EUROPEAN SCIENCE FOUNDATION
SETTING SCIENCE AGENDAS FOR EUROPE

Exploratory Workshops Scheme

Standing Committee for Life, Earth and Environmental Sciences (LESC)

ESF Exploratory Workshop on

Mesophyll conductance to CO_2: mechanisms, modeling and ecological implications

Sa Coma (Mallorca), Spain, 27 September – 1 October 2008

Convened by **Jaume Fexas,** Universitat de les Illes Balears, Palma de Mallorca, Spain

SCIENTIFIC REPORT

Contents

1. Executive summary

Organization and general overview

The Workshop was held at Hotel Sa Coma (Mallorca) over 3 days (Sunday 28th to Tuesday 30th September 2008). There were 28 participants coming from 9 different European plus 3 non-European countries. The participants included young (up to 10 participants below the age of 35) as well as senior researchers.

The Workshop was organized in a Hotel far from the main cities of the island, and arranged so that all the participants were staying at the same hotel with an all-included regime. In addition, extra activities including a guided wine tasting and a gala dinner were organized. Therefore, the surroundings allowed further additional interaction among participants after the sessions. The general atmosphere was of relax, kindness and great interaction. In particular, young researchers were able to interact and discuss with senior researchers, allowing them clarification of doubts and further planning of their future work. Senior researchers, on the other hand, could meet each other (some knew each other for a long time, but many did not), discuss their views with many specialists at the same time, and establish new collaborations for the future.

Regarding the scientific sessions, the most controversial issues concerning the subject of the Workshop were addressed with serious criticism but without competitiveness. The discussion sessions, which were held after each conference session, were very participative, and none of them lasted less than one hour. In total, about 14 hours were dedicated to oral presentations and up to another 6 hours to participant discussion.

Scientific objectives and agenda

The following objectives were totally fulfilled by the Workshop:

- **To review the current state-of-the-art** of knowledge on mesophyll conductance (g_m): its basis, regulation, and implications. This was achieved by the presentations and, specially, discussion among researchers involved in the whole range of aspects related to g_m knowledge. It was concluded that such an integrative share of knowledge was needed at this time, since this is the first time that the community of researchers involved in studies on g_m meet together in a single meeting specifically devoted to this subject. Results will be compiled in the form of articles in a special issue of a scientific journal.

- **To define the research priorities for the near future** concerning the topic of the workshop. In this aspect, important issues were raised during several discussion sessions, probably resulting in probably the most important outcome of the workshop program.

- **To promote interdisciplinary collaborations** among researchers involved in different aspects of g_m research across Europe. In the final Discussion session of the workshop, ideas for defining collaborations in terms of future research proposals were raised. In particular, it was decided to extend the community to molecular biologists, photobiologists and biophysicists, geneticists, other plant physiologists, forest researchers and agronomists, and to apply next year for an ESF Networking Program on "Determinants of plant productivity in response to environmental stresses".

Overall conclusions

1. Despite some methodological uncertainties, there is now ample consensus that there is really a "third player in the photosynthesis game". Until now, all photosynthesis models were based on the idea of two regulatory steps: stomatal regulation and carboxylation (Rubisco, Calvin cycle). Now it is clear that mesophyll or internal leaf CO_2 diffusion (i.e., g_m) is an equally important factor that can also be subject to regulation. Considering that the "two-steps" photosynthesis models are the feeding basis of plant productivity predictions, plants responses to the environment and climate change, carbon sink estimations, etc ..., neglecting g_m is an important issue that should be addressed. Therefore, it is important that a "broader scientific community" is not left out of this information.

2. Because of its importance, there is a need for consensus as to how to determine g_m, i.e., currently there is insufficient consensus on methodology". In this sense, many of the participants will prepare together a manuscript to reach a broad consensus concerning methodological aspects.

3. Moreover, we need to clarify the structural, molecular and physiological mechanisms. Consequently, an opportunity for interaction of ecophysiologists with plant molecular biologists, geneticists and breeders was detected.

4. On the other hand, there is a real need to implement the above mentioned global models to include g_m variations. In this sense, a good opportunity for interaction with modelers, atmospheric researchers, agronomists and forestry researchers was detected. Particularly, more research has to be conducted to solve the controversy about the effects of light intensity and CO_2 concentration on g_m.

