# Temporal constraints on leaf-level trait plasticity for EEO modelling

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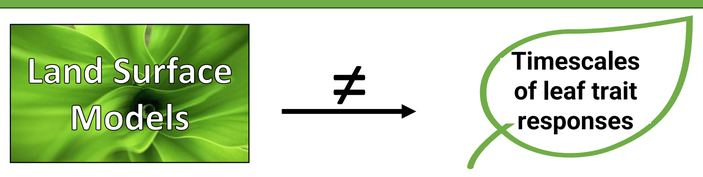
LEMONTREE Land Ecosystem Models based On New Theory, obseRvations and ExperimEnts

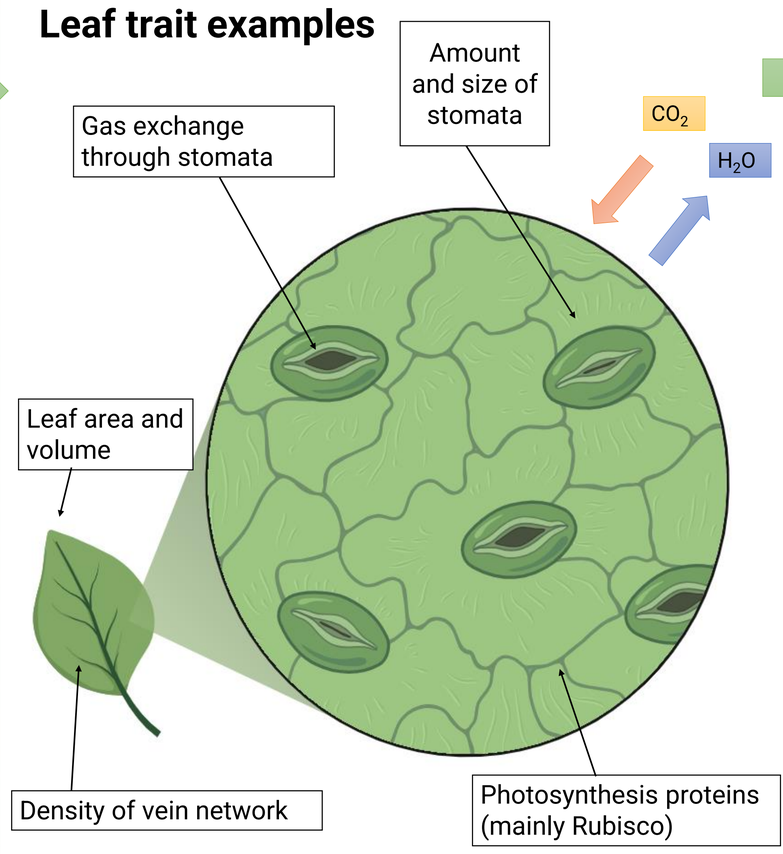
## INTRODUCTION




- **Leaf traits can respond to environmental changes on different timescales** ranging from seconds to millions of years, through processes of physiological responses, acclimation, and adaptation
- Current vegetation models (LSMs) do not do justice to these different timescales
- **Eco-evolutionary optimality (EEO)** theory: "plants adapt or acclimate to their environment, thereby eliminating uncompetitive plant strategies by natural selection" → more dynamic, but still lacking explicit timescales → leads to unrealistic predictions for vegetation modelling
- The **P-model** [1] is based on EEO theory

**Aim: identify the temporal constraints on key leaf-level EEO traits and outline potential interactions between traits to improve EEO modeling (specifically the P-model)**

### Leaf trait examples




## METHODS

**Step 1: identify timescales of key leaf traits with literature review**

Known coordination- and optimality theories:

- Coordination of stomatal conductance: $g_s/g_{smax}$ [2,3]
- Coordination of photosynthetic capacity and hydraulics ($A_{max}$ versus $K_{leaf}$) [4]
- Worldwide Leaf Economics spectrum (WLES) [5]
- P-model [1]:

$$a\,\frac{\partial(E/A)}{\partial\chi} = -b\,\frac{\partial(V_{cmax}/A)}{\partial\chi}$$

**Step 2: construct conceptual framework**

- x- axis = idealized gas exchange response
- y-axis = idealized biochemical response

→ Axes together: point of 'optimality'

