

STOMATA-A KEY FACTOR WITH MULTIPLE FUNCTIONS IN THE CONDITIONS OF GLOBAL CLIMATE CHANGE: A BRIEF OVERVIEW

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Abstract

The main components of climate change are carbon dioxide from the atmosphere, air temperature and drought. Considering the major changes of these parameters over time, nowadays especially, but also in the future, in order to cope properly with the new conditions, it is necessary to adjust the photosynthesis process in the sense of increasing its intensity and improving of water use efficiency. Because the stomata are formations of the epidermis involved in the process of carbon dioxide absorption (raw material in photosynthesis) and in its release (in the case of the respiration process), as well as in the release of water vapor during the transpiration, their behavior become defining for what it means not only the plants existence and their good functioning, but stomata influence is also extended and is not limited to just that. Besides the special importance for the physiological processes of plants, for plants own existence and good functioning, stomata also have significant effects for what the concentration of gases in the lower troposphere means and more than that, they can represent risks for vegetation or for human health. In view of the above, the purpose of this mini-synthesis is to present some new information on the central role played by stomata and especially their conductance property, under the conditions of climate change, in relation to the impact on plant productivity, on the carbon cycle in nature, as well as on water flow, but also on human health, with special reference to the conditions specific to the urban environment.

Key words: climate change, stomata, plant productivity, water use efficiency, carbon cycle, human health

INTRODUCTION

Global warming is a concept, but also a reality of today, as a result of multiple generating effects (e.g. anthropogenic activities which increase greenhouse gas emissions, as the increase in carbon dioxide) and it is well known that environmental climate change will influence our future [11], [48].

The main components of climate change are carbon dioxide from the atmosphere, air temperature and drought. Their changes will result in plants experiencing multiple co-occurring environmental stress factors and which require further studies [43].

As Xu et al. [56] mentioned, based on a more undisciplined management scenario, according to the Representative Concentration Pathway (RCP8.5) of Intergovernmental Panel on Climate Change (IPCC 2013), there has been a continuous increase in carbon dioxide concentration from $280 \mu\text{mol mol}^{-1}$ in 1750, to $400 \mu\text{mol mol}^{-1}$, today. It is also expected that it will reach a value of around $900 \mu\text{mol mol}^{-1}$ by the end of the 21st century. At the

same time, it is estimated that the temperature will increase with $2.6\text{--}4.8^\circ\text{C}$ at the end of this century.

Consequently, along the time, this topic has been the subject of numerous discussions, scientific conferences, and public policy debates in some countries [46], [44], being taken into consideration also the effects and reactions that these changes can have at the level of individual, communities and societies, as a whole [20]. As mentioned by Dryzek et al. [17], the subject begins with science, which initially identified the climatic change problem and continues with how it is received by society and government.

In addition to the global impact, the problem of increasing carbon dioxide is also worrying the scientific community, about the need to study plants morpho-physiological disorders that may have direct effects on photosynthesis. These include the changes that may occur in the cuticular waxes, as well as the response to the development of stomata, as a consequence of the chemical changes in the atmosphere [35].

Stomata complexes (as the “gatekeepers”) [31] are specialized formations located on the epidermis of leaves and plant stems, having as a main role the control of the gas exchanges between the plant and the environment [26], [55], namely the release of water vapors and the absorption of carbon dioxide (CO_2). The characteristics of these complexes are different in relation to the species' specificity, but the differences are also due to the specific environmental conditions, to which the stomata exhibit a strong sensitivity [58]. This control depends on the degree of opening of the stoma (ostiole), but also on the density of the stomata, and implicitly has consequences on gas exchanges in plants [39]. Both characteristics are under the influence of environmental factors on the one hand and on the other hand under internal control, especially a hormonal one [26]. Moreover, the regulation of the degree of opening of the ostiole is actively carried out by numerous abiotic and biotic factors, which has significant global implications on evapotranspiration and on the carbon cycles [33].