5. Finally, in order to integrate all these aspects, an application to an ESF Networking Programme with the subject "Determinants of plant productivity in response to environmental stresses" is planned for next year. In this application we will try to include people from many countries and from the different areas of knowledge mentioned above.

2. Scientific content of the event

In addition to the final program (see below), the scientific content of the event is reflected in the Abstracts presented by each participant (attached). Here we will only add a few comments on the highlights and most discussed aspects of each conference and of each Discussion session.

Session on 'Methodology to study g_m'.
Pons
It is generally possible to estimate g_m by combining measurements of gas exchange and chlorophyll fluorescence, but precautions has to be taken and tests of reliability performed. For instance, edge effects on commercial gas exchange cuvettes are an important limit, often neglected, for proper estimations of g_m.
The errors in the estimation of Rubisco specificity are inducing the most important biases in g_m estimations, while errors in chlorophyll fluorescence and respiration are also important but to a lesser extent.

Ribas-Carbo

When using the isotopic technique, the possible variations in the assumed constants induce relatively small differences (10%) in the estimation of g_m. However, big errors are induced due to the low precision of the most commonly used instruments, especially when having low CO_2 draw-downs (i.e. when using small chamber or leaves having low photosynthesis rates).

Brugnoli

It is possible to get a time-integrated estimate of g_m by measuring carbon isotope discrimination by extraction of recently synthetized sugars in leaves. This is useful for broad comparisons (e.g., many genotypes) and for field sampling.

Tcherkez

Some of the assumed 'constants' (e.g., discrimination by Rubisco) may not be so constant (more studies are needed to confirm this point).

It is suggested that carbonic anhydrase has little effect on g_m.

Barthel

Newly developed tunable laser diodes (TDLs) will allow fast and quite precise measurements of g_m. This will be useful to assess fast (seconds to minutes) changes of g_m, as well as for monitoring gm continuously in the field.

Douthe

Unreliable g_m values appear when using artificial CO_2 sources with $\delta^{13}C$ largely different from ambient air.

DISCUSSION SESSION ON "METHODOLOGY TO STUDY g_m"

There are problems common to all methods: (1) g_m is a 'residual' parameter (i.e., we measured two methods, they do not match, and we 'insert' a residual g_m value to make them match); (2) gas exchange and particularly the sub-stomatal CO_2 concentration (C_i) are perhaps bigger sources of error than chlorophyll fluorescence or isotope discrimination.

Nevertheless, if two or more of the different methods match each other, then we are more confident of the value because the underlying assumptions are different.

Concerning sensitivity analysis, these are not properly done because they are based on changing a single parameter separately, when in fact they aggregate to create a bigger error.

Session on 'Mechanisms regulating g_m'.

Genty

The gas-phase component of g_m, g_{ias} is much higher than the liquid phase component, g_{liq} in many species (i.e., the larger resistance is within the liquid phase of cells and/or organelles). Isotopic analysis suggest that the most limiting step of g_m is somewhere *inside* chloroplasts.

Sharkey

Phytochrome mutants have parts of chloroplasts very close to cell wall while others curved away. Gas exchange estimates suggest that the former parts have a very large g_m, while the others have very low. Therefore, the 'average' g_m is only slightly lower than in wild-types (WT).

Ancient plant species and/or Arabidopsis mutants with a single large and thin chloroplast have lower photosynthetic capacity but somewhat larger g_m: evolution have not favored increased g_m.

Cornic

CMSII mutants lacking mitochondrial Complex I present a low acclimation to high light. When grown at low light, g_m was about 0.1 mol m^{-2} s^{-1} in WT and CMS, but when grown at

high light g_m increased to 0.23 mol m^{-2} s^{-1} in WT but remained at 0.11 mol m^{-2} s^{-1} in CMS. Very similar differences are observed in Complex I mutants of other species.

Kaldenhoff / Uehlein

Data suggest that most PIP1-type aquaporins transport CO_2 across cell and chloroplast membranes. Indeed, even inserting human PIP1 but not PIP2 in plants has similar effect.

PIP1 have a different function in roots and leaves: this may be because they are slightly different (probably phosphorylation or differences in homo- and heterotetramers with PIP2). For instance, constructs PIP2:PIP1 in yeast with proportions 0:4 – 1:3 – 2:2 – 3:1 – 4:0 show an increasing order of water conductivity and decreasing order of CO_2 permeability.

