannels in the leaf tissue are applied for bionic purposes in analogous pumpless fluid transport systems on microfluidic platforms [8,9]. The mechanical characteristics of plant leaves were also studied [10,11]. Most studies investigating the relationship between stomatal development or behavior and photosynthesis were performed in the presence of steady light (square waves) [12,13]. The anatomical structure of a plant leaf stomata and the processes inside it must be discussed in order to evaluate the heat conversion processes in plant leaf stomata for the purpose of bionics.

Stomata come in a variety of shapes and sizes, and this may directly affect their functionality [14]. It is known that the number of stomata in 1 mm^2 of a leaf ranges up to 450 [15,16]. The maximum number of stomata per leaf area is limited by the size of the stomata, but the density and size of the stomatal vary greatly between species, resulting in different rates of gas exchange [17,18]. Plants with large and small stomata generally have higher water efficiency but also lower photosynthesis rates compared to plants with many but smaller stomata [19]. The size of the stomata opening in the leaves of different plants ranges from 0.17 to 239 μ m², and the total area of stomata openings accounts for 0.52 to 5.28% of the leaf surface [11,20,21]. Water is a very important element in the process of plant growth. The mechanism that controls the water balance and gas exchange in the plant is the opening and closing of the stomata of the plant leaf [22,23]. The stomata opening for physical and chemical reasons increases hydraulic/stomatal conductivity, loss of water, and finally, leaf turgor [24]. Stomatal conductivity is further regulated by opening and closing under a variety of environmental conditions [25–28]. Normally, when exposed to light, stomata open to absorb CO₂ [29]. However, about 90 to 95% of CO₂ reaches the inside of the leaf in the process of gas exchange only through stomata, whereas only 5 to 10% of plant metabolic gas diffuses through the epidermis and cuticle [11,20,21]. CO_2 , together with the ambient air, accessed the spongy tissue of the leaf through open stomata; metabolites (O_2 and water vapor) are also released into the environment through open stomata [24,30]. It is often stated that every stomata serves its own gas exchange system [31,32]. The shapes of stomata are different, and the size of their apertures changes from closed to fully opened [21,33]. Thus, although the effects of stomata size and density on gas exchange can be modeled [34,35], little is known about their effects on stomatic heat motor performance.

In the technical field, the potential energy of gas under pressure is converted into mechanical kinetic energy through thermodynamic processes in special complex channels [36]. Leaf stomata perform the function of energy conversion channels. Plant leaf stomata have shapes similar to the complex channels used in heat engines. Plant leaf stomata have very different anatomical shapes. These shapes depend not only on the biological processes inside the leaf and their anatomical structure but also on the climatic conditions of the habitat [33]. In heat engines, the shape of energy conversion channels does not change. The plant leaf can change not only the stomata shape but also the throughput of the gas flow. The flow in energy conversion channels of energy equipment is unidirectional [36]. The gas flow in plant leaf stomata is bi-directional. The plant leaf stomata shape is much more complicated compared to flow conversion channels in technical equipment [33].

The operation of the plant leaf heat engine (biological prototype) is based on the conversion of the potential energy of pressure in the leaf gas exchange system. This conversion occurs when temperature in the plant leaf tissues changes. The potential energy of gas pressure converted into kinetic energy in plant leaf stomata creates mechanical work that promotes the processes of gas and energy exchange between the plant leaf and the environment [1].

Investigation into bionic leaf stomata shows that the conversion of low temperature heat into mechanical energy is possible in very thin plates when the plate structure in principle resembles the anatomical structure of a plant leaf.

By dynamically controlling their pore openings, plants can regulate gas exchange as a first response to many environmental changes, including light intensity, temperature, humidity, and water availability [37–39]. During daylight hours temperature pulsations

occur in the plant leaf and the plant's heat engine (biological prototype of a heat engine) operates in the gas exchange and stomata system. This is based on the theory of thermodynamic processes in the plant leaf gas exchange system and the first and second laws of thermodynamics [40,41]. The thermodynamic cycle of the heat engine operating in the plant leaf is explained theoretically [1]. Here, we prove experimentally that a heat engine operates in a plant leaf.

The model was developed to understand how plant cells respond to changes in the environment, providing a thorough understanding of the plant's potting mechanism, which is both a heat engine and a protective part of the turgor. Although many physical models have been proposed that mimic the temperature studies of plant leaves, there are fewer studies on the modeling of plant leaf petals as a heat engine and the influence of light on leaf rotation. This research focused on the stomatal heat engine in gas exchange. The effects of stomatal morphology and stomatal distribution were described. However, it is important to note that stomatal characteristics are often interrelated and functionally aligned, as are the complex and interrelated mechanisms that often drive certain changes. Thus, the purpose of this article was to reveal and experimentally substantiate the theoretical assumptions that the transformation of heat into mechanical energy takes place in the plant leaf, which intensifies the assimilation process.

2. Materials and Methods

The values of the biological heat engine in a plant leaf and the occurring processes are minute. Using the capabilities of today's laboratory equipment, direct measurements cannot be performed. The operation of the plant leaf's heat engine (there are up to 450 stomata on 1 mm² of the leaf surface) can be demonstrated by indirect measurement. First of all, the theoretical basis were performed and described, based on which the theoretical predictions of the stomatal heat engine of the plant were presented. Under laboratory conditions, the plant leaf must receive a thermal input (in the form of illumination) and a temperature change in the plant leaf tissues must be created.

During experimental investigation, broad-leaved linden leaves (*Tilia platyphyllos Scop*) were used, for which half of each leaf was covered with a coating that prevented the action of plant leaf stomata. To obtain a rotary motion and to prove that the plant's stomata worked in the leaf, it was necessary to ensure that only half of the plant's stomata worked (Figure 1). The plant leaf size was variable to test the efficiency of the plant leaf. In our study, plant leaves with an area of $9.2 \pm 0.6 \text{ cm}^2$, $16.0 \pm 0.8 \text{ cm}^2$, $29.1 \pm 1.1 \text{ cm}^2$ and $52.5 \pm 1.9 \text{ cm}^2$ were used (Figure 2).



Figure 1. Scheme of evaluation of torsional deformations of a hanging plant leaf in a galvanometer thread: cross-section a–a—leaf suspension (rotation) axis; 1—a metal filament from a galvanometer; 2—active leaf blade surface area; 3—surface area of a leaf blade covered with heat reflecting coating; 4—light wave reflection mirror to measure the rotation of the leaf.



Figure 2. Broadleaf linden leaves (*Tilia platyphyllos Scop*): 1—leaf area 9.2 \pm 0.6 cm²; 2—leaf area 16.0 \pm 0.8 cm²; 3—leaf area 29.1 \pm 1.1 cm²; 4—leaf area 52.5 \pm 1.9 cm².

To determine the effect of environmental factors on plant leaves, the rotational movements of a freely hanging plant leaf about the axis of suspension were observed (Figure 1). To demonstrate which factors work and how a plant leaf reacts when providing light intensity (60 W) in a suspended plant leaf, the stamens began to work and created a driving force. For this, a study was carried out on plant leaves of the same size, a dead leaf, and leaves imitating a plant leaf made of paper and transparent film. To eliminate external physical factors, the research was carried out under a transparent glass hood. During the investigation, the change in temperature was determined by determining 9 measurements per second (6 repetitions). Simulated plant leaves of the same parameters were used.

The plant leaf motion instigated by the impulse from a light source was measured by the angle of leaf rotation around the axes of suspension. A special stand and an indirect measurement methodology were developed to test the rotations of the leaf around the axes of suspension. The research stand and the stand diagram are presented in Figure 3.



