

# Water and vegetation in a changing environment: Optimal adaptation, feedbacks and key trade-offs

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**Luxembourg Institute of Science and Technology**

**WAVE – Water and Vegetation in a changing environment**  
*Capturing change and feedbacks of vegetation, atmosphere  
and hydrology, with an open science approach*

<https://zenodo.org/communities/wave> Contact: [stanislaus.schymanski@list.lu](mailto:stanislaus.schymanski@list.lu)



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Fonds National de la  
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# ADAPTATION TO ELEVATED CO<sub>2</sub>

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Gedney et al. (2006):  
Nature 439(7078)

Elevated CO<sub>2</sub>

—

Stomatal conductivity

+

Evapo-transpiration

CO<sub>2</sub>-Adapt.

Carbon profit

Optimality

Trade-offs

BG 3.4  
EGU22-8841  
Schymanski et al.



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Gedney et al. (2006):  
Nature 439(7078)

**Short term**

Piao et al. (2007):  
PNAS 104(39)

**Medium term**

Elevated CO<sub>2</sub>

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Leaf area index

+

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Gedney et al. (2006):  
Nature 439(7078)

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PNAS 104(39)

Schymanski et al. (2015):  
AoB Plants 7

**Short term**

**Medium term**

**Long term**

Elevated CO<sub>2</sub>

—

Stomatal conductivity

+

Evapo-transpiration

+

Leaf area index

+

?

Plant types  
Rooting depths

?

CO<sub>2</sub>-Adapt.

Carbon profit

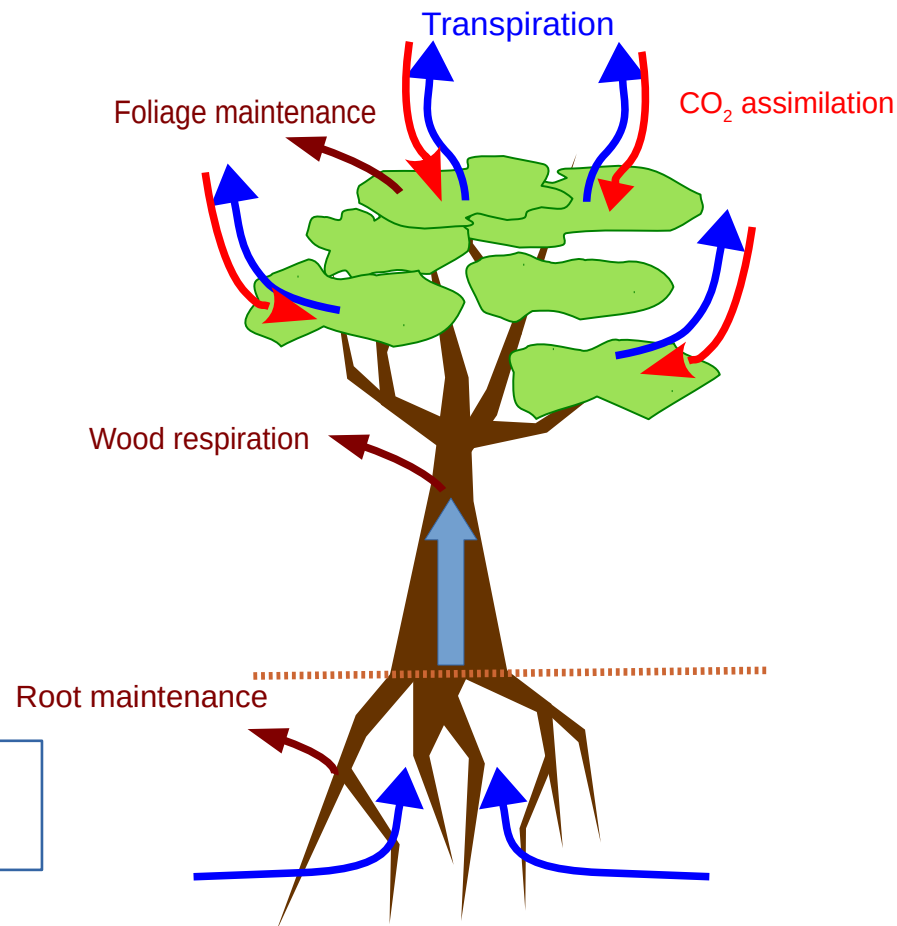
Optimality

Trade-offs

BG 3.4  
EGU22-8841  
Schymanski et al.

# GENERAL PRINCIPLES BEHIND VEGETATION RESPONSES?

- Carbohydrates as energy currency
- Leaf gas exchange determines gross income
- Trade-offs between carbon gain and loss guide economics
- Selective pressure for best use of resources to **maximise the Net Carbon Profit**



→ **Vegetation Optimality Model (VOM):**  
Schymanski et al. 2009, WRR 45

CO<sub>2</sub>-Adapt.

Carbon profit

Optimality

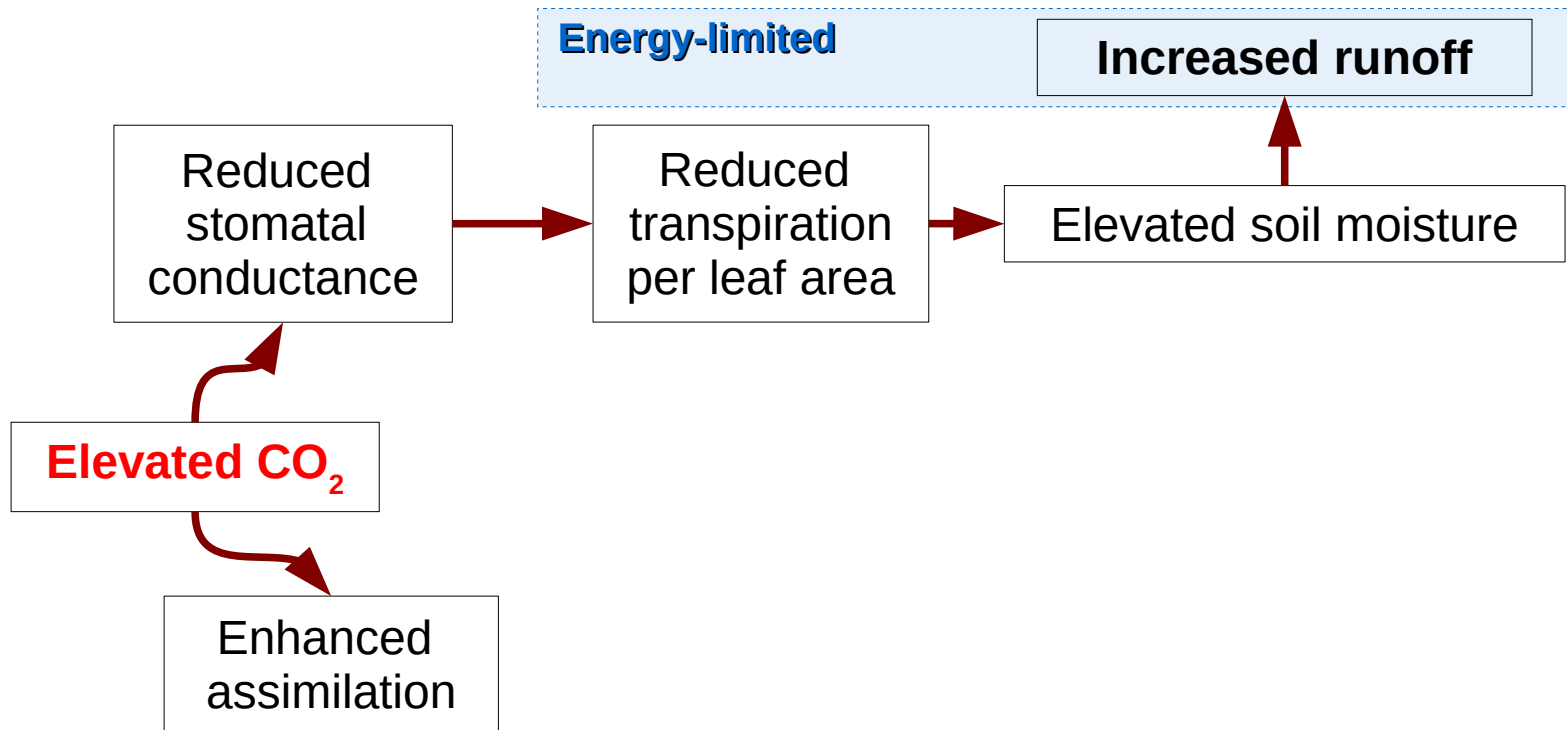
Trade-offs



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# ADAPTATION TO ELEVATED CO<sub>2</sub>: VEGETATION OPTIMALITY MODEL (VOM)