Tholen

There is a very high correlation between g_m and the surface of chloroplasts exposed to ias (S_c) in many different mutants and light treatments in Arabidopsis, but no effects of chloroplast arrangement on g_m in *Chenopodium album*.

Chloroplast movements are relatively fast (10-20 minutes under high light, but 60-90 minutes when back to low light), so they can explain some of the variations of g_m not related to long-term changes in leaf structure.

Reiter

Arabidopsis mutants deficient in major leaf CAs show reduced growth despite no apparent changes in g_m, but only when growth at low CO_2 (no effect at ambient CO_2).

Growth analysis predicts that 28% and 48% reductions in harvest biomass would correspond to 0.5-1% and 1-2% reductions in A_N and g_m, respectively (i.e., not measurable).

DISCUSSION SESSION ON "MECHANISMS REGULATING g_m"

g_{ias} seems much higher than g_{liq} except in very thick leaves, but this is subjected to uncertainties concerning the helox method. It would be worth testing it on many more species.

A systematic analysis of when g_m decreases and where (i.e., ias, cell wall, chloroplast envelope, etc ….) is needed.

Carbonic anhydrases:

Most evidences are suggesting a small role (early papers by Price, Williams, now Tcherkez, Genty). It is thought that the only important one could be inside the chloroplasts (i.e., where there is bicarbonate transport, since at a pH of 7.7-8.0 there would be about 50-times more HCO_3^- than CO_2).

Aquaporins:

Certainly there is fine evidence for their involvement, but unclear mechanism at the molecular level. There is now interest in mechanisms like "gating", vesicle traffic or tetramerization, but no evidence due to the lack of knowledge about the basics of CO_2 movement through biological membranes. Gating of aquaporins does not seem a general mechanism.

S_c and chloroplast movements:

These are compatible with the idea of aquaporin-facilitated, and there seems to be good matching between the evidences of Sharkey, Tholen, and others.

This is also compatible with the observed higher g_m in sun leaves, since the latter is related to volume effects, not to positional effects.

Mitochondrial rearrangements:

There are clear and well-demonstrated effects on g_m, but intriguing reasons.

Cell wall:

Using carbonic anhydrase as a probe, the results suggest that about 1/3 of g_m may occur at the cell wall.

Session on 'Environmental effects on g_m'.

Warren

Soil and atmospheric water stress affect g_m differently.

Under nitrogen limitation and leaf ageing g_m does not limit photosynthesis.

Shading the lower leaves results in increased g_m in the non-shaded upper leaves.

Galmés

Mesophyll conductance limits photosynthesis under water stress very similarly in different leaf habits and growth forms and it limits even more during re-watering.

The relationship between g_s and g_m is apparently linear, except perhaps under re-watering.

Costa

There are big differences in g_m between grapevine cultivars from 0.116 mol m^{-2} s^{-1} in Cabernet Sauvignon to 0.501 mol m^{-2} s^{-1} in Touriga. These differences are strongly decoupled from stomatal conductance.

Gallé

Strong differences in the response of g_s and g_m to water stress and recovery are observed, depending on growing environment.

There is also some acclimation (homeostasis) of g_m to water stress in some species.

Centritto

The relationship between g_s and g_m is apparently linear between rice cultivars and treatments, in agreement with very little differences in water use efficiency (WUE), but the relationship is not so clear when measured using the sugars method.

The two methods yield more similar results the more stressed the plants are.

Perez-Martin

There are complex interactions between species, light, VPD and water stress affecting g_m.

Tsonev

Cadmium (Cd) stress could injure chloroplast structure and reduce the activity of carbonic anhydrase. It certainly affects g_m.

Evans

Light response of g_m can be an artifact due to different sampling areas (within leaf depth) of the gas exchange and the fluorescence signal, and this will depend as well on the actinic light quality and on the weighted absorbance of each leaf layer.

Isotopic determinations demonstrate that light does not affect g_m, and CO_2 has only a small effect at least between 200 and 500 ppm CO_2.

Loreto

When increasing blue light, this may be absorbed by carotenoids rather than chlorophyll, lowering fluorescence and hence underestimating g_m.

Still, the effect of blue light on g_m is very fast (1-2 minutes), i.e., faster than chloroplast movements.

Monti

There are complex interactions between light and age affecting g_m.

DISCUSSION SESSION ON "ENVIRONMENTAL EFFECTS ON g_m"

Natural environments are composed of multiple variables that change dynamically and in complex interactions. Limits in understanding the effects of environment are due to very limited knowledge on the mechanisms regulating g_m.