## LITERATURE REVIEW RESULTS

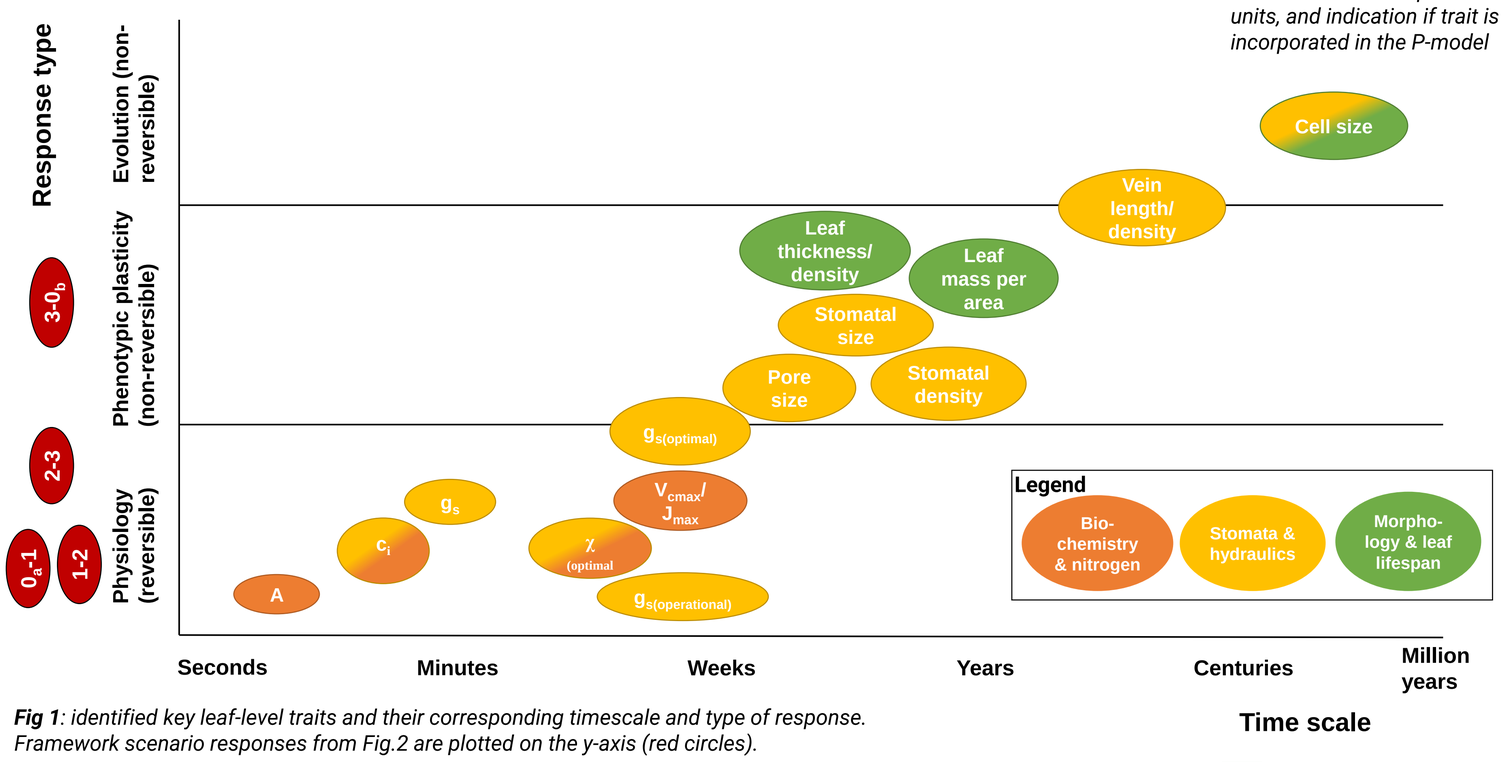



*Fig 1: identified key leaf-level traits and their corresponding timescale and type of response. Framework scenario responses from Fig.2 are plotted on the y-axis (red circles).*

***Table 1:** Trait descriptions and units, and indication if trait is incorporated in the P-model*

| Leaf-trait | Units | Description | In P-model? |
|---|---|---|---|
| A* | $mol \cdot m^{-2} \cdot s^{-1}$ | Photosynthesis rate | ✓ |
| $C_i$ | $mol \cdot mol^{-1}$ | Intercellular CO2 concentration | ✓ |
| $g_s$* | $mol \cdot m^{-2} \cdot s^{-1}$ | Stomatal conductance | ✓ |
| $g_{s(operational)}$ | $mol \cdot m^{-2} \cdot s^{-1}$ | Operational stomatal conductance | |
| $g_{s(optimal)}$* | $mol \cdot m^{-2} \cdot s^{-1}$ | Optimal stomatal conductance according to P-model | ✓ |
| $\chi_{(optimal)}$* | unitless | Optimal $c_i$:$c_a$ ratio as calculated from the P-model | ✓ |
| $V_{cmax}$* | $mol \cdot m^{-2} \cdot s^{-1}$ | Maximum carboxylation rate | ✓ |
| $J_{max}$* | $mol \cdot m^{-2} \cdot s^{-1}$ | Maximum electron transport rate | |
| Pore length | µm | Stomatal pore length | |
| Pore width | µm | Stomatal pore width, assumed equal to pore depth | |
| Stomatal density | $stomata \cdot mm^{-2}$ | Number of stomata per leaf area | |
| Stomatal size | $\mu m^{-2}$ | Stomatal length multiplied by stomatal width | |
| Vein length | µm | Vein length per unit area | |
| Vein density | $\mu m \cdot mm^{-2}$ | Vein density per unit area | |
| Cell size | µm | Cell length or cell width, e.g. stomata or epidermal cells | |
| $g_{s(max)}$ | $mol \cdot m^{-2} \cdot s^{-1}$ | Anatomical maximum stomatal conductance | |
| Leaf thickness | $cm^{-3} \cdot m^{-2}$ | Leaf volume per area / leaf volume to area ratio | |
| Leaf density | $g \cdot cm^{-3}$ | Leaf dry mass per leaf volume | |
| LMA | $g \cdot m^{-2}$ | Leaf dry mass per leaf area | |