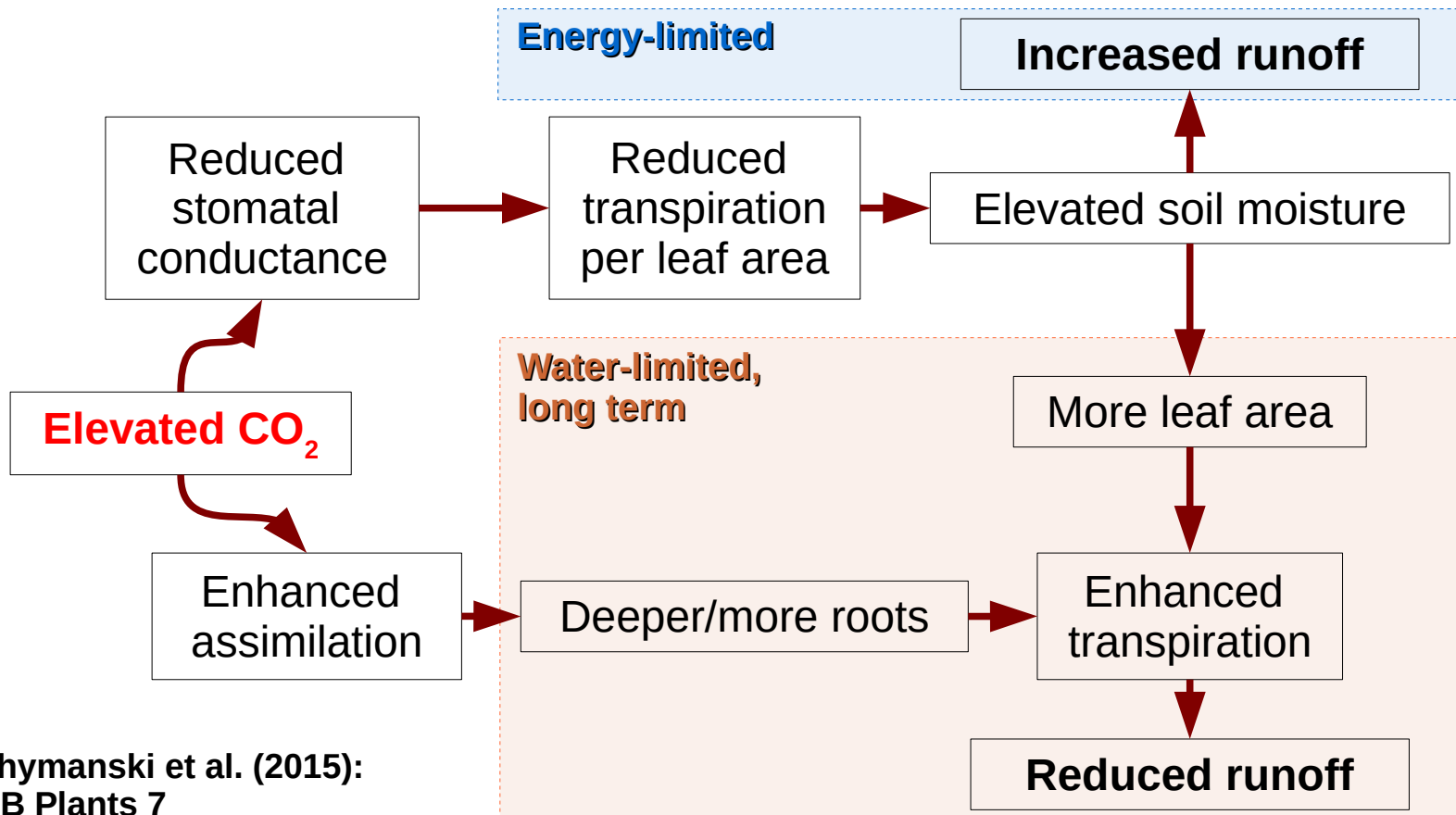
CO<sub>2</sub>-Adapt.  
Carbon profit  
**Optimality**  
Trade-offs



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# ADAPTATION TO ELEVATED CO<sub>2</sub>: VEGETATION OPTIMALITY MODEL (VOM)



Schymanski et al. (2015):  
AoB Plants 7

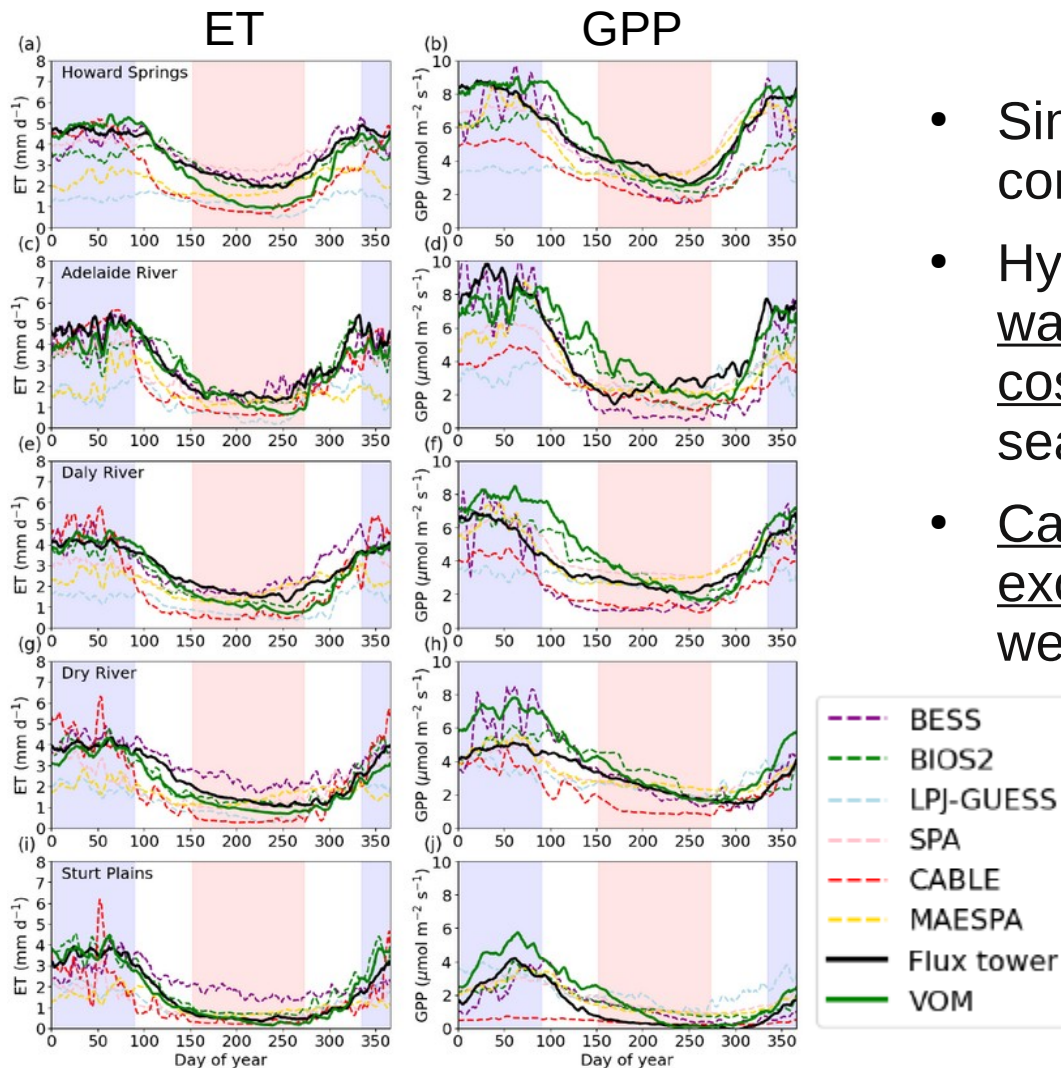
CO<sub>2</sub>-Adapt.  
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**Optimality**  
Trade-offs