Taking into account the fact that through the stomata a high proportion of gas exchanges between the leaf and the environment is ensured (95%), the preoccupations to reduce water losses and implicitly to improve the water use efficiency (WUE) should be considered. Beside WUE, another major indicator of the ability of plants to adapt to climate change (e.g. precipitation, temperature) is the carbon use efficiency (CUE) [15], cited by Masri et al. [37], as a ratio between the rate of net carbon uptake (net primary production) and gross carbon uptake (gross primary production).

Stomata manipulation represents an effective means to achieve these major objectives of the current period, characterized by the reduction of water availability [31], next to other new technologies, comprised in the concept of “smart” agriculture [22].

Besides the special importance of the physiological processes of plants, for their own existence and good functioning, stomata also have significant effects for what the concentration of gases in the lower

troposphere means and more than that, they can represent risks for vegetation or for human health [2].

In view of the above, the purpose of this mini-synthesis is to present some new information on the central role played by stomata and especially their conductance property, under the conditions of climate change, in relation to the impact on plant productivity, on the carbon cycle in nature, on water flow, but not at the end on human health, with special reference to the conditions specific to the urban environment.

MATERIALS AND METHODS

This short bibliographic synthesis has been elaborated mainly on the basis of scientific information present in recent publications, indexed in internationally recognized databases. The data relevant to the topic of interest were systematized and discussed, so that finally some conclusions were drawn regarding the importance of the topic under discussion, as well as the need to approach it with interest in future research.

RESULTS AND DISCUSSIONS

The behavior of the stomata in the case of high temperatures

Progress has been made regarding the assessment of the consequences of drought on terrestrial plants and of the effects of climatic achievements on the functions at the ecosystem level. So, recent discoveries lead to the need to revise current opinions on the functional coordination between stomata and their hydraulic characteristics and respectively to offer a mechanistic framework for modeling plant mortality under drought conditions [36].

At the same time, Sperry et al. [49] succeeded on the basis of several mathematical formulas, in which they included different characteristics, to argue and quantitatively demonstrate the concept of a new and synthetic model regarding the stomata responses at the leaf level scale. As Wolf et al. [54] pointed out, several physiologically based stomata algorithms have the potential to

improve the simulation of carbon, water and energy flows in some models, which leads to increased confidence in the systems for predicting vegetation response to extreme climate change.

Local species are the ones that help maintain the functioning of the ecosystem and studies carried out by Craine et al. [12] suggest that different grasslands around the globe have the potential to withstand drought, if species tolerant to this abiotic stress factor are widespread locally. Moreover, Gago et al. [22] noticed that within the “smart” agriculture, for a more efficient use of water, among the new technologies applied, those designed to regulate the irrigation program (such as innovative technologies “Unmanned Aerial Vehicles – UAVs” equipped with remote sensors, to scale up levels from leaf to whole plant water status) are of interest, too. Their studies opened the challenge for the multidisciplinary and integrative approach of the concept of WUE.

As a result of climatic change, there was registered an increase in the frequency, magnitude and duration of the heat waves [41]. Thus, the climatic models, such as those in the Coupled Model Intercomparison Project (CMIP5) highlight the significant increase in the frequency and severity of these extremes [28]. So, urgent understanding the mechanisms that lead to these undesirable results is required [14].

The stomata control of energy, water and carbon dioxide flows is a key component in terms of vegetation and atmosphere, coupling within the models of terrestrial systems. In this context, Bonan et al. [7] presented a framework for modeling the stomata conductance, which includes the connections between the gas exchanges that take place at the leaf level, the hydraulic constraints at the plant level, and the soil-plant-atmosphere system. The purpose of such a model was that of optimizing the photosynthetic carbon gain, on the unit of water loss, simultaneously avoiding dehydration caused by a low potential of water at the leaf level. With a view to a more robust modeling of carbon and water cycles, the recommendation of Masri et al. [37], for those dealing with this aspect is to