## CONCEPTUAL FRAMEWORK

*Fig. 2: Conceptual framework and scenarios of idealized leaf-level gas exchange and photosynthesis to environmental changes, illustrated with identified key leaf traits from figure 1.*

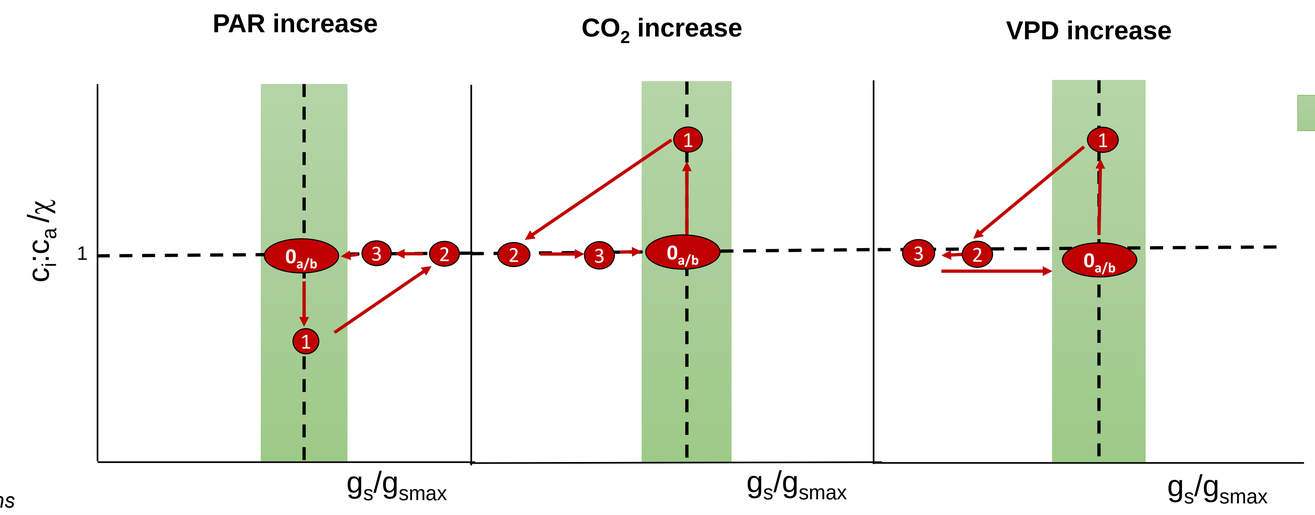



***Table 2:** Conceptual framework scenario response descriptions*

| Response + timescale | PAR increase | $CO_2$ increase | VPD increase |
|---|---|---|---|
| *$0_a$ Initial state* | | | |
| $0_a$→1 instantaneous | A increase, $c_i$ decrease | Increase in $C_a$ | Increase in VPD |
| 1→2 minutes | Stomatal opening | Stomatal closure | Stomatal closure |
| 2→3 weeks | $V_{cmax}$ upregulation | $V_{cmax}$ downregulation | $V_{cmax}$ upregulation |
| 3→$0_b$ months-years | New leaf with higher $g_{smax}$ | New leaf with lower $g_{smax}$ | New leaf with lower $g_{smax}$ |
| *Net photosynthesis rate* | *Increased* | *Increased* | *Slightly decreased* |

## LIMITATIONS

- Leaf-level responses only, though in reality whole-plant and community processes at play (e.g. competition for resources, symbiotic interactions, resource allocation)
- Framework is idealized, also non-functional responses possible and different strategies with the same optimality aim

## DISCUSSION & CONCLUSION

- Tight coordination between leaf trait of biochemistry, gas exchange, and morphology to aim for optimality
  - Especially stomatal and hydraulic traits
  - Cell size may be driver of coordinated traits
- $\chi_{(optimal)}$ is not similar to $c_i$:$c_a$ as currently defined → different response timescales
  - Proposed redefinition $\chi_{(optimal)}$: "acclimated $c_i$:$c_a$ jointly controlled by $g_{s(operational)}$ (instead of $g_s$), and acclimated $V_{cmax}$"

**Acknowledging the costs, benefits, and constraints of leaf-level responses is a way forward in connecting plant ecophysiology with EEO modelling, thereby contributing to the improvement of EEO modelling, and in particular the P-model.**

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