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## VEGETATION OPTIMALITY PREDICTS ET &amp; GPP



- Similar or better results than conventional models
- Hydrology feedback and water uptake and transport costs important for dry season fluxes
- Canopy light absorption & gas exchange limits important for wet season fluxes

Nijzink, R. C. et al. (2022): HESS 26(2)  
<https://doi.org/10.5194/hess-26-525-2022>

CO<sub>2</sub>-Adapt.  
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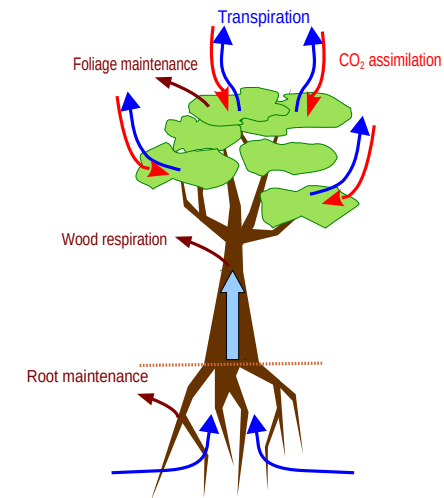
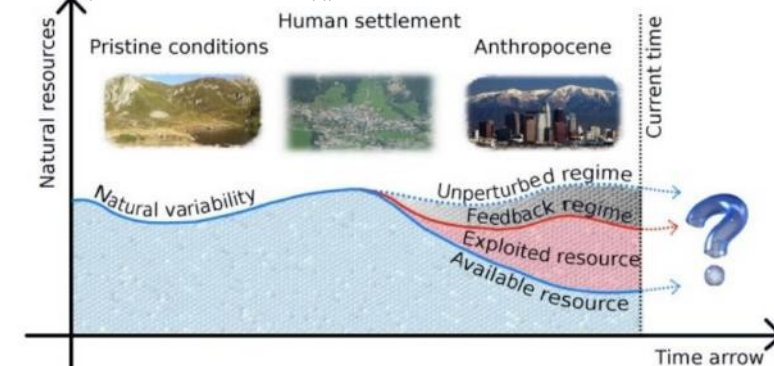
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# PROMISES AND CHALLENGES OF OPTIMALITY-BASED MODELLING

- General principles → performance in the past should indicate performance in the future
- Need to quantify physical and biological limits
- Need to quantify trade-offs between costs and benefits of carbon investments

## “Change in Hydrology and Society”

(Montanari et al., 2013, HSJ 58(6))



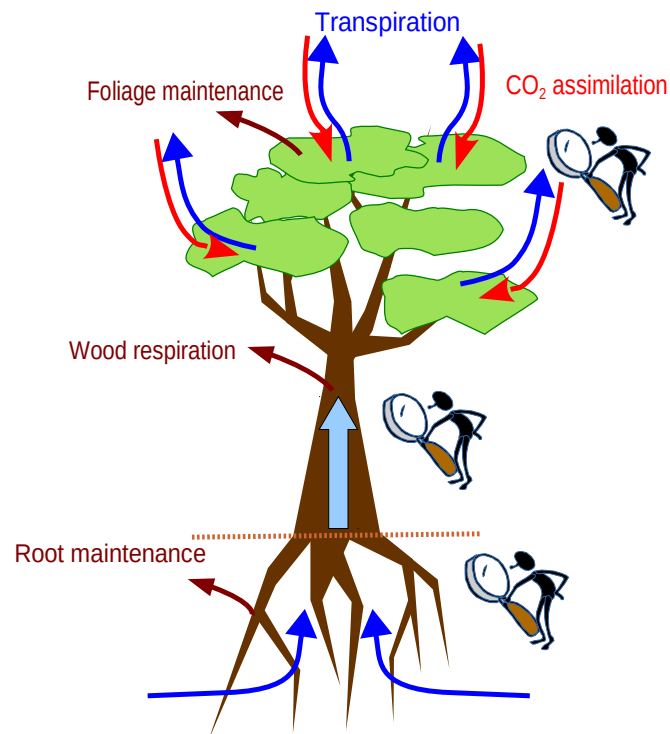
CO<sub>2</sub>-Adapt.  
Carbon profit  
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# NEED TO QUANTIFY PHYSICAL LIMITS AND TRADE-OFFS RELATED TO C INVESTMENT



- Nijzink et al.: LAI and light interception: [EGU22-2886.html](https://www.eur01.safelinks.com/m/q/EGU22-2886.html)
- Thakur et al.: Leaf vs. canopy resistances: [EGU22-4268.html](https://www.eur01.safelinks.com/m/q/EGU22-4268.html)
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- Ceolin et al.: Root system dynamics experiments: [EGU22-5306.html](https://www.eur01.safelinks.com/m/q/EGU22-5306.html)



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# APPENDIX...

**CO<sub>2</sub>-Adapt.**  
**Carbon profit**  
**Optimality**  
**Trade-offs**

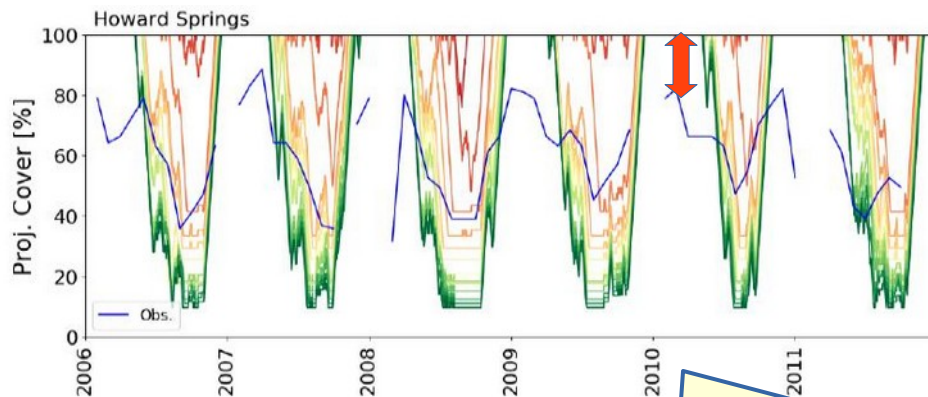
**BG 3.4**  
**EGU22-8841**  
**Schymanski et al.**



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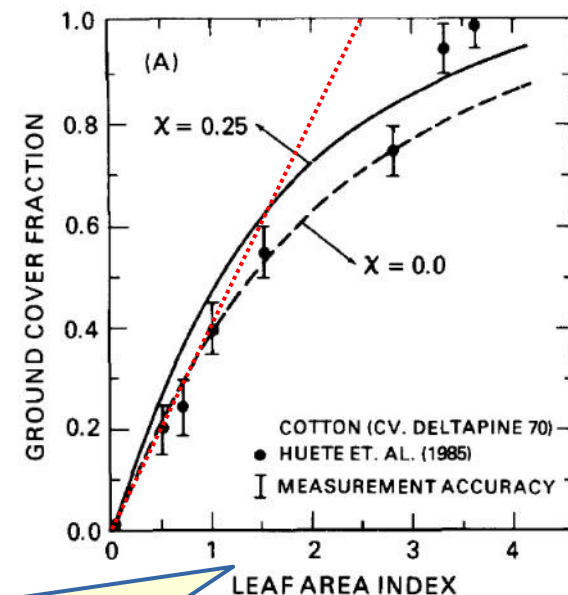
# TRADE-OFFS RELATED TO LAI AND CANOPY LIGHT CAPTURING



Assumption in the VOM: LAI of 2.5 results in full cover (100% light interception)

Why do plants waste so much leaf area instead of growing one big leaf?