re-examine the patterns of stomata conductance and soil-vegetation interactions. As De Kauwe et al. [13] mentioned, in climatic models such as the CMIP5 model, the land surface is represented by modules in which photosynthesis and transpiration (via stomata conductance) are inherently coupled. Practically: the high temperatures cause the reduction of the rate of photosynthesis due to the direct effects on the enzymatic phase of the photosynthesis; intensification of the respiration process takes place; the stomata conductance decreases due to an increased of vapor pressure deficit value. In addition to the above, De Kauwe et al. [14] specified that finding additional evidence regarding the decoupling of photosynthesis from stomata conductance (reducing photosynthesis to near zero, but increasing transpiration into the boundary layer) in the case of elevated temperatures would involve revising the hypotheses existing in current climate models, with no negligible implications for developments based on the role of the land surface in amplifying temperature extremes. Genetic engineering is an effective means to improve the tolerance of plants to heat stress. For example, in rice leaf blade, the strong expression of OsMDHAR4 (monodehydroascorbate reductase) protein (a key enzyme in the maintenance of the ascorbate acid pool through the ascorbate acid - glutathione cycle) was identified in chloroplast, due to heat treatment. Unlike the wild type, the osmdhar4 mutant expressed an improved tolerance to heat stress, while OsMDHAR4 overexpression line showed enhanced sensitivity to heat stress. Also, in the rice leaves, the authors found that suppression of the gene OsMDHAR4 indicated the closing of the stomata and the accumulation of hydrogen peroxide. An overexpression of this gene caused an increase of the degree of openness of the stomata, while the hydrogen peroxide content decreased [34]. Moreover, they found that suppression of OsMDHAR4 promoted stomata closure and hydrogen peroxide accumulation, while overexpression of OsMDHAR4 increased stomata opening and

decreased hydrogen peroxide content in rice leaves.

Under climatic changes, worldwide, at the level of agriculture it is registered an increase in the combined incidence of drought and thermal stress [57]. Temperature changes in the direction of their increase are a factor that affects inclusive stomata conductance. Although high temperatures would be expected to result in decreased of stomata conductance due to a decreased of leaf water potential and increased transpiration, Urban et al. [51] studies have highlighted an increase in stomata conductance for poplar (*Populus deltoides x nigra*) and loblolly pine (*Pinus taeda*) at an increase in temperature by 10 °C, from 30°C to 40°C, at a constant vapor pressure deficit of 1 kPa. In part, the authors' explanation was that at high temperatures the degree of viscosity at the xylem and mesophyll solution was decreased, which increased conductivity. The beneficial effect on the plant of increasing the stomata conductance is to maintain the proper temperature, thanks to the intensification of transpiration.

Plant species respond differently to temperature increase, as demonstrated also in two dominant tree species of the subtropical forest [53]. Thus, although there are changes in the stomata morphology and sensitivity to water deficiency, the species *Schima superba* found a conservative strategy, that is, a reduction in stomata density, but a constant maintenance of the stomata size, as a possible measure to prevent the loss of water and at the same time with the cost of reducing carbon gain. However, in *Syzygium rehderianum*, a balance has been achieved between what is the loss of water by transpiration and the absorption of carbon dioxide, by reducing the stomata size, but without affecting their density. Such behavior allowed the photosynthesis process to unfold even under high temperature conditions.

As Le et al. [32] emphasized, in the conditions of the climatic changes due to the increase of the temperature and of the precipitation reduction during the summer, an increase of the evapotranspiration for all the cultures is registered, with impact of reducing the water

storage in the soil, as well as of the surface runoff. This also causes changes in the water cycle, as evidenced when the maize crop expanded to meet the demand for bioenergy has been replaced by miscanthus and switchgrass, that use more water for total evapotranspiration per season, by approximately 58% and 36%, respectively, as compared to maize.

Different behavior was found by Zhu et al. [39] too, respectively an increase in the plant stomata density and its shape index under urban conditions, as the temperature increased, while the stomata area decreased significantly. And in this case, plants resort to an ecological compensation strategy to adapt to the particular growing environmental conditions.

The negative impact of temperature increase on photosynthetic efficiency and on the physiology of stomata has been recently demonstrated in olive [25]. A marked reduction of RuBisCO enzyme activity, a deterioration in photosystem II, as well as a reduction of stomata conductance was determined. Therefore, the authors recommended the selection of olive varieties with a higher tolerance to thermal stress, as well as strategies to avoid the impact of high temperatures, in the context of developing a sustainable agriculture in the Mediterranean area.