Figure 3. Line diagram of experimental stand to test heat conversion in a plant leaf: 1—metal filament to suspend the leaf; 2—transparent hood; 3—beam reflection mirror; 4—leaf holding mechanisms; 5—test item; 6—test item retaining rack; 7—stand foot; 8—height control handle; 9—stands; 10—specular reflection (laser point); 11—illumination source; 12—suspended leaf height adjustment mechanism; 13—mirror illumination laser; 14—stand fixing mechanisms; 15—motion monitoring ruler; 16—light source device; 17—laser beam; 18—laser beam reflecting from the mirror.

The research object (plant leaf and plant leaf simulation model) was suspended on a metal filament for which the mechanical properties were known. The metal filament was required to be very thin because the gas flow leaving the plant leaf stomata creates a very small mechanical reactive force. A metal filament (1) with a mirror (3) from a mirror galvanometer M 17/13 was used to suspend the plant leaf. The hair cross-section was as follows: $6.9 \times 6.9 \mu m$. The length of the filament was 100 mm. The plant leaf was fixed by means of a special retaining mechanism (4) under the mirror (3) (Figure 3).

The plant leaf used for testing (5) was specially prepared according to the test type and goal. Prior to suspending, half of the leaf surface along the axis of suspension was covered with a light-reflecting material, namely aluminium foil ($\varepsilon = 0.039-0.057$) [42]. When a half-covered leaf receives a light beam emitting source (further–light source) (Table 1), the sides of the leaf along the axis of suspension receive different amount of heat from the heat-emitting source. On the side of the leaf not covered with foil, the light source stimulates the processes of exchange between the system of the plant cavities and stomata and the environment; the plant leaf stomata engine then begins operating. When the stomata engine on the side of the leaf not covered with the foil begins working, the hanging plant leaf receives an impulse to rotate around the axis of suspension. The hanging plant leaf's rotation movement is then transferred to the metal filament (1) on which the leaf is hanging. The plant leaf's rotation angle is transmitted via the beam mirror (3) and specular reflection (laser point) (10) to the leaf rotation angle monitoring ruler (15) (Figure 3).

Table 1. Correlation of light source power W under normal conditions in W/m^2 .

Light source power, W	150	100	60	40
Energy content under normal conditions W/m ²	1135.9	1011.8	330.6	181.8
Energy content under normal conditions W/cm ²	0.114	0.101	0.033	0.018

After being protected from the environment by the hood (2), the motion capture equipment (4; 3; 1) was set up by attaching the plant leaf to the hanging stand (12). When the laser device (13) was turned on, a red point laser beam (17) was obtained, which was directed towards the mirror (4) hanging above the plant leaf, which was connected to the calibrated galvanometer thread (1). After focusing the beam received by the laser (18) from the reflection mirror (4) to the observation ruler (15), we obtained a clearly visible laser reflection point (10) in the reflection ruler. Next, we turned on the light source (11), which illuminated the plant leaf (5) and observed the leaf turning process.

The research ruler (15) consisted of a circle with a diameter of 1.49 m. The height of the stand wall was 0.53 m. The wall was divided into 360 divisions. The value of one division in the wall was 1° . A source of light intensity (11) was placed inside the stand, with a distance of 30 cm from the test object. The power of the light source was varied from 40 W to 150 W and used for 11 s on.

As a source of light and illumination, an incandescent lamp with a wide light spectrum with bleached glass and a tungsten filament lamp of 40 W, 60 W, 100 W, 150 W electric power were used. Measurements were performed with an AX-203 light meter (error $\pm 5\%$). Table 1 shows the energy content in W/m² under normal conditions.

The constructed stand and the methodology of testing a specially prepared leaf allowed us to create different temperatures on different sides of the leaf along the axis of suspension and observe the work of thermal energy conversion into mechanical energy as performed by thermodynamic processes in leaf stomata (plant leaf rotation around the axis of suspension).

The research was closely related to temperature measurements, which changed the illuminance of the plant leaf. Low-thickness, thin research objects such as plant leaves, plant stems, as well as interventions in the deep tissues of a plant leaf represent some of the most difficult physical measurements. This is because the leaves of the plant are thin which makes it difficult for them to live, and can affect vital processes. Accurate temperature measurements were determined according to the physical data of the temperature sensor.

The design and dimensions of the sensor and, most importantly, the way it is attached to the object under investigation should be taken into account. Temperature measurement was performed with temperature sensors made of Cu-CuNi wires with a welding point diameter of 0.07 mm. The temperature sensors were connected to a special Normal ZA 9000-FSU Cu-CuNi connector, which connects to the electronic device ALMEMO 2590-9 V5. Temperature sensors were fixed on the surface of the plant leaf according to the isotherm with a length of at least 100 sensor diameters. The temperature was recorded with the temperature measuring accumulator ALMEMO 2590-9 V5. The collected data were stored in the measuring device ALMEMO 2590-9. Through the device connector (ZA-9000-FSU), the temperature sensor wires were connected to the device in the ALMEMO 2590-9 v5 connector with the memory chip. After conducting the measurements, the measurement data of the ALMEMO 2590-9 V5 data storage medium were transferred to a computer, where further data processing was carried out using a special program ARM-Control, and the obtained measurement readings were transferred to Microsoft Excel.

Experimental studies examined the temperature change of plant leaves for illumination using different light sources, determining the dependence of their rotation on the area of the leaf and the dependence of the rotation on the power of the heat source. The light sources used were only switched on for a limited time, i.e., up to 11 s, because after 11 s the plant leaf had turned, the leaf movement process changed and the leaf began to vibrate and oscillate. During the investigation, the change in temperature was determined by determining 9 measurements per second (6 repetitions). Using the obtained research results and the theoretical basis, a theoretical model of the dependence of the angle of rotation on the given light source was derived.

After the measurements were made, a regression equation was derived from the data results to determine the dependence. The derivative of the angular velocity of plant leaf rotation with respect to time was determined (for the test time—11 s):

ί

$$\upsilon = \frac{\varphi \cdot \frac{\pi}{180}}{t},\tag{1}$$

where:

 ω —angular speed of plant leaf rotation, rad/s;

 φ —plant leaf rotation angle, degrees;

t is the rotation time of the plant leaf.

In the statistical analysis, the data obtained during the investigation were analyzed using Microsoft Office Excel software. Experimental data were processed using the student *t*-test and summarized as means \pm standard deviations. Differences were considered significant at p < 0.05. To evaluate the results of plant leaf temperature changes using different power sources, the results of the dependence of the leaf rotational speed on the area of the active part of the leaf using different power sources were evaluated using multiple regression analysis.

3. Theoretical Substantiation of Gas Flow in Leaf Stomata

The exchange of oxygen and carbon dioxide in leaves (as well as the loss of water vapor in transpiration) occurs through stomata [43]. The anatomical structure of stomata varies [32,44]. Stomata have different forms and a different aperture area from closed to fully opened. Gas inside the stomata moves in both directions. In all cases, the anatomical structure of stomata is presented as a complex gas flow channel [21,33,45]. Based on the similarity of the gas flow (along engineered channels) theory, the anatomical structure of plant leaf stomata supposedly is a channel with a nozzle and a diffusor [36,42]. The nozzle inside the leaf turns into a diffusor and vice versa depending on the gas flow direction (from the leaf to the environment or from the environment to the leaf) as can be seen in Figure 4. For technical equipment it is not possible to change the gas flow direction in the nozzles [42,46,47]. We believe that the direction of gas flow leaving the plant leaf stomata is parallel (or near parallel) to the nozzle axis. The investigation into the gas flow along



complex channels in engineering systems [42,48,49] resulted in creating the fundamentals of modern energy theory and the development of the first energy machines.