Reality: cover fraction is non-linear function of LAI



Choudhury (1987): RSE 22

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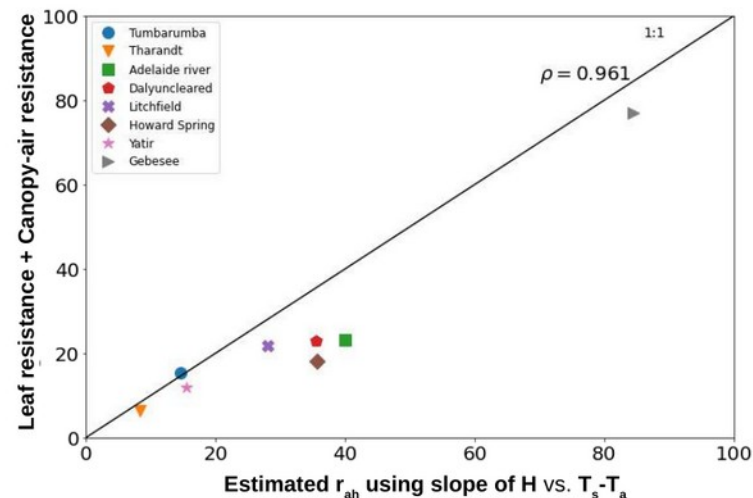
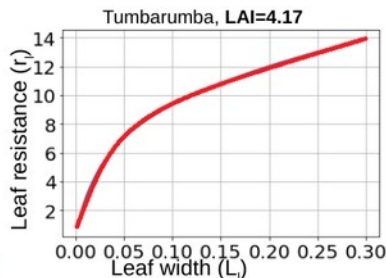
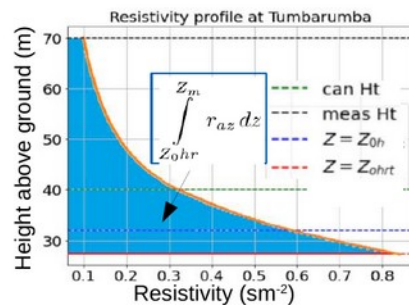
Nijzink et al.: LAI and light interception: [EGU22-2886.html](https://www.egu22.eu/abstracts/EGU22-2886.html)



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# PHYSICAL LIMITS OF CANOPY GAS EXCHANGE

## Our model: Canopy-air space + Leaf boundary layer



gitanjali.thakur90@gmail.com

Thakur et al.: Leaf vs. canopy resistances: [EGU22-4268.html](https://doi.org/10.1111/egus.4268)

CO<sub>2</sub>-Adapt.  
Carbon profit  
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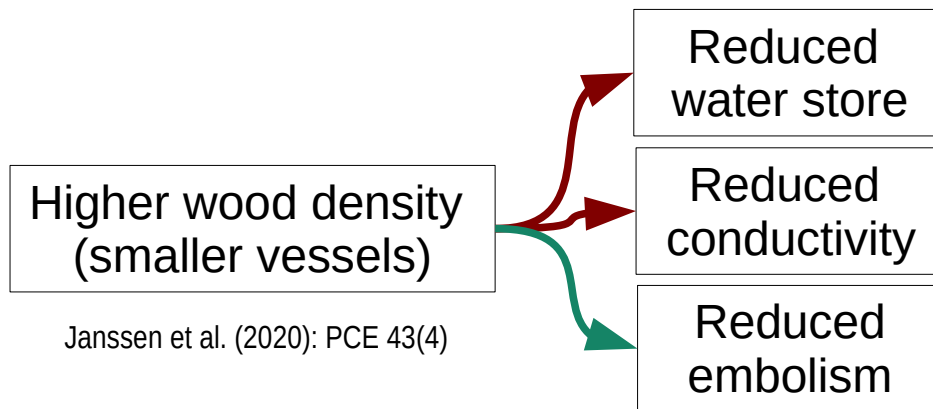
BG 3.4  
EGU22-8841  
Schymanski et al.



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# TRADE-OFFS RELATED TO WATER TRANSPORT AND STORAGE

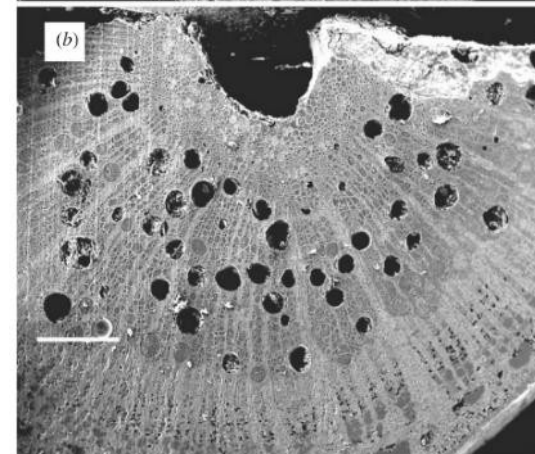
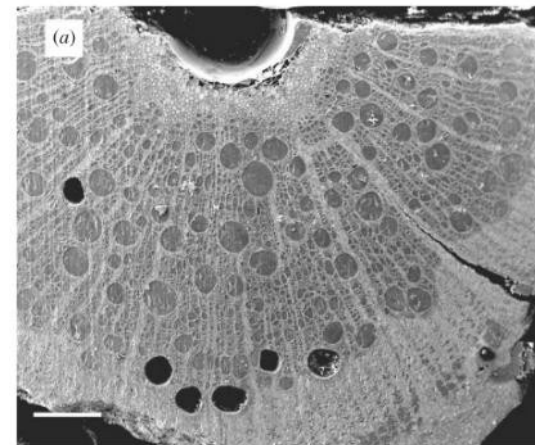


Janssen et al. (2020): PCE 43(4)

## OPEN QUESTIONS:

- How to measure conductivity?
- How often do xylem vessels need to be replaced?
- How expensive is embolism repair?

Krieger et al.: Plant hydraulic conductivity experiments: [EGU22-5357.html](https://www.eurac.edu/en/education/graduate-program/eu22-5357.html)



Canny et al. (2007): Func. Plant Biol. 34(2)

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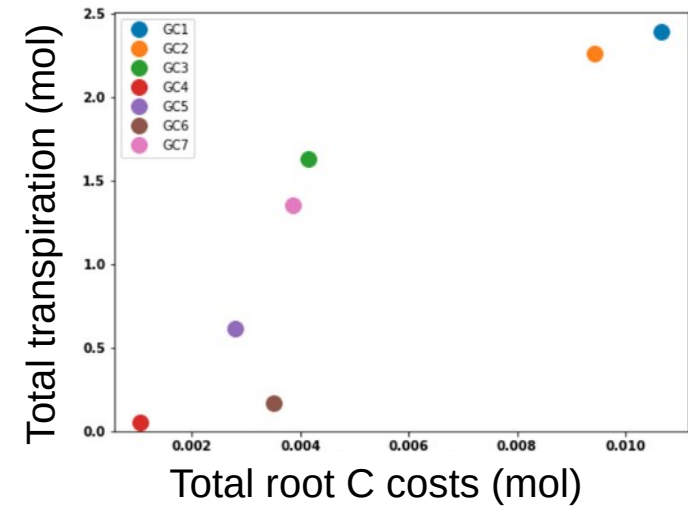
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# TRADE-OFFS RELATED TO ROOT UPTAKE

## OPEN QUESTIONS:

- How much C investment per water uptake?
- How does trade-off change with environmental conditions?