More measurements are needed to confirm/discern the effects of light intensity and CO_2 concentration. Also, there is a need to study the effects of many nutrients deficiency / toxicity on g_m.
A possible integrative factor is pH, since the apoplast is very acidic when transpiration is low and basic when high, this would explain while there is a specific CA outside the plasmalemma where if pH was always constant there will only by CO_2 and not HCO_3^-.

Session on 'Ecological implications of g_m'.

Terashima

The increase in photosynthesis after transition from shade to sun conditions in 12 different species correlated with increased S_c.
g_m/S_c correlated negatively with cell wall thickness, suggesting a significant role for the cell wall in limiting g_m. It may be affected by wall composition, pH, water potential …. Effects of apoplast pH on g_m should be studied.

Niinemets

It would be important to consider the extremely different leaf structures along plant kingdom (Arabidopsis is not representative of all plants).
For instance, a very good correlation was found between LMA and g_m when varying with altitude in *Metrosideros polymorpha* in Hawaii.

Hassiotou

Banksia species present a relatively high g_m considering their very high LMA.
In all these species except two there was a strong effect of C_i on g_m, but the slope was less pronounced as LMA increased. Also in these species reduced light resulted in apparently reduced g_m.
Remarkably, all these species presented very similar CO_2 drawdown (C_a-C_i and C_i-C_c), i.e., photosynthetic capacity was co-regulated with conductances.

Tosens

There are complex interactions between light, water stress and leaf structure affecting g_m.

Diaz-Espejo

Previous attempts of modeling photosynthesis including g_m have set a constant value, or a value that is a linear function of g_s or N content, which now we know is not true.
A fairly conservative atmosphere to chloroplast CO_2 drawdown (C_a-C_c) may be used to produce an empirical model to estimate g_m and then use it for improving model photosynthesis estimations.

Dreyer

Despite possible effects of g_m carbon 13 discrimination ($\Delta^{13}C$) in plant dry matter is still a good indicator of WUE when comparing genotypes, treatments, locations … for a given species, but not when comparing different species.

Flexas

There is a reasonable relationship between leaf intrinsic water-use-efficiency (A_N/g_s) and the ratio of mesophyll to stomatal conductance (g_m/g_s) in nature, but this is not achieved in transgenic plants possibly because of pleiotropic effects (need to test promoter-inducible transgenes).

DISCUSSION SESSION ON "ECOLOGICAL IMPLICATIONS OF g_m"

Debate: how do we quantify the importance of g_m? (1. plot A_{max} vs g_m, but better use photosynthetic capacity which is independent of g_m; 2. based on C_i-C_c; 3. use a mass-based rather than an area based unit). Most people favor the second option.
Question: what is the cost/benefit of maintaining g_m? Insufficient knowledge on the mechanisms regulating g_m impede answering this question.

Probably the mechanism(s) are moving from biochemical to structural mechanisms when increasing time and/or size scale.
Effects of g_m on WUE, NUE, …: further studies urged.

3. Assessment of the results, contribution to the future direction of the field

There were four scientific sessions in the Workshop, the conclusions of each of them are summarized below, together with an assessment of the contribution of the Workshop to the future direction of the field.

Session on 'Methodology to study g_m'.

1. When using any of the methods to estimate g_m, tests have to be done and reported to demonstrate the validity of the assumptions used.

2. When not testable, a sensitivity analysis must be provided. However, this must take into account the factors not separately, but integrated to test their combined effect on g_m calculation.

3. It is important to compare the results of two or more different methods with different underlying assumptions.

Session on 'Mechanisms regulating g_m'.

1. In most species, but not all, the most important limitation to CO_2 diffusion is in the liquid phase of cells (i.e., $g_{ias} >>> g_{liq}$).

2. Leaf structural properties (leaf mass per area, cell wall thickness) may account for the most invariable components of g_m, while chloroplast movements and biochemical components of the leaf may account for dynamic short-term variations.

3. Concerning dynamic changes, apparently there is little evidence for the involvement of carbonic anhydrases and more evidence for the involvement of chloroplast movements and some aquaporins, although to understand the exact mechanisms further studies and transgenic approaches are required.

Session on 'Environmental effects on g_m'.