Figure 4. Diagram of gas flow along the plant leaf stoma: gas flow cross-sections a-a and b-b.

Based on the general theory of gas flow in channels [36], we previously claimed that the critical pressure ratio β_k in the plant's gas exchange system p_1 and the environment p_2 can be reached ($\beta_k = p_1/p_2 = 0.528$ for diatomic gases), and the gas flow effluence through the leaf stomata to the environment will depend on the pressure in the internal gas exchange system of the plant leaf [36,42]. The motion of the plant leaf is caused by mechanical force. This force is created by thermodynamic processes in the leaf's gas exchange system as the gas flows to the environment by means of the plant leaf stomata. In nature, thermodynamic processes in mesophyll cells (gas exchange system) are caused by a change in the temperature of leaf tissues. Under the test conditions, temperature change in the plant leaf was induced using a thermal impulse from heat from a light source. The changing temperature caused changes in the gas pressure in the gas exchange system. Following higher gas pressure and higher potential energy created by the gas pressure in the plant leaf gas exchange system, the gas flows into the environment with lower pressure. The potential energy of gas pressure transformed into kinetic energy of the gas flow in the plant leaf stomata led to a rotating movement of the specially prepared suspended plant leaf. The mechanical work performed by the torque and transmitted to the suspended plant leaf depends on the reaction of the gas flow displaced through the plant leaf stomata, i.e., the reactive force generated by the outflowing gas.

The analysis of the plant leaf stomata. seen as a channel (Figure 4) where the potential energy of the gas pressure is converted into kinetic energy of the flow, with the application of the first law of thermodynamics leads to the following:

- The torque around the leaf suspension axis depends on the leaf surface area. Torque
 increases with a higher leaf surface area. Subsequently, the rotational speed of the leaf
 also increases.
- Torque depends on the difference in gas pressures $\Delta p = p_2 p_1$. With a higher difference between the pressures in the leaf's gas exchange system and the environment, the outgoing gas flow increases and the rotational force acting on the leaf also increases. Consequently, the rotational speed of the leaf depends on differential pressure $\Delta p = p_2 p_1$. Gas pressure p_1 in the plant leaf stomata framework changes depending on the plant leaf temperature, i.e., the pressure increases at a higher temperature. Temperature pulsations in the plant leaf produce pressure pulsations in the gas exchange system of the plant leaf. Therefore, when the plant leaf is exposed to heat flow in the form of a light source, the leaf's temperature increases and the pressure in the leaf's gas exchange system also increases. With higher pressure, the gas flow displaced

through the plant leaf stomata generates a higher reactive force on the illuminated side of the suspended leaf. The rotational speed of the leaf will also increase.

- The velocity of the gas flow leaving the plant leaf stomata has a substantive effect on the rotational speed of the leaf. This factor alone cannot be evaluated as it is directly related and depends on $\Delta p = p_2 - p_1$.

The experimental tests described below measuring the rotation of a suspended leaf (with a different surface area of the leaf and the source of the heat acting on the leaf) confirm the theoretical statement that, in nature, low temperature thermal energy is converted into kinetic energy by the flow of gas inside plant leaf stomata.

4. Results

4.1. Variation of Plant Leaf Temperature for Lighting Using Different Light Sources

To experimentally confirm the thermal engine (biological prototype of the thermal engine) operating in the formation of the stomatal system of the plant leaf, we studied the dependence of leaf rotation on the area of the leaf blade and the dependence using different power sources for lighting. The question arises as to how these processes would take place under analogous conditions in dead materials that do not have the structure of the stomatal system. What is the difference between a real living plant leaf and a simulated plant leaf? First, the way a living plant leaf reacts to a light source was determined compared to dead plant leaves and imitation leaves. Thus, the study was carried out using leaves of a living plant (broad-leaved linden *Tilia platyphyllos Scop*), leaves of a dead plant and leaves imitating plant leaves made of paper and transparent film.

From the research results (Figure 5), it was found that when a light source of 60 W was used, a significant difference was found between a living plant leaf (curve 1) and a dead plant leaf (curve 2), paper (curve 3) and transparent film (curve 4) (p < 0.05, n = 6). The results of the live plant leaf show a significantly higher rotation angle, which reached 97.0 \pm 3.8° at 11 s, than the dead plant leaf (25.5 \pm 1.5°) and the models of leaf-imitating leaflets made of paper (26.7 \pm 1.4°) and transparent film (24.3 \pm 1.2°).



Figure 5. Comparative data of a plant leaf and other materials in a transparent glass enclosure under the influence of a light source with a power of 60 W: 1—a broad-leaved linden (*Tilia platyphyllos Scop*) leaf; 2—dead leaf of broad-leaved linden (*Tilia platyphyllos Scop*); 3—white paper imitation plant leaf; 4—stabilized transparent 50 μ m thick polyethylene film imitation plant leaf (p < 0.05, n = 6).

There was no significant difference (p < 0.05, n = 6) in the data of the dead plant leaf (curve 2), the transparent 50 µm thick polyethylene film imitation plant leaf (curve 4) and the white paper imitation plant leaf (curve 3). The difference between these curves in the time interval of 11 s was about $2.4 \pm 0.3^{\circ}$. However, as we can see, these materials were

still given a boost. The angle of rotation was determined by the heat generated by the light source. The difference between a live plant leaf and a dead plant leaf was 71.5° (73.7°), between a live plant leaf and paper it was 70.3° (72.5°), and between a live plant leaf and film it was 72.7° (74.9°). These differences reflected the difference between a leaf of a living plant that exists in nature and simulated models. It can be postulated that the substantial increase in the rotation angle of living plant leaves was caused by the heat engine (biological prototype of the heat engine) operating in the structure of the stomatal system of the plant leaf.

Plant leaf temperature measurements revealed that the temperature of plant leaf tissues is directly related to the power of the illumination source (the flow of heat). When the maximum temperature in the leaf is achieved, the temperature begins dropping. This process reveals the biological adaptation of a plant leaf to the new situation of energy exchange, i.e., energy balance.

Figure 6 presents the variation of plant leaf temperature for lighting under 11 s of different power sources (60 W; 100 W; 150 W). As we can see, the initial temperature of the plant reached 25.9 \pm 0.1 °C. The plant leaf reached its maximum temperature at 11 s under the influence of the light source. After turning on the light source, the heat in the plant leaf began to rise and after 11 s the temperature of the plant leaf reached 30.7 \pm 0.1 °C with a 150 W (curve 1) light source, 30.0 \pm 0.1 °C with a 100 W (curve 2) light source and with a 60 W (curve 3) light source—28.3 \pm 0.1 °C. So, in this case, an energetic exchange of gases with the environment in the plant leaf occurred, wherein the stomata of the plant leaf performed mechanical work, as a result of which the plant cooled down.



Figure 6. The change in the plant leaf temperature when illumination sources of different power are used (the length of light impulse is 11 s): 1—change in the plant leaf temperature with 150 W lamps; 2—100 W; 3—60 W (p < 0.05, n = 6).