The results obtained by Anav et al. [2] can be used to improve the representation of the effects of soil water stress on vegetation, with chemical transport models and for a better description of biogeochemical and biophysical feedbacks, within the soil-plant-atmosphere complex system, in response to the climate changes that lead to the existence of higher temperatures and conditions of increased drought.

As Chaves et al. [10] noticed, because the dilemma of "carbon compromise and leaf temperature" must be considered, in the case of semi-arid areas, genotypes that can simultaneously meet several requirements would be appropriate to successfully cope with the action of high temperatures: 1. to have the capacity to maximize the absorption of water from the soil (either through the

presence of a vigorous root system and / or the use of suitable rootstocks); 2. to have the ability to regulate the stomata conductance, so as to allow the amount of water lost through transpiration to be reduced, to the unit of carbon fixed (to be characterized by an increased of WUE) and at the same time to ensure the optimization of the water use in relation to the growth cycle phase; 3. to adjust the surface of the vegetal carpet according to the available water; 4. to exhibit characteristics that they allow the avoidance of heat (such as paraheliotropic movements) or heat resistance, at the level of the leaf mesophyll level; 5. to maintain cool canopies in case of irrigation application, in order to cope with periods of enhanced temperatures.

The behavior of the stomata in the case of high CO₂ level

At the plant level as an organism, the stomata are a major factor in the control of water loss and carbon dioxide absorption, respectively and at the ecosystem level they represent the main constraint regarding the continuous flow of water within the soil-plant-atmosphere system. Thus, an increase in CO₂ concentration modifies the stomata conductance and water use of plants, which may have a considerable effect on the hydrological cycle [27]. Therefore, for the future management of water resources, especially in the water-limited areas, it is necessary to treat with interest the responses of different plants and the hydrological cycle that lead to the increase of CO₂ in the dry and wet areas. The overall estimates of the conductance of the plant carpet and of the evapotranspiration are of particular importance in terms of realigning the water cycle in nature and the energy partition [47].

Stomata conductance has major influences on photosynthesis and handling this feature can improve crop productivity and yield. Therefore, the natural variation of this feature and the identification of genomic regions involved may represent unexploited targets in future plant breeding programs [21].

Although known and accepted for a long time (about 40 years), the theory regarding the opening of the stomata until the carbon obtained balances the water lost during that

time, is not in accordance with the competition for water between plants. Wolf et al. [54] developed an alternative theory according to which plants can maximize carbon gain without reducing water loss. Both theories, both the classic and the latter, are added two characteristics: 1. water flow through xylem that can be adversely affected as the water potential in xylem decreases; 2. the costs of feeding with carbon due to the reduced potential of the water, in combination with other mechanisms, which include the restoration of the damage caused at the xylem level. The authors have mentioned that the last alternative for carbon-maximization optimization is consistent with plant competition, because it yields an evolutionary stable strategy (ESS) - species, with the ESS stomata behavior that will outcompete all others.

Generally, an increase in carbon dioxide levels leads to a decrease in stomata conductivity, but also to stomata density [5] which can reduce the use of water by vegetation and can affect the climate [8]. Moreover, this behavior is a well-known response, characteristic of C3-type plants, which manages to reduce water losses, while maintaining the process of carbon dioxide absorption [30]. If from the point of view of the fixation of carbon dioxide during the photosynthesis, an increased of its concentration in the environment becomes limiting due to the decrease of the stomata conductance, at the same time it can increase the WUE. As a result, the growth of plants can be favoured, even in the context of climate change, which is associated with an increase in periods of water shortage [50]. The significantly improvement of the functioning of a tropical forage species grown in the field was also suggested by the results obtained by Habermann et al. [24], under elevated atmospheric carbon dioxide concentration, combined with a warmer environment. In this case, the stomata opening control and stomata anatomy were mainly due by elevated CO₂, and warming influence was noticed especially on photosystem II activity, as well as on antioxidant system, as a mean to defence to abiotic stress, such as drought.