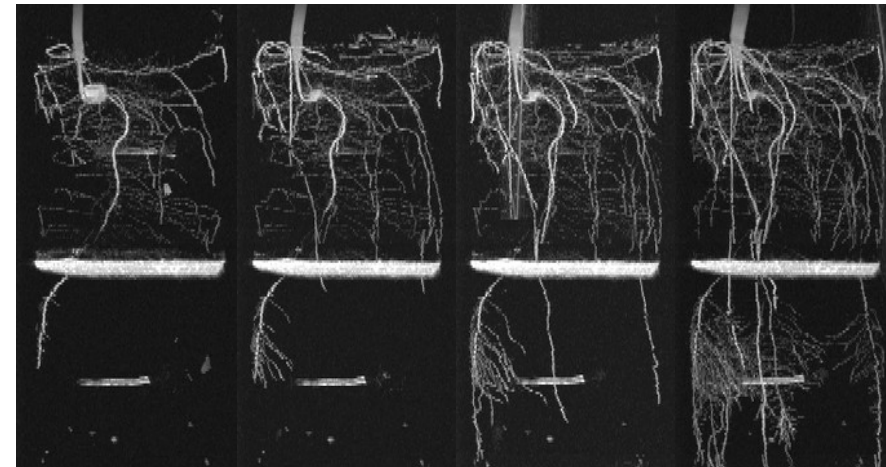
Osuebi et al.: Shoot vs. root C flux experiments: [EGU22-5798.html](https://doi.org/10.1111/1365-3113.12579)



## OPEN QUESTION:

- How quickly can the root system adjust to changing environment?

Ceolin et al.: Root system dynamics experiments: [EGU22-5306.html](https://doi.org/10.1111/1365-3113.12579)



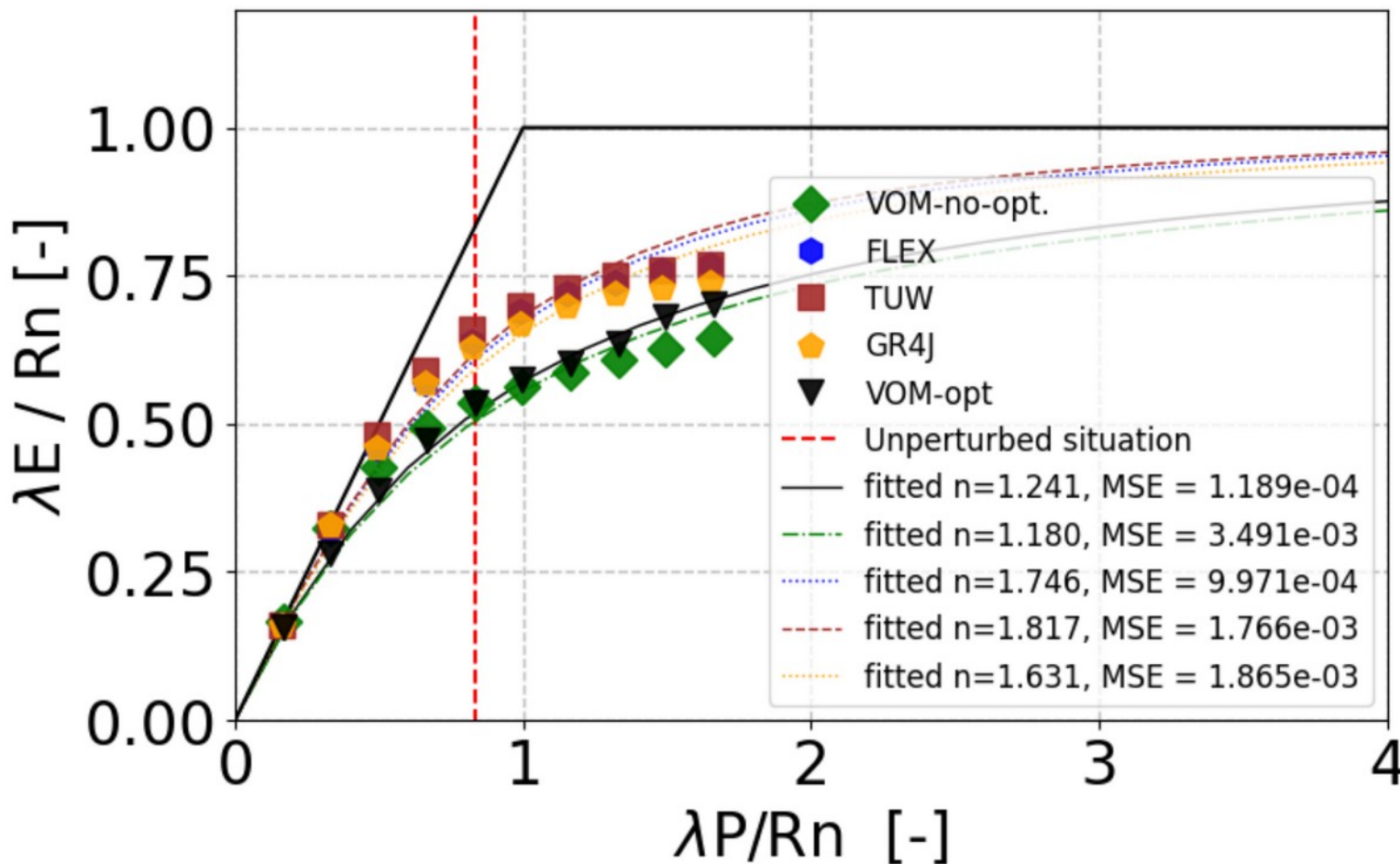
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# OPTIMALITY PREDICTS CONVERGENCE ON BUDYKO CURVE

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Nijzink, R. C., & Schymanski, S. J. (2022). HESSD 1–29.  
<https://doi.org/10.5194/hess-2022-97>

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Peak Charles NP, Western Australia

Terrestrial ecosystem responses to global change:  
integrating experiments and models to understand  
carbon, nutrient, and water cycling  
Convener: Benjamin Stocker | Co-conveners: Teresa  
Gimeno, Karin Rebel, Sönke Zaehle  
Presentations | Fri, 27 May, 08:30–11:50 (CEST)  
Room 3.16/17

Gedney et al. (2006):  
Nature 439(7078)

CO<sub>2</sub>-Adapt.

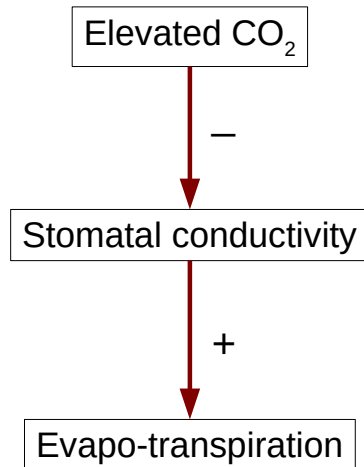
Carbon profit

Optimality

Trade-offs

BG 3.4  
EGU22-8841  
Schymanski et al.

2



In 2006, Gedney et al. pointed out that the response of vegetation to increasing atmospheric CO<sub>2</sub> concentrations is a reduction in ET, and likely responsible for globally increasing stream flow.