From the results of the research data, it can be seen (Figure 6) that when a plant leaf is provided with heat (including the mass of the plant leaf) from a light source lasting 11 s, the temperature of the leaf varies linearly (linear); in all cases, the coefficient of determination reached $R^2 = 0.997$, which was close to 1, i.e., the derived regression model fit the obtained data. Evidently, the process of heating the mass (including the mass of the plant leaf) depends on the amount of heat provided. This short-term process of heating the plant leaf tissue highlights the influence of further studies, with a duration of 11 s, on the temperature of the plant leaf tissue.

4.2. The Relationship between the Rotation of the Plant Leaf and the Leaf Blade Surface Area

In a theoretical analysis of gas displacement from a gas exchange system of the plant leaf through the leaf stomata, we found that the rotational force created by the displaced gas flow depends on the leaf blade surface area nF. The rotational force increased with an increase in the leaf blade surface area. A higher rotational force must then increase the angular velocity of the plant leaf.

Specially prepared leaves of a broad leaved lime (*Tilia platyphyllos Scop*) with different leaf blade surface areas were used for the experimental tests. The relationship between leaf rotation and leaf blade surface area was tested by applying the same heat generated by a light source. The relationship between leaf rotation and leaf blade surface area is presented in Figure 7, for which the power of the light source was 150 W (luminous lux of 1400 lm). An 11-s interval, for which the relationship between the plant leaf angular velocity and the luminous lux was linear (since the coefficient of determination R^2 is close to 1), was chosen for the analysis. The data in Figure 7 show that when an increased area of the plant leaf is illuminated, the rotation angle also increases; the rotation angle of the plant leaf with an area of 9.2 ± 0.6 cm² reached 44° after 11 s, 16.0 ± 0.8 cm²— 92° , 29.1 ± 1.1 cm²— 143° and 52.5 ± 1.9 cm²— 165° .



Figure 7. Broad leaved lime (*Tilia platyphyllos Scop*) leaf testing results (heat producing source power is 150 W) (n = 6): 1—the curve illustrates the angular velocity in degrees of a plant leaf with active blade surface area of 9.2 ± 0.6 cm²; 2—active blade surface area is 16.0 ± 0.8 cm²; 3—active blade surface area is 29.1 ± 1.1 cm²; 4—active blade surface area is 52.5 ± 1.9 cm². The dashed line marks the 11 s limit.

The largest angular velocity using a 150 W light source was obtained with a leaf with the largest active surface area of 52.5 ± 1.9 cm² (Curve 4, Figure 7). Data analysis with Curve 4 revealed that the biggest leaf reacted the fastest and experienced the greatest change in angular velocity. The reason for faster rotation is a 1.81 times greater leaf blade surface area (52.5/29.1) compared to Curve 3, 3.28 times greater leaf blade surface area (52.5/16.0) compared to Curve 2, and 5.70 times greater leaf blade surface area (52.5/9.2) compared to Curve 1. With a higher leaf blade surface area, the average angular velocity of the leaf changed from 0.070 to 0.262 rad/s (Figure 8).



Figure 8. The relationship between the broad leaved lime (*Tilia platyphyllos Scop*) leaf blade angular velocity and active surface area (n = 6).

The analysis of the change in the average angular velocity of the suspended plant leaf revealed that this change was related to the amount of heat received by the plant leaf. At the regular thermal flux q and with the rotation of the plant leaf at angle α in relation to the light source, the surface area of the leaf receiving the thermal flux q from a 150 W light source reduces. Logically, we may expect that the angular velocity of the leaf will reduce with a lower thermal flux. The calculations of average angular velocities for the leaves with active leaf blade surface areas of $9.2 \pm 0.6 \text{ cm}^2$; $16.0 \pm 0.8 \text{ cm}^2$; 29.1 ± 1.1 and $52.5 \pm 1.9 \text{ cm}^2$ confirmed that the average angular velocity of the leaf drops in accordance with a reduced thermal flux (Figure 8).

4.3. The Relationship between the Rotation of the Plant Leaf and the Power of Heat-Emitting Source

The theoretical analysis of gas displacement of the internal gas exchange system in the leaf through the stomata revealed that the rotational force generated by the outgoing gas flow depended on the gas pressure difference $\Delta p (\Delta p = p_2 - p_1)$. At a higher difference of pressures in the internal gas exchange system of the leaf and in the ambient environment, the rotational force of the leaf increased. The ambient pressure did not change during the investigation. The gas pressure p_1 in the plant leaf stomata and gas circulation framework changed depending on the plant leaf temperature. Plant leaf temperature pulsations caused pressure pulsations in the leaf's gas exchange system. At a higher pressure in the leaf's gas exchange system, the gas displaced into the environment generated a higher reactive force of the outgoing flow acting on the illuminated side of the suspended leaf. Figure 9 illustrates the relationship between the angular velocity of the broad leaved lime (Tilia *platyphyllos Scop*) leaf (active surface area 25.0 ± 1.0 cm²) and the power of light sources at the same light exposure duration. A heat emission duration of 11 s was selected because the function of the plant leaf temperature and supplied heat flow is linear in this period (since the coefficient of determination R^2 is close to 1). It was found that the highest values were achieved when the light source was of higher power. From the research data, it was found that when illuminating a plant leaf with an area of 25.0 ± 1.0 cm² with a 40 W light source, after 11 s, the rotation angle reached 31°, with a 60 W light source—97°, with a 100 W light source—131° and with a 150 W light source—134°. As we can see, the difference between 100 W and 150 W power light sources was 2.2%, so it is believed that the exposure of the leaf to light sources with a higher power than 150 W did not make a considerable difference, because the stomata of the plant leaf no longer possessed a greater angle of rotation.



Figure 9. The relationship between the angular velocity of the broad leaved lime (*Tilia platyphyllos Scop*) leaf (active surface area $25.0 \pm 1.0 \text{ cm}^2$) and the power of heat-emitting source (the length of light source is 11 s): 1—angular velocity of the leaf with 40 W light source; 2—60 W; 3—100 W; 4—150 W. The dashed line marks the 11 s limit.

Calculations of the average angular velocity of the leaf when the power of the light source was 40, 60, 100, and 150 W proved that the angular velocity of the leaf changed with the rotation of the leaf and the change in heat received by the leaf. The data of angular velocities are presented in Figure 10, showing that with the change in the power of the light source, the angular velocity of the leaf changed from 0.049 to 0.213 rad/s.



Figure 10. The relationship between the angular velocity of the broad leaved lime (*Tilia platyphyllos Scop*) leaf (leaf rotation) and the power of light source.

After analyzing the reason for the change in the suspended leaf's angular velocity, it was found to be related to the amount of heat received by the plant leaf and the rotation of the leaf. The decrease in the supplied heat with the turn of the leaf blade may be observed in the diagram presented in Figure 11.



Figure 11. Plant leaf rotation scheme: A—suspended plant leaf; B—heat flow change with plant rotation evaluation diagram; a–a—leaf suspension (rotation) axis; 1—a metal filament from a gal-vanometer; 2—active leaf blade surface area; 3—surface area of a leaf blade covered with heat reflecting coating; 4—light wave reflection mirror to measure the rotation of the leaf; 5—heat flux *q*; 6—plant leaf position (initial) perpendicular to the heat (light) waves; 7—plant leaf position after rotation at angle α .

The reason for the change in the suspended leaf's angular velocity (Figures 8 and 10) was indicated to be related to the amount of heat received by the plant leaf. At the regular thermal (heat) flux q and with the rotation of the plant leaf at angle α in relation to the light source, the surface area of the leaf receiving the thermal flux q from the light source reduced. The drop in the supplied heat with the turn of the leaf blade can be seen in the diagram presented in Figure 11.