1. There is substantial evidence for the response of g_m to leaf development and ageing, acclimation to growing light intensity, water and salt stress. More studies are required concerning the effects of vapor pressure deficit, altitude and, specially, the effects of many nutrients deficiency / toxicity.

2. It is of particular importance to discern the possible short-term effects of light intensity (and quality) and CO_2 on g_m, because they affect the reliability of some of the methods used for g_m estimation. Presently, the results appear somewhat contradictory, although a closer inspection suggests that they are not necessarily mutually exclusive.

3. Finally, evidence was presented at the workshop for strong interactions between different environmental variables and their effects on g_m. Therefore, although there is still a need to study single factor effects, it is important to consider that these can change when different environmental factors interact together.

Session on 'Ecological implications of g_m'.

1. There are some general relationships between g_m and either leaf structure, photosynthesis capacity, stomatal conductance, WUE, etc …

2. Poor understanding of the mechanisms regulating g_m limits our capacity to fully understand the above mentioned relationships.

3. Despite limits in mechanistic understanding, the generality of the above relationships can be used to model g_m and to include g_m effects on leaf and plant models of productivity. This is a priority for the immediate future.

Contribution of the Workshop to the future direction of the field.

1. For the first time, the scientific community involved in research on g_m met together in a single Workshop with this specific subject. This served to identify the general agreements, as well as the controversial aspects and the needs for future research. As said before, the workshop has also allowed to establish relationships and cooperation among scientist working on this topic.

2. As the main conclusion, there is now ample consensus that g_m is an important limiting factor for photosynthesis that can be subject to rapid regulation. Its importance is similar to that of stomatal regulation and photosynthetic capacity. It is important to clearly inform to the "broader scientific community" about it. Therefore, a Special Issue of Journal of Experimental Botany on "Mesophyll conductance to CO_2" will help. Such issue is planned with about 15 research contributions by participants in the Workshop plus three consensus multi-authored papers on the main subjects of the workshop: (1) Protocols for measuring g_m; (2) Mechanisms regulating g_m; and (3) Global aspects and implications of g_m for plant modeling.

3. On the other hand, in order to clarify the mechanisms that regulate g_m there is a need for interaction with molecular biologists, geneticists, and other plant physiologists, while for implementing plant models to include g_m regulation there is a need for interaction with forest researchers and agronomists. Therefore, it was decided to extend the community and to apply next year for an ESF Networking Programme on "Determinants of plant productivity in response to environmental stresses".

4. Final program

The final program was that detailed below. Despite the last-minute withdrawal of participants of Andrea Monti and Norbert Uehlein for health resons, the program was unaffected since their contributions were presented by Jaume Flexas and Ralf Kaldenhoff, respectively.

27th September 2008
20:00 Reception and documentation

28th September 2008
8:30 Documentation

9:00 Opening session. Arja Kallio (ESF), Hipólito Medrano (UIB), Jaume Flexas (Organiser)

9:30 Session on 'Methodology to study g_m'. Chairs: A. Díaz-Espejo, M. Ribas-Carbo.
- Thijs Pons: Measurements of mesophyll conductance by means of gas exchange in combination with chlorophyll fluorescence: evaluation of potential errors
- Miquel Ribas-Carbo: Isotopic methods for g_m measurements

10:30 Coffee break

11:00 Session on 'Methodology to study g_m'. Chairs: A. Díaz-Espejo, M. Ribas-Carbo.
- Enrico Brugnoli: The application of carbon isotopes in recently assimilated carbohydrates to estimate mesophyll conductance in ecophysiological studies
- Guillaume Tcherkez: On the effect of heavy water on $^{12}C/^{13}C$ fractionation in photosynthesis
- Matthias Barthel: Using high frequency stable isotope laser spectrometry to investigate the influence of drought on the mesophyll conductance to CO_2
- Cyril Douthe: Investigating intrinsic water-use-efficiency in tree species with combined gas exchange and on-line $^{13}CO_2$ isotope discrimination with a tunable diode laser: system description and first results

12:20 Discussion session on 'Methodology'. Chairs: J. Evans, B. Genty.