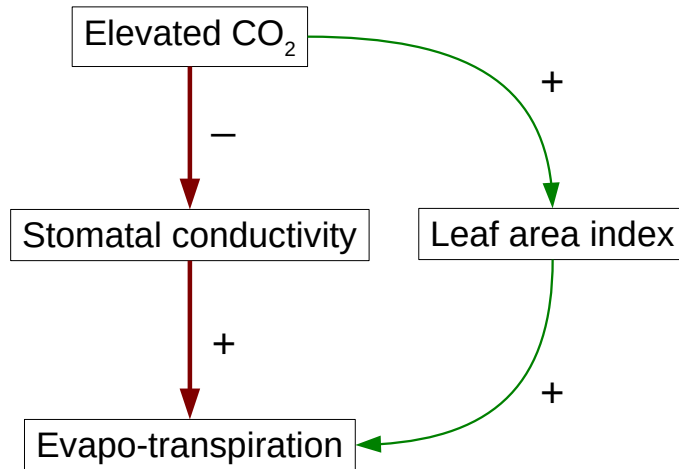
## ADAPTATION TO ELEVATED CO<sub>2</sub>

Gedney et al. (2006):  
Nature 439(7078)

Piao et al. (2007):  
PNAS 104(39)

**Short term**

**Medium term**



CO<sub>2</sub>-Adapt.

Carbon profit

Optimality

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BG 3.4  
EGU22-8841  
Schymanski et al.

However, this response might just be a short-term effect. Piao et al. used a different model and pointed out that the reduced stomatal conductance could be compensated for by an increase in leaf area, largely negating the effect of CO<sub>2</sub> on evapotranspiration.

## ADAPTATION TO ELEVATED CO<sub>2</sub>

Gedney et al. (2006):  
Nature 439(7078)

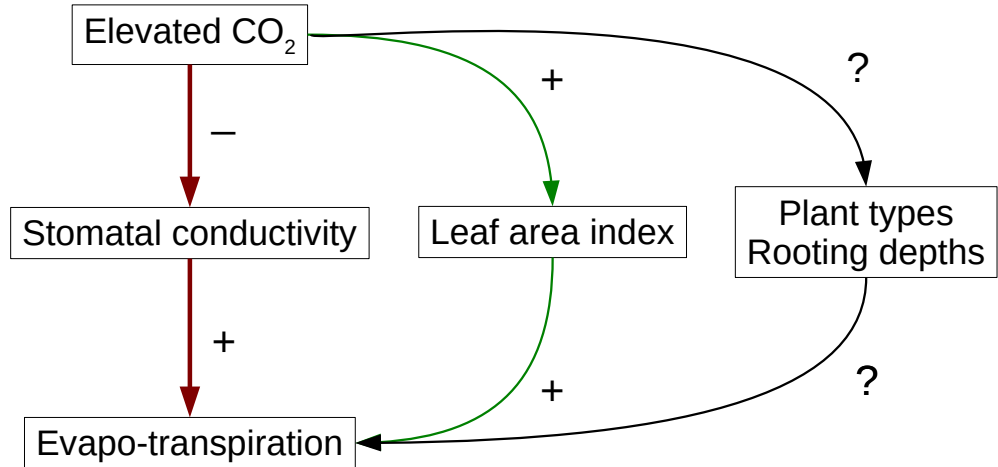
Piao et al. (2007):  
PNAS 104(39)

Schymanski et al. (2015):  
AoB Plants 7

**Short term**

**Medium term**

**Long term**



CO<sub>2</sub>-Adapt.

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BG 3.4  
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Schymanski et al.

4

However, in the long-term, other things could change, too, such as species compositions, rooting depths etc. leading to a different net effect again. To predict such long-term responses to unseen environmental conditions, we cannot resort to past observations alone, but we need to go back to basic principles.

## GENERAL PRINCIPLES BEHIND VEGETATION RESPONSES?

CO<sub>2</sub>-Adapt.

Carbon profit

Optimality

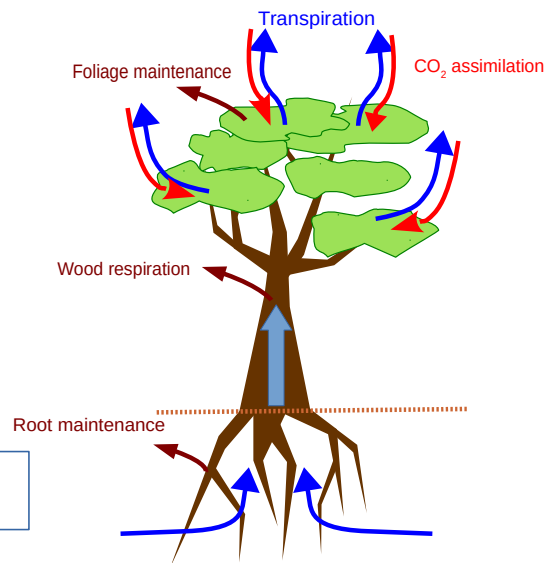
Trade-offs

BG 3.4  
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5

- Carbohydrates as energy currency
- Leaf gas exchange determines gross income
- Trade-offs between carbon gain and loss guide economics
- Selective pressure for best use of resources to **maximise the Net Carbon Profit**

→ Vegetation Optimality Model (VOM):  
Schymanski et al. 2009, WRR 45



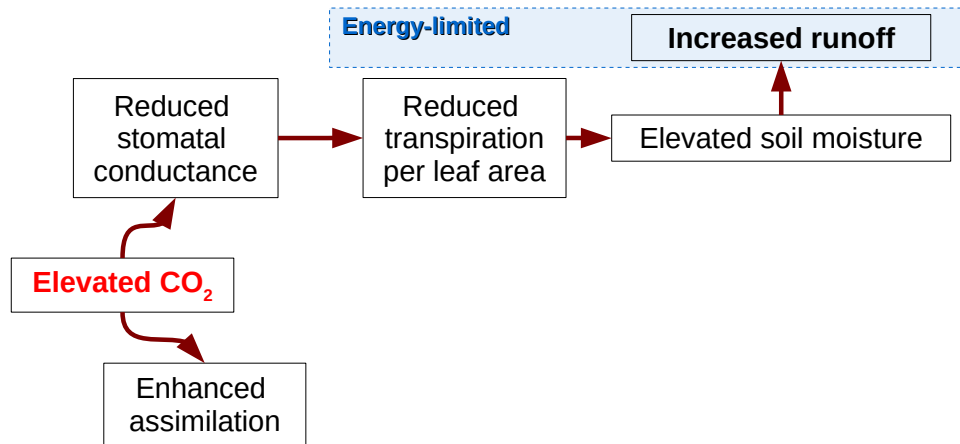
What might be the general principles guiding the adaptation of vegetation to its environment? Plants support life on our planet by using solar energy to turn CO<sub>2</sub> into carbohydrates. If we consider carbohydrates as energy currency, we find that leaf gas exchange determines the gross income, while a lot of other plant organs assist in supplying the leaves with water and nutrients and exposing them to light. The trade-offs between carbon gain, structural investment and maintenance loss are likely to guide the adaptation to their environment. Furthermore, if there is a selective pressure for best use of resources, we could imagine that vegetation self-optimises for maximum net carbon profit. This hypothesis is the basis of the VOM, which dynamically optimises vegetation properties and water use in order to maximise the long-term NCP.

## ADAPTATION TO ELEVATED CO<sub>2</sub>: VEGETATION OPTIMALITY MODEL (VOM)

CO<sub>2</sub>-Adapt.  
Carbon profit  
**Optimality**  
Trade-offs

BG 3.4  
EGU22-8841  
Schymanski et al.