The reduced surface area of the active plant leaf blade with the change of the leaf position with respect to the light source at angle α can be calculated using the following Equation:

$$\Delta F_x = F_{xB} - F_{xC} = F(1 - \cos \alpha), \tag{2}$$

where *F* is the plant leaf surface area, in cm^2 ;

 ΔF_x is the reduced surface area of the active plant leaf blade with the change of the leaf position with respect to light source, in cm²;

 F_{xB} , F_{xC} is the projection of the plant leaf surface area in positions 6 and 7 (Figure 11B), in cm²;

 α is the angle of the plant leaf position with respect to light source.

The second reason is the change in the amount of heat absorbed by the leaf in the form of light waves when the leaf rotates with respect to the heat-emitting source. When the leaf rotates with respect to the light source, the rate of heat (light) absorption by the leaf changes because the travelling time of lightwaves in semi-transparent tissues of the leaf increases.

The third reason is related to other factors influencing the rotation of the leaf; however, it is not possible to evaluate the said factors due to the limited scientific information available.

The tests revealed that a suspended (specially prepared) leaf rotates around the suspension axis after it receives the flux of a light source (in the form of light waves) causing a temperature changes in the plant leaf tissues. Leaves with a bigger leaf blade surface area rotate faster due to the greater torque in the suspended leaf system.

5. Discussion

In the case of our research, after keeping the light source on for 11 s (with a 150 W light source it reached 30.7 \pm 0.1 °C, with 100 W—30.0 \pm 0.1 °C and with 60 W—28.3 \pm 0.1 °C) and when the temperature reaches the maximum temperature in the plant leaf, a temperature decrease is observed, which was also described by a study of energy balance presented by Klešnin [50]. According to Merlot et al. [51], leaf temperature depends not only on the water vapor conductivity of stomata, but also on many other environmental and plant variables, including absorbed net radiation, humidity, air temperature, and boundary layer conductivity, which also determine leaf energy balance. In relation to these issues, there is still a debate as to whether the cooling of the leaves is mainly due to convection or transpiration. Classes of stomatal behavior, with the potential to alter stomatal responses to environmental factors, were discussed by Merlot et al. [51] and Daszkowska-Golec and Szarejko [52]. The researchers found that when the protective cells swelled, the stomata opened because the ions and osmolytes in them increased size, which caused them to move away from each other, resulting in an increase in the aperture of the stoma. Conversely, when the closure possesses the opposite mechanism, the protective cells contract when ion leakage occurs [51].

Plant stomatal pairs respond to the environment by facilitating transpiration cooling for mesophilic enzyme activity, CO₂ uptake, and transpiration water loss [53,54]. According to Schymanski et al. [55] and Page et al. [56] it was found that leaf dynamics respond to brief changes in microclimate and lighting. The temperature of the leaves of a plant is thought to be highly dependent on physiological properties [57], and the temperature gradient between leaves and air is paramount to the exchange of water and energy between plants and the atmosphere [56]. In general, some researchers suggest that the dynamics of transpiration vary depending on the climatic zone [58,59] and the time of day and season [60,61]. Additionally, it is further determined by the angle of the sun, the cloud cover, and the shade [62,63], due to the overlapping leaves, different spectral properties, and light intensity [12]. Hartt and Kortschak [64], Urban et al. [3] and Blonder and Michaletz [65] found that the temperature of the leaf tissues of a plant depends on the power of the source used for illumination, which also increases the temperature of the leaf. We confirmed this with our research, which found that the temperature of the leaf and the angle of rotation increase with the increase in the power of the light source, where when illuminating a plant leaf with an area of 25.0 ± 1.0 cm² with a 40 W light source (at the same time radiating heat), after 11 s, the angle of rotation reaches 31° , for a 60 W power light source— 97° , a 100 W power light source—131° and a 150 W power light source—134°. However, we also found that the rotation angles of plant leaves exposed to higher power sources (100 W and 150 W) were not large and reached 2.2%. Thus, it is believed that light sources with increased power (>100 W) acting on the leaves do not provide a considerably greater effect difference, because the stomata of the plant leaf stop developing a greater angle of rotation. Although other studies demonstrated that temperature did not affect stomatal [66,67], Weston and Bauerle [68] and Lahr et al. [69] demonstrated that elevated temperatures caused stomatal closure.

Rapid changes in the flux density of photosynthetic photons allow for rapid changes in leaf temperature, and higher conductivity provides greater vapor cooling and potential protection from heat [12,55]. When sunflower leaves have open stomata, an increase in leaf temperature may increase latent heat flux, but evaporative cooling may simultaneously inhibit the rise in leaf temperature, resulting in a lower constant leaf temperature than when stomata are closed [55]. It was also noted that the amount of leaf water affects the slope of leaf temperature fluctuations and the stomatic conductivity affects the amplitude. Leakey et al. [70] and Schymanski and Zwieniecki [55] found that the internal heat capacity of a leaf failed to significantly reduce the temperature of the leaves. Merlot et al. [51] argued

that leaf temperature can be used as an indicator to detect mutants with altered stomatal control because transpiration causes leaf cooling.

During the experimental studies, it was found that a temperature rise occurred with a linear dependence during the daylight hours, while keeping the light source on for 11 s (60 W; 100 W; 150 W). When analyzing the literature sources, it was observed that regardless of the light source, when the light is turned on, the temperature changes through the layer (temperature kinetics) show an exponential growth [71–73]. However, in the case of our study, the subjects were examined during daylight hours with an additional sudden light source, while in the reviewed literature, the studies were presented for a longer period from dark to light.

Much attention has been paid to the issues of stomatal responses to light sources [74–77]. Studies have shown that the size and density of leaf dentate changed over geological terms, where structural changes are interpreted using gas diffusion theories as improvements in the regulation of gas exchange in plants [17,78-82]. As reported, the reflectance and transmittance spectra of leaves are determined by the following two factors: the absorption of the chemical content, which is related to the wavelength; and repeated reflection, the permeability caused by the light scattering in the leaves, and the absorption that is related to the refractive index and the internal structure of the leaves [83]. Mechanically, when a model of stomatal motion is studied and transpiration is revealed, the diffuse gas flow F (expressed in moles per unit area) through the perforated sheets of the stomatal depends on the driving force (i.e., the difference in concentration along the diffusion path) and the conductivity g (mol $L^{-2} T^{-1}$) of various obstacles between the subatomic cavity and the ambient atmosphere [15]. Studies have been performed even with the developed bionic material and according to Yang et al. [7] spectral and persistence experiments show that the bionic composite reflects almost the same reflectance spectrum as the green leaf reflectance spectrum. However, data on how one responds to various light sourced for the movement of the sheet and when exposed to the heat engine are not provided.

In the case of our research, it can be observed that leaves responds to light sources and this depends on the light output, the flux of a light source, the distance between the source and the plant leaf and the anatomical features of the plant leaf. Our research provides a theoretical basis for the development and exploration for ways to intensify the process of assimilation in plants. Thus, in future we can also model specific technological engineering solutions using the investigated regularities of the plant leaf and the established principles, which could be applied in indoor horticulture, greenhouses, or other contexts.