13:30 Lunch

15:00 Session on 'Mechanisms regulating g_m'. Chairs: R. Kaldenhoff, D. Tholen.
- Bernard Genty: CO_2 transfer in the mesophyll: physical and biochemical components
- Tom Sharkey: Chloroplast size and location effects on mesophyll conductance
- Gabriel Cornic: The CMSII mutation and the mesophyll conductance

16:30 Coffee break

17:00 Session on 'Mechanisms regulating g_m'. Chairs: R. Kaldenhoff, D. Tholen.
- Ralf Kaldenhoff (for Norbert Uehlein): Physiological consequencies of plant aquaporin CO_2 conductivity

- Ralf Kaldenhoff: Molecular basis of plant aquaporin CO_2 conductivity
- Danny Tholen: The effect of chloroplast movements on mesophyll conductance in *Arabidopsis thaliana*
- Ilja Reiter: *Arabidopsis* lines deficient in major leaf carbonic anhydrases show reduced growth in low CO_2

18:45 Discussion session on 'Mechanisms regulating g_m'. Chairs: I. Terashima, G. Cornic.

29th September 2008

9:30 Session on 'Environmental effects on g_m'. Chairs: E. Brugnoli, N. Uehlein.
- Charles Warren: Environmental variation in mesophyll conductance
- Jeroni Galmés: Mesophyll CO_2 limitations on carbon assimilation in natural vegetation during drought stress and recovery

10:30 Coffee break

11:00 Session on 'Environmental effects on g_m'. Chairs: E. Brugnoli, N. Uehlein.
- Miguel Costa: Non-stomatal limitations of photosynthesis in different cultivars of *Vitis vinifera* subjected to deficit irrigation
- Alex Gallé: Photosynthesis limitation in response to drought stress: some insights on acclimation and recovery
- Mauro Centritto: Response of photosynthesis, carbon isotope discrimination and mesophyll conductance to water deficits during reproductive stage in rice
- Alfonso Pérez: Effect of air vapour pressure deficit on mesophyll conductance
- Tsonko Tsonev: Mesophyll conductance to CO_2 in heavy metals treated plants

13:30 Lunch

15:00 Session on 'Environmental effects on g_m'. Chairs: E. Brugnoli, N. Uehlein.
- John Evans: Does internal conductance vary with irradiance?
- Francesco Loreto: Impact of blue light on mesophyll conductance
- Jaume Flexas (for Andrea Monti): Bottom up mesophyll conductance under diverse light levels in *Brassica carinata*

16:30 Coffee break

17:00 Discussion session on 'Environmental effects on g_m'. Chairs: Ü. Niinemets, F. Loreto.

30th September 2008

9:30 Session on 'Ecological implications of g_m'. Chairs: J. Galmés, T. Pons.
- Ichiro Terashima: Variation of mesophyll conductance depending on plant functional type: roles of chloroplast surface area, cell wall thickness and cooporins
- Ülo Niinemets: Structural controls of internal diffusion conductance: scaling from leaf to globe

10:30 Coffee break

11:00 Session on 'Ecological implications of g_m'. Chairs: J. Galmés, T. Pons.

- Foteini Hassiotou: How do leaf structure, CO_2 and irradiance influence mesophyll conductance in sclerophylls?

- Tiina Tosens: Photosynthetic capacity as depending on leaf anatomical structure and internal gas exchange resistance in *Populus tremula*

13:30 Lunch

15:00 Session on 'Ecological implications of g_m'. Chairs: J. Galmés, T. Pons.

- Antonio Díaz-Espejo: Photosynthesis modeling in olive trees: effects of mesophyll conductance

- Erwin Dreyer: Estimating intrinsic water-use efficiency in trees: interferences between the ^{13}C isotopic signal and internal conductance to CO_2?

- Jaume Flexas: Involvement of mesophyll conductance to CO_2 in leaf-level water-use-efficiency