6



Schymanski et al. (2015):  
AoB Plants 7

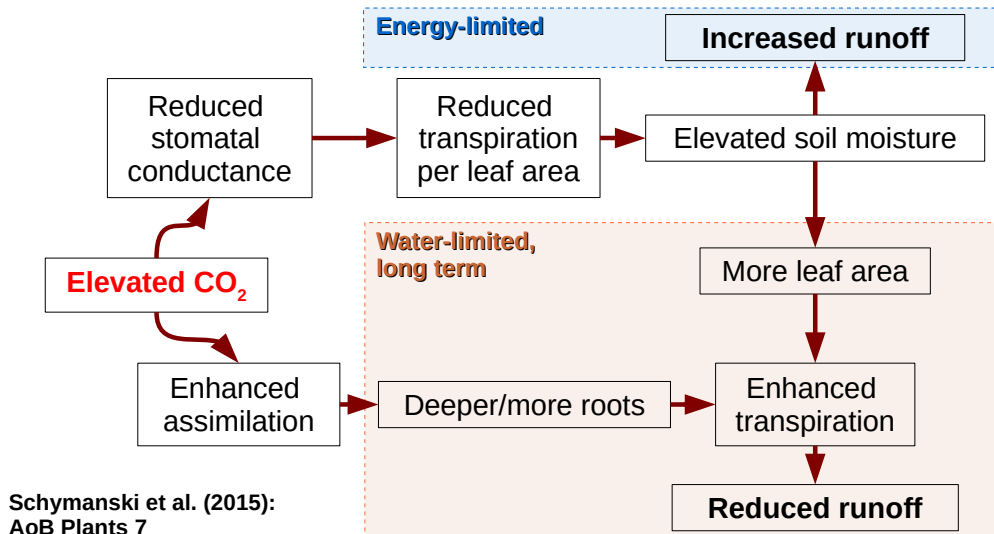
The VOM predicted that eCO<sub>2</sub> would indeed result in enhanced assimilation and reduced transpiration in the short term, which would then result in elevated soil moisture and increased runoff. However, in the long term, this response was limited to energy-limited ecosystems. For water-limited ecosystems, elevated soil moisture allowed more plants to grow and hence resulted in increased leaf area, whereas at the same time, enhanced assimilation allowed to produce deeper or more roots, together enhancing transpiration and eventually reducing runoff. So we clearly have to distinguish between energy-limited and water-limited ecosystems, and also between short-term and long-term responses, as they can be quite opposite.

## ADAPTATION TO ELEVATED CO<sub>2</sub>: VEGETATION OPTIMALITY MODEL (VOM)

CO<sub>2</sub>-Adapt.  
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7



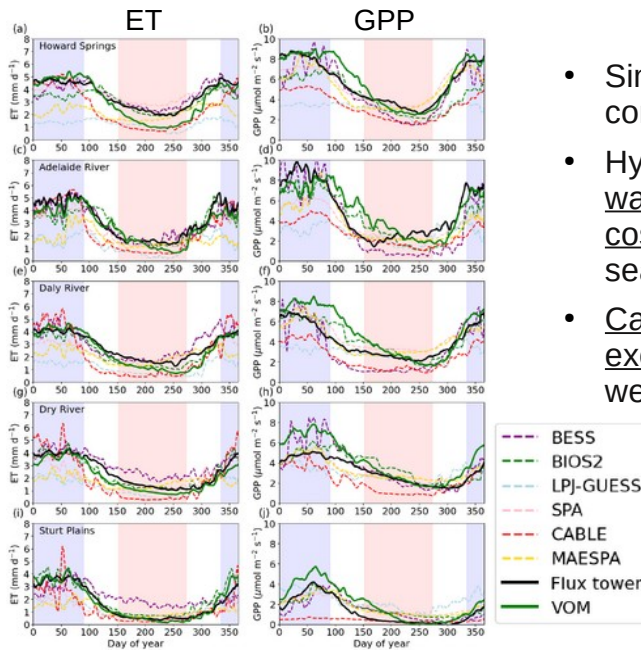
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## VEGETATION OPTIMALITY PREDICTS ET & GPP

CO<sub>2</sub>-Adapt.  
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BG 3.4  
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Schymanski et al.

8



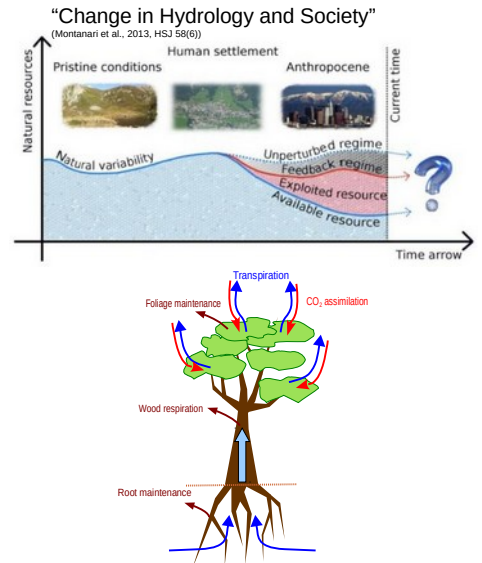
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Nijzink, R. C. et al. (2022): HESS 26(2)  
<https://doi.org/10.5194/hess-26-525-2022>

More recently, the VOM was compared with a range of established vegetation models along an aridity gradient in Australia, and it turned out that the model performed similarly or better than conventional models. Here you see the observations in black and the VOM results in green, with ET on the left and GPP in the right column. All the dashed lines refer to the other models. Please check out the paper in HESS for details. What we also learned here is that hydrology feedback and water uptake and transport costs are important for dry season fluxes, whereas canopy light absorption and gas exchange limits are important for wet season fluxes.

## PROMISES AND CHALLENGES OF OPTIMALITY-BASED MODELLING

- General principles → performance in the past should indicate performance in the future
- Need to quantify physical and biological limits
- Need to quantify trade-offs between costs and benefits of carbon investments



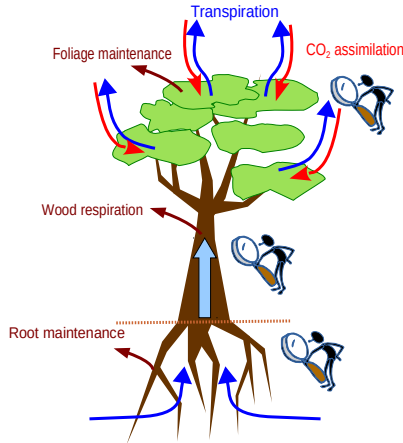
The above results highlight some of the promises of optimality-based modelling, as optimality enables prediction instead of extrapolation, and therefore can be used to predict vegetation behaviour under unseen conditions. Furthermore, since it is based on a general principle, its performance in the past should be indicative of its performance in the future. However, for the model to give meaningful results, we need to accurately quantify the physical and biological limits of plant-environment interaction, and the trade-offs between costs and benefits of carbon investments.

## NEED TO QUANTIFY PHYSICAL LIMITS AND TRADE-OFFS RELATED TO C INVESTMENT

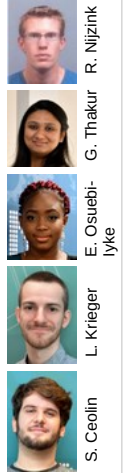
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10



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With this, I thank you for your interest in our work and leave you with a summary of our attempts to simulate vegetation response to change based on first principles.