6. Conclusions

- 1. The presented experimental studies of the rotation of a suspended plant leaf (from the surface area of the plant leaf and the light flux given to the leaf) confirm the theoretical statements about the internal engine of the plant leaf, which activates the assimilation process with its surrounding environment.
- 2. In a natural or artificial environment, the low-potential heat energy is converted into kinetic—mechanical energy of the gas flow in the petiole of the plant leaf. When the energy of the light flow is supplied to the plant leaf, the motor of the plant leaf begins to work, which intensifies the energy and gas exchange with the environment. This is shown by the observed difference between the live plant leaf and simulated plant leaf models, which ranged from 70.3° to 72.7° (72.5–74.9%).
- 3. It was established that after providing the plant leaf with a light source flow (in the form of heat rays) with a power of 150 W and causing a temperature change in the tissues of the plant leaf, the hanging plant leaf rotated around the hanging axis, whereby a plant leaf with an area of $9.2 \pm 0.6 \text{ cm}^2$ had a rotation angle of 44° , $16.0 \pm 0.8 \text{ cm}^2$ — 92° , $29.1 \pm 1.1 \text{ cm}^2$ — 143° and $52.5 \pm 1.9 \text{ cm}^2$ — 165° . As the plant leaf area increased, so did the angular rotation speed, which ranged from 0.070-0.262 rad/s, respectively.
- 4. By analyzing the influence of light sources on the rotation angle of a plant leaf, it was found that when illuminating a plant leaf with an active leaf area of $25.0 \pm 1.0 \text{ cm}^2$

with a 40 W light source, after 11 s, the rotation angle reaches 31° , with a 60 W light source it reaches 97° , with a 100 W light source it reaches 131° and with a 150 W light source it reaches 134° . When the power of the light source changes from 40 to 150 W, the angular rotation speed of the plant leaf also changes—0.049–0.213 rad/s.

Author Contributions: Author Contributions: Conceptualization, T.Ū. and P.A.S.; methodology, T.Ū. and P.A.S.; investigation, T.Ū.; data curation, T.Ū., S.P. and R.Č.; writing—original draft preparation, T.Ū. and P.A.S.; writing—review and editing, T.Ū., S.P. and R.Č.; visualization, T.Ū. and S.P. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

References

- 1. Sirvydas, P.A.; Kucinskas, V.; Kerpauskas, P.; Uksas, T. The Principle of Transforming the Solar Energy to Mechanical Energy in the Plant Leaf Stomata Engine. *Energetika* 2014, *60*, 19–26.
- 2. Kramer, P.J.; Boyer, J.S. Stomata and Gas Exchange. In *Water Relations of Plants and Soils*; Chapter 8; Academic Press, Inc.: Cambridge, MA, USA, 1995; pp. 257–282.
- Urban, J.; Ingwers, M.W.; McGuire, M.A.; Teskey, R.O. Increase in Leaf Temperature Opens Stomata and Decouples Net Photosynthesis from Stomatal Conductance in Pinus Taeda and Populus Deltoides X Nigra. J. Exp. Bot. 2017, 68, 1757–1767. [CrossRef] [PubMed]
- Chen, Z.; Chen, G.; Dai, F.; Wang, Y.; Hills, A.; Ruan, Y.; Zhang, G.; Franks, P.J.; Nevo, E.; Blatt, M.R. Molecular Evolution of Grass Stomata. *Trends Plant Sci.* 2017, 22, 124–139. [CrossRef]
- 5. Ye, H.; Yuan, Z.; Zhang, S. The Heat and Mass Transfer Analysis of a Leaf. J. Bionic Eng. 2013, 10, 170–176. [CrossRef]
- 6. Yuan, Z.; Ye, H.; Li, S. Bionic Leaf Simulating the Thermal Effect of Natural Leaf Transpiration. J. Bionic Eng. 2014, 11, 90–97. [CrossRef]
- Yang, Y.; Liu, Z.; Hu, B.; Man, Y.; Wu, W. Bionic Composite Material Simulating the Optical Spectra of Plant Leaves. J. Bionic Eng. 2010, 7, S43–S49. [CrossRef]
- He, J.; Mao, M.; Li, D.; Liu, Y.; Jin, Z. Characterization of Leaf-Inspired Microfluidic Chips for Pumpless Fluid Transport. J. Bionic Eng. 2014, 11, 109–114. [CrossRef]
- 9. Peng, Y.; Liu, W.; Chen, W.; Wang, N. A Conceptual Structure for Heat Transfer Imitating the Transporting Principle of Plant Leaf. Int. J. Heat Mass Transf. 2014, 71, 79–90. [CrossRef]
- 10. Faisal, T.R.; Khalil Abad, E.M.; Hristozov, N.; Pasini, D. The Impact of Tissue Morphology, Cross-Section and Turgor Pressure on the Mechanical Properties of the Leaf Petiole in Plants. *J. Bionic Eng.* **2010**, *7*, S11–S23. [CrossRef]
- 11. Wang, S.; Ren, L.; Liu, Y.; Han, Z.; Yang, Y. Mechanical Characteristics of Typical Plant Leaves. J. Bionic Eng. 2010, 7, 294–300. [CrossRef]
- Vialet-Chabrand, S.R.M.; Matthews, J.S.A.; McAusland, L.; Blatt, M.R.; Griffiths, H.; Lawson, T. Temporal Dynamics of Stomatal Behavior. *Plant Physiol.* 2017, 174, 603–613. [CrossRef]
- Matthews, J.S.A.; Vialet-Chabrand, S.; Lawson, T. Acclimation to Fluctuating Light Impacts the Rapidity of Response and Diurnal Rhythm of Stomatal Conductance. *Plant Physiol.* 2018, 176, 1939–1951. [CrossRef] [PubMed]
- 14. Woolfenden, H.C.; Baillie, A.L.; Gray, J.E.; Hobbs, J.K.; Morris, R.J.; Fleming, A.J. Models and Mechanisms of Stomatal Mechanics. *Trends Plant Sci.* 2018, 23, 822–832. [CrossRef] [PubMed]
- 15. Lehmann, P.; Or, D. Effects of Stomata Clustering on Leaf Gas Exchange. New Phytol. 2015, 207, 1015–1025. [CrossRef] [PubMed]
- 16. Dow, G.J.; Berry, J.A.; Bergmann, D.C. The Physiological Importance of Developmental Mechanisms that Enforce Proper Stomatal Spacing in Arabidopsis Thaliana. *New Phytol.* **2014**, 201, 1205–1217. [CrossRef] [PubMed]
- Franks, P.J.; Berner, R.A.; Beerling, D.J. Maximum Leaf Conductance Driven by CO₂ Effects on Stomatal Size and Density Over Geologic Time. *Proc. Nat. Acad. Sci. USA* 2009, 106, 10343–10347. [CrossRef]
- 18. Zarinkamar, F. Stomatal Observations in Dicotyledons. Pak. J. Biol. Sci. 2007, 10, 199–219. [CrossRef]
- 19. Drake, P.L.; Froend, R.H.; Franks, P.J. Smaller, Faster Stomata: Scaling of Stomatal Size, Rate of Response, and Stomatal Conductance. *J. Exp. Bot.* **2013**, *64*, 495–505. [CrossRef]
- 20. Nobel, P.S. Physicochemical and Environmental Plant Physiology; Elsevier Science & Technology: London, UK, 2005.
- 21. Šlapakauskas, V. Augalų Ekofiziologija; Lututė: Kaunas, Lithuania, 2006; p. 413.
- 22. Düring, H. Stomatal and Mesophyll Conductances Control CO2 Transfer to Chloroplasts in Leaves of Grapevine (*Vitis Vinifera* L.). *Vitis Geilweilerhof* **2003**, 42, 65–68.