An absolute necessity is to know whether manipulation of the stomata guard cells (in terms of the balance between carbon dioxide absorption and water loss by transpiration) to improve the response to increased carbon dioxide concentration can lead to increased photosynthesis efficiency [55]. In this context, a positive result was obtained by Dunn et al. [19] in wheat, where the expression of genes for manipulation of epidermal patterning factor (EPF) was achieved by reducing the density of stomata, and the increase of WUE was recorded in the case of a moderate reduction (<50% reduction in stomata density on leaves prior to tillering). The authors pointed out that the result is a promising one and can be a means to be followed during the breeding of the wheat plants, in order to cope with the deficiencies regarding the water supply under restricted environments, without registering losses of yield. Also, Caine et al. [9], by genetic engineering dedicated to reducing the number of stomata (through the overexpression of OsEPF1 in the epidermis) have been obtained a very productive rice cultivar (IR64), with a smaller number of stomata and at the same time, with a lower stomata conductance.

In contrast, Purcell et al. [42] demonstrated the fact that in an environment with a high concentration of carbon dioxide (hot and dry climate, with a high vapor pressure deficit), the stomata conductance increases, and it has a global significance for what the future modeling of the soil-vegetation – climate feedbacks. Although in many cases, a decrease in stomata conductance was recorded as the concentration of carbon dioxide increases, but, if the biomes were exposed to drought conditions, the increase in stomata conductance became one of the specific responses.

Stomata behavior in urban environment

The behavior of the stomata is of interest not only from the point of view of their influence on the productivity of plants evaluated, for example as net photosynthesis. If we refer to the urban environment, very exposed in terms of the number of inhabitants, associated with the incidence of the polluting factors derived from the intense traffic, the increase of the

concentration of carbon dioxide, as well as of the pollutants in the air are very harmful to the health of the people.

Associated with the conditions mentioned above, the air temperature is higher and it is well known the “urban heat island” (UHI) phenomena, [40] cited by [38]. This is mainly due by modification of surface properties that permit a greater solar radiation absorbtion, as well as a reducing of the convective cooling, associated with a lower water evaporation rates [23].

Ballinas and Barradas [3] highlighted the complexity of mitigating the UHI phenomenon and the need for the involvement of multidisciplinary teams (urban developers, ecologists, architects, engineers, climatologists, geographers, sociologists, etc.). They should take into account the characteristics of key native species, so, the obtained results, respectively the recommended procedures or techniques, will be suitable for a particular city. The authors emphasize that the measures taken in urbanism must stop the growth of this phenomenon and lead to a more sustainable city.

An excellent meta-analysis has recently been performed on the key pathways through which green and blue space affect both urban canopy and boundary layer temperatures. All aspects have been examined from the perspectives of city-planning, urban climatology and climate science [23]. The authors consider that especially in the countries where rapid urbanization is expected, within the framework of the urban planning policy, the way in which the green and blue space infrastructure is applied should lead to mitigating the adverse effects of the UHI and to increasing the climate resilience. For instance, Alizadeh and Hitchmough [1] highlight the need to design a multi-layered vegetation community and a dynamic public landscape, consisting of a mixture of marine climate species and Mediterranean species from southern Europe, proven to have a high level of sustainability in current and future climate scenarios for United Kingdom.

In addition to other indicators used to monitor and characterize the situation, the features of

the stomata have proven to be useful. From this point of view, the decrease in the number of stomata, of the stomata indices and of the number of epidermal cells at the surface unit, with the increase of the length and the breadth of the stomata and respectively of the size of the epidermal cells have been shown to be possible biomarkers regarding the auto pollution [52].

Studies in Gothenburg, Sweden, by Konarska et al. [29] confirmed that trees can counteract heat stress in urban area, through shading and transpiration. They also have shown a positive correlation between the intensity of transpiration and the rate of air cooling in the presence of trees, compared to an area without vegetation. This beneficial effect was recorded around the period of sunset and no cooling effect due to transpiration has been noticed later in the night, or during daytime.