## APPENDIX...

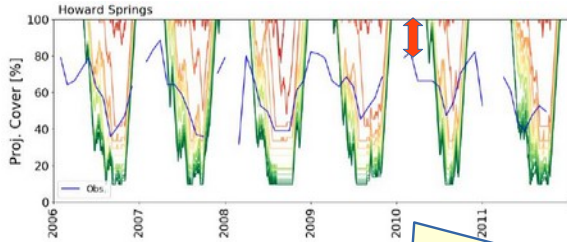
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**CO<sub>2</sub>-Adapt.**  
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**BG 3.4**  
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**Schymanski et al.**

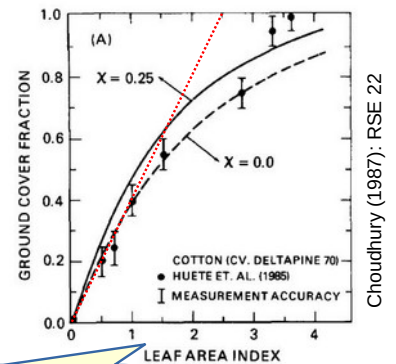
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Choudhury (1987): RSE 22

Nijzink et al.: LAI and light interception: [EGU22-2886.html](https://doi.org/10.5194/egus22-2886)

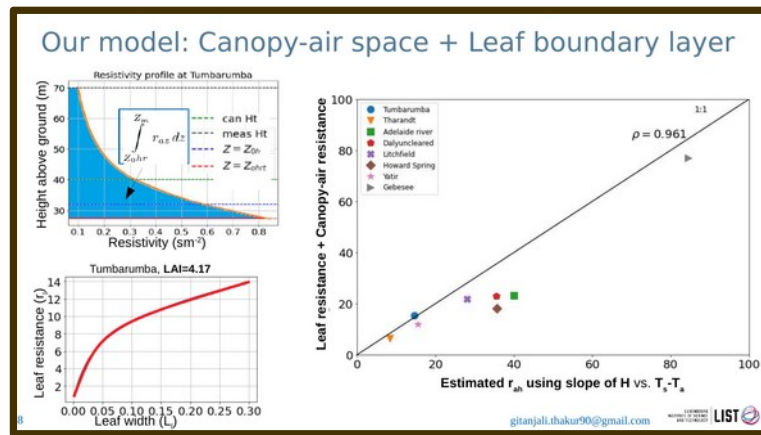
One problem is that the leaf turnover costs in the VOM were calculated based on the assumption that a LAI of 2.5 results in full cover. This was due to a linear extrapolation and neglect of the strong non-linearity between LAI and ground cover fraction at higher LAI values. But this makes us wonder why plants waste so much leaf area instead of growing just one big leaf.

## PHYSICAL LIMITS OF CANOPY GAS EXCHANGE

CO<sub>2</sub>-Adapt.  
 Carbon profit  
 Optimality  
 Trade-offs

BG 3.4  
 EGU22-8841  
 Schymanski et al.

13



Thakur et al.: Leaf vs. canopy resistances: [EGU22-4268.html](https://www.egu22.eu/Program/AbstractDetails.aspx?id=4268)

This is what we set out to do in a series of research projects, two of which focus on quantifying the heat and mass transfer resistance from the leaf surface to the atmosphere, and the light interception by leaves in a canopy.

## TRADE-OFFS RELATED TO WATER TRANSPORT AND STORAGE

CO<sub>2</sub>-Adapt.  
Carbon profit  
Optimality  
**Trade-offs**

Higher wood density  
(smaller vessels)

Janssen et al. (2020): PCE 43(4)

Reduced  
water store

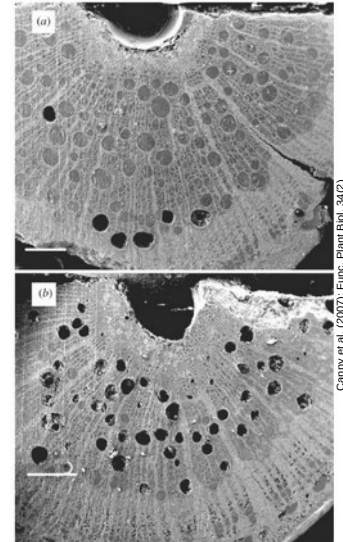
Reduced  
conductivity

Reduced  
embolism

### OPEN QUESTIONS:

- How to measure conductivity?
- How often do xylem vessels need to be replaced?
- How expensive is embolism repair?

Krieger et al.: Plant hydraulic conductivity experiments: [EGU22-5357.html](https://www.egu22-8841.eu/EGU22-5357.html)



Canny et al. (2007): Func. Plant Biol. 34(2)

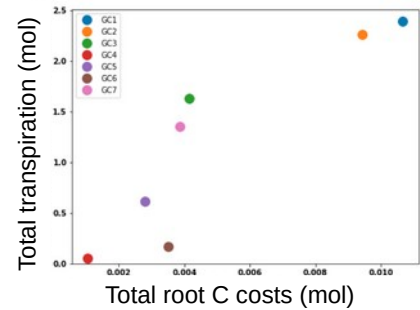
Another project investigates the trade-off between wood density or vessel size and water storage capacity, hydraulic conductivity and embolism vulnerability, where the open questions range from the basic question how to actually measure conductivity, to the longevity of xylem vessels and the carbon costs of embolism repair.

## TRADE-OFFS RELATED TO ROOT UPTAKE

### OPEN QUESTIONS:

- How much C investment per water uptake?
- How does trade-off change with environmental conditions?

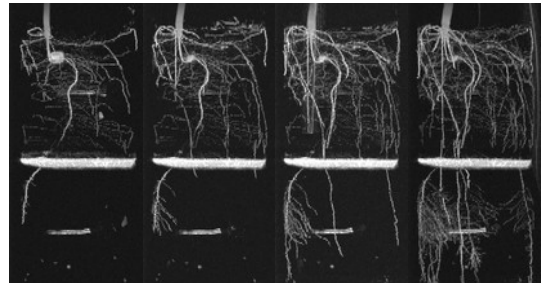
Osuebi et al.: Shoot vs. root C flux experiments: [EGU22-5798.html](https://www.egu22.eu/Programme/Abstracts/Abstracts/EGU22-5798.html)



### OPEN QUESTION:

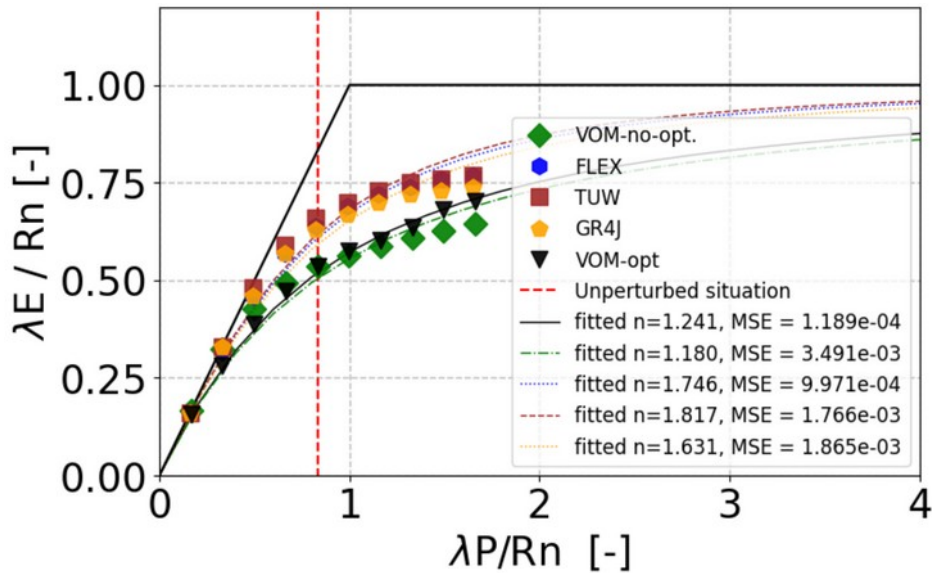
- How quickly can the root system adjust to changing environment?

Ceolin et al.: Root system dynamics experiments: [EGU22-5306.html](https://www.egu22.eu/Programme/Abstracts/Abstracts/EGU22-5306.html)



Yet another two projects focus on the trade-off between root c investment and maintaining a given water uptake capacity under different environmental conditions, and how quickly roots can actually adapt to a changing environment.

## OPTIMALITY PREDICTS CONVERGENCE ON BUDYKO CURVE



Another interesting result of the Vegetation Optimality Model is that it explains response of vegetation water use to changes in precipitation. Catchments world-wide follow the empirical Budyko curve and it is commonly assumed that the response of ET to changes in climate can be simulated by moving a catchment along its own Budyko curve. In a recent paper in HESSD, we found that only if vegetation is allowed to optimally adjust to each new precipitation setting, the catchment does indeed move along the Budyko curve, otherwise the sensitivity to rainfall is smaller than the empirical curve.