- Voelker, S.L.; Brooks, J.R.; Meinzer, F.C.; Anderson, R.; Bader, M.K.-F.; Battipaglia, G.; Becklin, K.M.; Beerling, D.; Bert, D.; Betancourt, J.L.; et al. A Dynamic Leaf Gas-Exchange Strategy is Conserved in Woody Plants Under Changing Ambient CO₂: Evidence from Carbon Isotope Discrimination in Paleo and CO2 Enrichment Studies. *Glob. Chang. Biol.* 2016, 22, 889–902. [CrossRef]
- Ache, P.; Bauer, H.; Kollist, H.; Al-Rasheid, K.A.S.; Lautner, S.; Hartung, W.; Hedrich, R. Stomatal Action Directly Feeds Back on Leaf Turgor: New Insights into the Regulation of the Plant Water Status from Non-invasive Pressure Probe Measurements. *Plant J. Cell Mol. Biol.* 2010, 62, 1072–1082. [CrossRef] [PubMed]
- 25. Rahnama, A.; James, R.A.; Poustini, K.; Munns, R. Stomatal Conductance as a Screen for Osmotic Stress Tolerance in Durum Wheat Growing in Saline Soil. *Funct. Plant Biol. FPB* **2010**, *37*, 255. [CrossRef]
- Cano, F.J.; Sanchez-Gomez, D.; Rodrigues-Calcerrada, J.; Warren, C.R.; Gil, L.; Ismael, A. Effects of Drought on Mesophyll Conductance and Photosynthetic Limitations at Different Tree Canopy Layers. *Plant Cell Environ.* 2013, 36, 1961–1980. [CrossRef] [PubMed]
- 27. Fanourakis, D.; Bouranis, D.; Giday, H.; Carvalho, D.R.A.; Rezaei Nejad, A.; Ottosen, C. Improving Stomatal Functioning at Elevated Growth Air Humidity: A Review. J. Plant Physiol. 2016, 207, 51–60. [CrossRef]
- Varela, S.A.; Weigandt, M.N.; Willems, P.; Bianchi, E.; Diez, J.P.; Gyenge, J.E. Physiological Status of Conifer Seedlings Treated with Radiation, Drought and Frost Stress Mitigation Techniques: A Laboratory Assessment. New For. 2015, 47, 87–103. [CrossRef]
- Kim, H.; Goins, G.D.; Wheeler, R.M.; Sager, J.C. Stomatal Conductance of Lettuce Grown Under or Exposed to Different Light Qualities. Ann. Bot. 2004, 94, 691–697. [CrossRef]
- 30. Hedrich, R.; Shabala, S. Stomata in a Saline World. Curr. Opin. Plant Biol. 2018, 46, 87–95. [CrossRef]
- 31. Jarvis, P.G. Stomatal Physiology; Cambridge University. Press: Cambridge, UK, 1981.
- 32. Willmer, C.; Fricker, M. Stomata; Springer: Berlin/Heidelberg, Germany, 2012.
- 33. Lambers, H.; Oliveira, R.S. Plant Physiological Ecology, 3rd ed.; Springer: Cham, Switzerland, 2019.
- 34. Franks, P.J.; Farquhar, G.D. The Effect of Exogenous Abscisic Acid on Stomatal Development, Stomatal Mechanics, and Leaf Gas Exchange in Tradescantia Virginiana. *Plant Physiol.* **2001**, *125*, 935–942. [CrossRef]
- Boer, H.J.; Price, C.A.; Wagner-Cremer, F.; Dekker, S.C.; Franks, P.J.; Veneklaas, E.J. Optimal Allocation of Leaf Epidermal Area for Gas Exchange. New Phytol. 2016, 210, 1219–1228. [CrossRef]
- 36. Švenčianas, P.; Adomavičius, A. Inžinerinė Termodinamika; Technologija: Kaunas, Lithuania, 2011; p. 308.
- 37. Hetherington, A.M.; Woodward, F.I. The Role of Stomata in Sensing and Driving Environmental Change. *Nature* 2003, 424, 901–908. [CrossRef]
- Shimazaki, K.; Doi, M.; Assmann, S.M.; Kinoshita, T. Light Regulation of Stomatal Movement. Ann. Rev. Plant Biol. 2007, 58, 219–247. [CrossRef] [PubMed]
- Harrison, E.L.; Arce Cubas, L.; Gray, J.E.; Hepworth, C. The Influence of Stomatal Morphology and Distribution on Photosynthetic Gas Exchange. *Plant J.* 2020, 101, 768–779. [CrossRef] [PubMed]
- 40. Planck, M. Treatise on Thermodynamics; Dover Publications: Dover, UK, 1987.
- 41. Moran, M.J. Fundamentals of Engineering Thermodynamics, 8th [revised] ed.; Wiley: Hoboken, NJ, USA, 2014.
- Drobavičius, A.; Garbavičius, J.; Gimbutis, G.S.; Kajutis, K.; Krukonis, V. Bendroji Šiluminė Technika; Mintis: Vilnius, Lithuania, 1974; p. 572.
- Von Caemmerer, S.; Farquhar, G.D. Some Relationships between the Biochemistry of Photosynthesis and the Gas Exchange of Leaves. *Planta* 1981, 153, 376–387. [CrossRef]
- 44. Ziegler, H. The evolution of stomata. In *Stomatal Function*; Zeiger, E., Farquhar, G.D., Cowan, I.R., Eds.; Stanford University Press: Stanford, CA, USA, 1987; pp. 29–57.
- Franks, P.J.; Farquhar, G.D. The Mechanical Diversity of Stomata and its Significance in Gas-Exchange Control. *Plant Physiol.* 2007, 143, 78–87. [CrossRef]
- 46. Gimbutis, G.; Kajutis, K.; Krukonis, V. Šiluminė Technika; Mokslas: Vilnius, Lithuanisa, 1993.
- 47. Van Wylen, G.J.; Sonntag, R.E. Fundamentals of Classical Thermodynamics, 2ed. ed.; Wiley: New York, NY, USA, 1973.
- 48. Martinaitis, V. Techninė Termodinamika ir Šilumokaita; Technika: Vilnius, Lithuania, 2003; p. 163.
- 49. Baehr, H.D. *Thermodynamik*, 3rd ed.; Springer: Berlin/Heidelberg, Germany, 1973; p. 440.
- 50. Kleshnin, A.F. Die Pflanze und das Licht. Neu bearbeitete und ergänzte Ausgabe; Akademie–Verlag: Berlin, Germany, 1960; p. 620.
- Merlot, S.; Mustilli, A.; Genty, B.; North, H.; Lefebvre, V.; Sotta, B.; Vavasseur, A.; Giraudat, J. Use of Infrared Thermal Imaging to Isolate Arabidopsis Mutants Defective in Stomatal Regulation. *Plant J. Cell Mol. Biol* 2002, 30, 601–609. [CrossRef] [PubMed]
- 52. Daszkowska-Golec, A.; Szarejko, I. Open or Close the Gate—Stomata Action Under the Control of Phytohormones in Drought Stress Conditions. *Front. Plant Sci.* 2013, *4*, 138. [CrossRef]
- Meinzer, F.C.; McCulloh, K.A. Xylem Recovery from Drought-Induced Embolism: Where is the Hydraulic Point of no Return? Tree Physiol. 2013, 33, 331–334. [CrossRef]
- Brodribb, T.J.; McAdam, S.A.M.; Jordan, G.J.; Martins, S.C.V. Conifer Species Adapt to Low-Rainfall Climates by Following One of Two Divergent Pathways. Proc. Nat. Acad. Sci. USA 2014, 111, 14489–14493. [CrossRef]
- Schymanski, S.J.; Or, D.; Zwieniecki, M. Stomatal Control and Leaf Thermal and Hydraulic Capacitances Under Rapid Environmental Fluctuations. *PLoS ONE* 2013, *8*, e54231. [CrossRef]