16:30 Coffee break

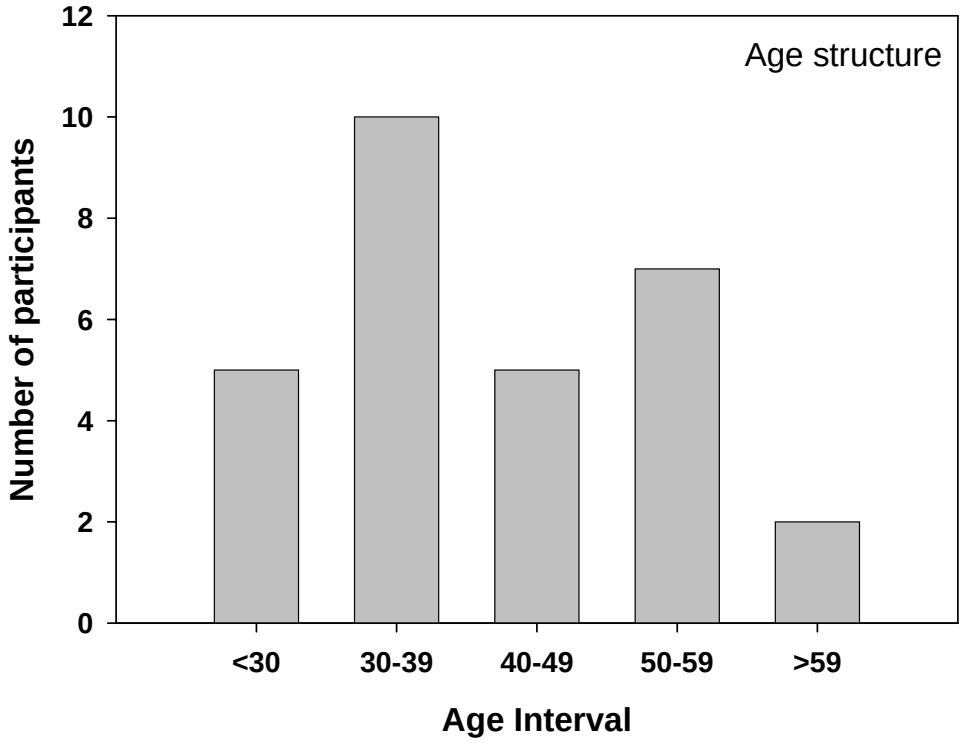
17:00 Discussion session on 'Ecological implications of g_m'. Chairs: E. Dreyer, C. Warren.

18:00 Conclusions of the workshop and closing session. Chairs: T. Sharkey, J. Flexas.

5. Statistical information on participants

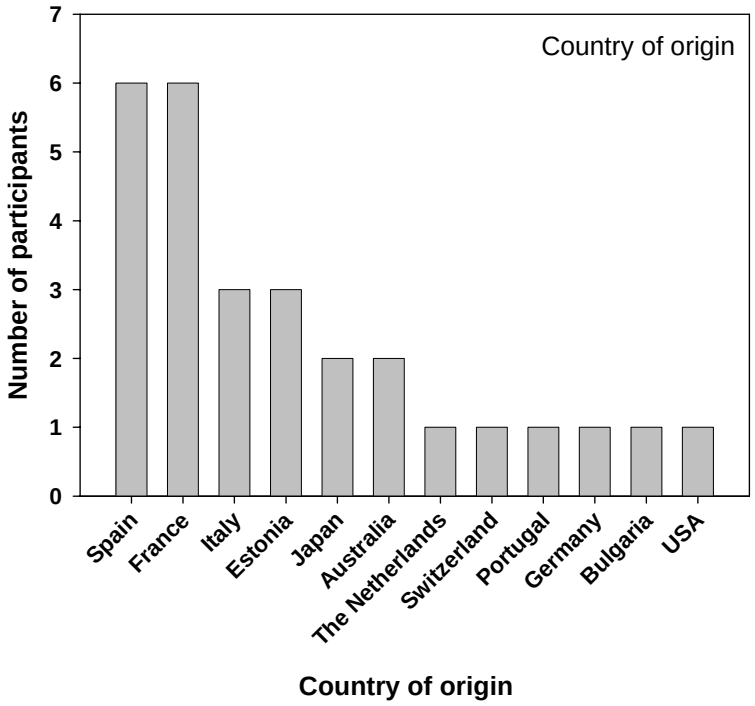
A total of 28 participants attended the Workshop, including most of the researchers currently involved on g_m. A search on ISI Web of Knowledge using the terms 'mesophyll conductance' and/or 'leaf internal conductance' reveals only a few names of researchers with more than 3 papers in this area that could not attend the meeting: G.J. Ethier and N.J. Livingston (University of Victoria, Canada), and G.D. Farquhar and S. von Caemmerer (Australian National University, Australia). This analysis also reveals the imbalance in the gender of researchers involved in this field, the majority of them being men with only very few women. This was also reflected in the composition of participants in the Workshop (26 men and 2 women). However, it must be said that it was almost impossible to include more women because very few other women are working in this field. Senior researcher Suzanne von Caemmerer could not be invited because of the ESF limits concerning non-European participants), and the same was true for young researcher Margaret Barbour (New Zealand). Other women recently researching on g_m include Manuela Chaves, from Portugal (she was invited but declined due to other responsibilities), María Fernanda Ortuño (not possible to be included due to excess Spanish participants) and the organizer's PhD students Alicia Pou and Magdalena Tomàs (which were actually present in the workshop as staff members of the organization).