It is obvious that vegetation (in parks, gardens, etc.) as one of the effective remediation strategies has become useful including by extending the green walls of perennial and annual herbaceous plants. These, in addition to the many beneficial functions in terms of reducing pollution, but also increasing urban biodiversity, have the role of reducing the concentration of carbon dioxide thanks to the sequestration of significant amounts of carbon dioxide, at the plant level, as well as in the soil, through known physiological processes. Such a positive potential has been shown both in the case of grass species and shrubs (the perennial herbaceous species *Rudbeckia fulgida* var. *sullivantii* 'Goldstrum', *Erigeron karvinskianus*, *Veronica longifolia*, *Filipendula vulgaris*, *Gaura lindheimeri*, *Campanula persicifolia*, the perennial aromatic *Origanum vulgare*, *Salvia nemorosa* and *Achillea millefolium*, also the shrub *Lonicera pileata*), whose increased photosynthetic capacity, marked stomata conductance and intense transpiration have been shown to be more suitable for carbon dioxide absorption, as well as gaseous pollutants [4]. Many of the studied species have proven to be suitable for urban planning programs and due to a low emission of volatile organic compounds (VOCs),

respectively characterized by low to moderate ozone forming potential (OFP) values. However, the species of the shrub category did not have the same potential (for the removal of the pollutants and for the storage and sequestration of the carbon, respectively) due to their specific morphological and anatomical characteristics (smaller leaf surface and specific structure).

Besides this, plants having the ability to absorb gas from the atmosphere if the stomata are open, a change in their behavior consequently affects the concentration of compounds remaining in the lower atmosphere. Thus, for example, in case of lower soil moisture, stomata conductance decreases and as a consequence there is a decrease in the amount of O₃ (ozone) removed by dry deposition, a process carried out during the summer, correlated with the marked limitation of stomata conductivity due mainly to soil moisture [2].

Climate is one of the key factors affecting the health of forests, but, even in temperate Romanian forest, the studies conducted by De Marco et al. [16] emphasized the obvious influence of ozone on defoliation and highlighted the need for its control in order to improve the health and vitality of the forest. Ozone reduces stomata conductance and consequently influences both the carbon dioxide assimilation and the WUE. Also, the improvement of knowledge regarding its impact on different signaling stages at the cellular level, as well as on the functioning of the ion channels involved in the movements can lead to the explanation of different types of responses to many and varied environmental conditions [18].

Urban greenery has proven to be a key component of the landscape architecture theory since the mid-19th century, with a positive impact on ventilation, improved sanitation and healthier indoor conditions. Moreover, in the specialized literature, the contribution of urban greenness to the physical and mental well-being was mentioned, more so in dense urban areas. The construction of green buildings represents part of the green economy meant to have less damaging effects on the environment and

bring substantial benefits to the society as a whole, but also to each individual [6]. It should not be neglected that the net effects of urban greening on local microclimate, emissions, and air quality result from multiple competing physical and chemical processes that are highly site-specific. So, the use of genetically modified plants that have a tolerance to higher temperatures under global climate change could be one of the very promising prospects [45].

CONCLUSIONS

Global warming is a concept, but also a reality of today, as a result of multiple generating effects and it is well known that environmental climate change will influence our future [1]. The main components of climate change are carbon dioxide from the atmosphere, air temperature and drought. Their changes will result in plants experiencing multiple co-occurring environmental stress factors [3]. Because the stomata are formations of the epidermis involved in the process of carbon dioxide absorption (raw material in photosynthesis), but also of its release (in the case of the respiration process), as well as the release of water vapor during the transpiration, their behavior become defining for what it means not only the plants existence and good functioning, but their influence is also extended and is not limited to just that. Besides the special importance of the physiological processes of plants, for their own existence and good functioning, stomata also have significant effects for energy, carbon and water flow cycles, for what the concentration of gases in the lower troposphere means and more than that, they can represent risks for vegetation, or for human health.

Future researches are needed with a view to clearly understand stomata functioning mechanism, their multiple functions for plant own life and for plants productivity, as well as for other additional functions, including those regarding the reduction of environmental pollution and preserving people health. Only thus, further, by biotechnological approaches

the stomata behavior can be manipulated, as well the proper plant species can be recommended for a local area, according to the specifically conditions, mainly nowadays, when the climate changes are greatly extended over the world.

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