- 56. Page, G.F.M.; Liénard, J.F.; Pruett, M.J.; Moffett, K.B. Spatiotemporal Dynamics of Leaf Transpiration Quantified with Time-Series Thermal Imaging. *Agric. For. Meteorol.* **2018**, 256–257, 304–314. [CrossRef]
- 57. Berry, J.; Bjorkman, O. Photosynthetic Response and Adaptation to Temperature in Higher Plants. *Ann. Rev. Plant Physiol.* **1980**, 31, 491–543. [CrossRef]
- Wang, L.; Good, S.P.; Caylor, K.K. Global Synthesis of Vegetation Control on Evapotranspiration Partitioning. *Geophys. Res. Lett.* 2014, 41, 6753–6757. [CrossRef]
- Wang, R.; Yu, G.; He, N.; Wang, Q.; Zhao, N.; Xu, Z.; Ge, J. Latitudinal Variation of Leaf Stomatal Traits from Species to Community Level in Forests: Linkage with Ecosystem Productivity. Sci. Rep. 2015, 5, 14454. [CrossRef]
- Assmann, S.M.; Wang, X. From Milliseconds to Millions of Years: Guard Cells and Environmental Responses. *Curr. Opin. Plant Biol.* 2001, 4, 421–428. [CrossRef]
- 61. Dubbert, M.; Piayda, A.; Cuntz, M.; Correia, A.C.; Costa E Silva, F.; Pereira, J.S.; Werner, C. Stable Oxygen Isotope and Flux Partitioning Demonstrates Understory of an Oak Savanna Contributes Up to Half of Ecosystem Carbon and Water Exchange. *Front. Plant Sci.* **2014**, *5*, 530. [CrossRef] [PubMed]
- 62. Chazdon, R.L.; Pearcy, R.W. The Importance of Sunflecks for Forest Understory Plants. Bioscience 1991, 41, 760–766. [CrossRef]
- Way, D.A.; Pearcy, R.W. Sunflecks in Trees and Forests: From Photosynthetic Physiology to Global Change Biology. *Tree Physiol.* 2012, 32, 1066–1081. [CrossRef]
- 64. Hartt, C.E.; Kortschak, H.P. Translocation of 14C in the Sugarcane Plant during the Day and Night. *Plant Physiol.* **1967**, *42*, 89–94. [CrossRef]
- 65. Blonder, B.; Michaletz, S.T. A Model for Leaf Temperature Decoupling from Air Temperature. *Agric. For. Meteorol.* **2018**, 262, 354–360. [CrossRef]
- Cerasoli, S.; Wertin, T.; McGuire, M.A.; Rodrigues, A.; Aubrey, D.P.; Pereira, J.S.; Teskey, R.O. Poplar Saplings Exposed to Recurring Temperature Shifts of Different Amplitude Exhibit Differences in Leaf Gas Exchange and Growth Despite Equal Mean Temperature. *AoB Plants* 2014, *6*, 2014. [CrossRef]
- von Caemmerer, S.; Evans, J.R. Temperature Responses of Mesophyll Conductance Differ Greatly between Species. *Plant Cell Environ.* 2015, 38, 629–637. [CrossRef] [PubMed]
- Weston, D.J.; Bauerle, W.L. Inhibition and Acclimation of C(3) Photosynthesis to Moderate Heat: A Perspective from Thermally Contrasting Genotypes of Acer Rubrum (Red Maple). *Tree Physiol.* 2007, 27, 1083–1092. [CrossRef] [PubMed]
- 69. Lahr, E.C.; Schade, G.W.; Crossett, C.C.; Watson, M.R. Photosynthesis and Isoprene Emission from Trees Along an Urban-Rural Gradient in Texas. *Glob. Chang. Biol.* 2015, 21, 4221–4236. [CrossRef]
- Leakey, A.D.B.; Scholes, J.D.; Press, M.C. Physiological and Ecological Significance of Sunflecks for Dipterocarp Seedlings. J. Exp. Bot. 2005, 56, 469–482. [CrossRef] [PubMed]
- 71. Kaňa, R.; Vass, I. Thermoimaging as a Tool for Studying Light-Induced Heating of Leaves Correlation of Heat Dissipation with the Efficiency of Photosystem II Photochemistry and Non-Photochemical Quenching. *Environ. Exp. Bot.* **2008**, *64*, 90–96. [CrossRef]
- 72. Vialet-Chabrand, S.; Lawson, T. Dynamic Leaf Energy Balance: Deriving Stomatal Conductance from Thermal Imaging in a Dynamic Environment. J. Exp. Bot. 2019, 70, 2839–2855. [CrossRef]
- Bajons, P.; Klinger, G.; Schlosser, V. Determination of Stomatal Conductance by Means of Infrared Thermography. *Infrared Phys. Technol.* 2005, 46, 429–439. [CrossRef]
- 74. Karlsson, P.E.; Assmann, S.M. Rapid and Specific Modulation of Stomatal Conductance by Blue Light in Ivy (*Hedera Helix*): An Approach to Assess the Stomatal Limitation of Carbon Assimilation. *Plant Physiol.* **1990**, *94*, 440–447. [CrossRef]
- Grantz, D.A.; Assmann, S.M. Stomatal Response to Blue Light: Water use Efficiency in Sugarcane and Soybean. *Plant Cell Environ*. 1991, 14, 683–690. [CrossRef]
- Assmann, S.M.; Lee, D.M.; Malkus, P. Rapid Stomatal Response to Redlight in Zea Mays. *Photochem. Photobiol.* 1992, 56, 685–689. [CrossRef]
- 77. Lawson, T.; von Caemmerer, S.; Baroli, I. Photosynthesis and Stomatal Behaviour. In *Progress in Botany* 72; Springer: Berlin/Heidelberg, Germany, 2010; pp. 265–304.
- 78. Raven, J.A. Selection Pressures on Stomatal Evolution. New Phytol. 2002, 153, 371–386. [CrossRef] [PubMed]
- Berry, J.A.; Beerling, D.J.; Franks, P.J. Stomata: Key Players in the Earth System, Past and Present. *Curr. Opin. Plant Biol.* 2010, 13, 232–239. [CrossRef] [PubMed]
- De Boer, H.J.; Lammertsma, E.I.; Wagner-Cremer, F.; Dilcher, D.L.; Wassen, M.J.; Dekker, S.C. Climate Forcing due to Optimization of Maximal Leaf Conductance in Subtropical Vegetation Under Rising CO. *Proc. Nat. Acad. Sci. USA* 2011, 108, 4041–4046. [CrossRef] [PubMed]
- Assouline, S.; Or, D. Plant Water use Efficiency Over Geological Time—Evolution of Leaf Stomata Configurations Affecting Plant Gas Exchange. PLoS ONE 2013, 8, e67757. [CrossRef]
- 82. Buckley, T.N.; Schymanski, S.J. Stomatal Optimisation in Relation to Atmospheric CO2. New Phytol. 2014, 201, 372–377. [CrossRef]
- 83. Woolley, J.T. Reflectance and Transmittance of Light by Leaves. Plant Physiol. 1971, 47, 656–662. [CrossRef]