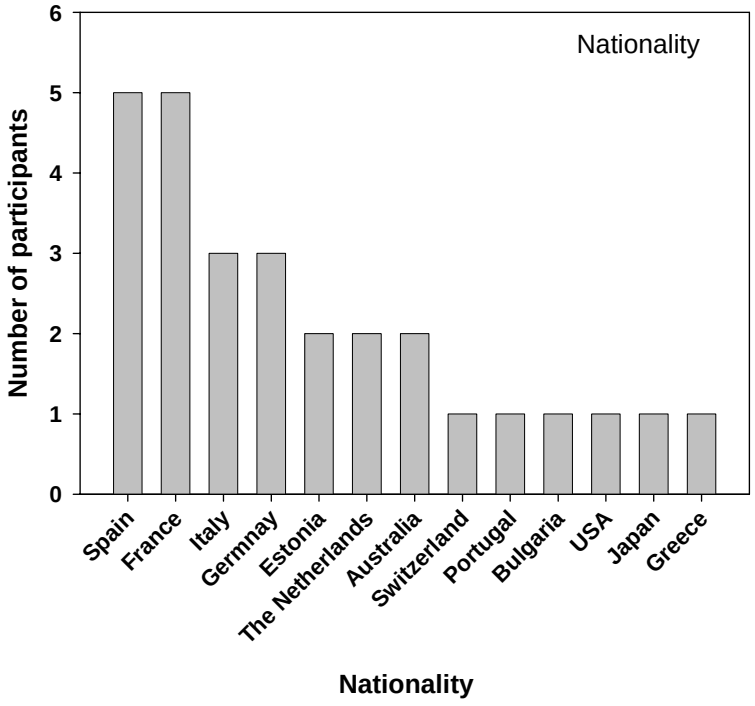
Concerning the age structure (see figure below), the participants included up to 5 very young researchers (under 30 years), 10 young researchers (below 40 years) and 13 senior researchers (above 40 years). In this sense, there was a good balance that allowed young researchers to interact with (and learn from) senior researchers, while the abundance of researchers between 30 and 40 years old ensured that the field will be active for many years.



Regarding the countries of origin of the participants, the Workshop included people from 9 European plus 3 non-European countries, while attending to the nationality of the participants there was people from 10 European plus 3 non-European countries (see

figures below). This broad composition reinforces the possibility of ample European and non-European collaboration.





6. Final list of participants

List

Participant	Country	Role	e-mail
1. Barthel, Matthias	Switzerland	Participant	matthias.barthel@ipw.agrl.ethz.ch
2. Brugnoli, Enrico	Italy	Invited speaker	enrico.brugnoli@ibaf.cnr.it
3. Centritto, Mauro	Italy	Participant	mauro.centritto@ibaf.cnr.it
4. Cornic, Gabriel	France	Invited speaker	gabriel.cornic@u-psud.fr
5. Costa, Miguel	Portugal	Participant	miguelc@itqb.unl.pt
6. Díaz-Espejo, Antonio	Spain	Scientific committee	adiaz@irnase.csic.es
7. Douthe, Cyril	France	Participant	Cyril.Douthe@nancy.inra.fr
8. Dreyer, Erwin	France	Invited speaker	dreyer@nancy.inra.fr
9. Evans, John Richard	Australia	Invited speaker	john.evans@anu.edu.au
10. Flexas, Jaume	Spain	Organizer	jaume.flexas@uib.es
11. Gallé, Alexander	Spain	Participant	alexander.galle@uib.es
12. Galmés, Jeroni	Spain	Invited speaker	jeroni.galmes@uib.es
13. Genty, Bernard	France	Invited speaker	bernard.genty@cea.fr
14. Hassiotou, Foteini	Estonia	Participant	fhassiotou@gmail.com
15. Kaldenhoff, Ralf	Germany	Invited speaker	kaldenhoff@bio.tu-darmstadt.de
16. Loreto, Francesco	Italy	Scientific committee	francesco.loreto@ibaf.cnr.it
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