

Peer review status:

This is a non-peer-reviewed preprint submitted to EarthArXiv.

Croplands as thermodynamic agents in a high-CO₂ world

David Helman^{1,2*}

¹Department of Soil and Water Sciences, Institute of Environmental Sciences, The Robert H. Smith Faculty of Agriculture, Food and Environment, Hebrew University of Jerusalem, Rehovot 7610001, Israel

²The Advanced School for Environmental Studies, Hebrew University of Jerusalem, Jerusalem, Israel

*Corresponding author (david.helman@mail.huji.ac.il)

Abstract

Rising atmospheric CO₂ is widely expected to influence crops through physiological pathways, yet croplands are also extensive physical interfaces that regulate land–atmosphere energy exchange. Despite covering 12–15% of Earth’s ice-free land surface, their role in surface energy balance under elevated CO₂ remains poorly constrained. Most CO₂ enrichment studies have not explicitly resolved the surface energy balance, and current models rely on simplified representations of canopy physical properties. As a result, potential CO₂-driven changes in radiative exchange, aerodynamic coupling, and energy partitioning remain largely untested. Here I propose a thermodynamic framework for crop–atmosphere interactions that identifies these missing pathways and formulates testable hypotheses linking canopy processes to boundary-layer dynamics. Resolving these mechanisms is essential for improving projections of land–atmosphere coupling and agricultural climate risk.

For more than four decades, the effects of rising atmospheric CO₂ on crops have been interpreted primarily through plant physiology. In C₃ species, elevated CO₂ enhances photosynthesis while often reducing stomatal conductance, thereby improving water-use efficiency. These responses have been observed consistently across species, climates, and experimental approaches, and underpin current expectations of CO₂ fertilization in crop models and climate assessments^{1–4}. Within this framework, canopy temperature is typically treated as a secondary outcome, assumed to respond to changes in transpiration and evaporative cooling⁵.

This physiological framing has delivered major advances. It has clarified the interactions among CO₂, water availability, nitrogen supply, and temperature^{2,6,7}; explained declines in grain protein and mineral concentrations under elevated CO₂^{8–10}; and helped explain diminishing yield benefits under heat and drought stress¹¹. Despite these advances, the prevailing physiological framing implicitly assumes that the crop canopy’s physical environment remains unchanged or that any relevant changes can be inferred solely from water fluxes. As a result, croplands are often represented in models with simplified or static physical properties^{4,12–15}, likely limiting their ability to capture CO₂-driven changes in surface energy exchange.

More fundamentally, most experimental and modelling approaches have not explicitly resolved the surface energy balance as a primary outcome of CO₂ enrichment, leaving key physical pathways unconstrained. This limitation extends beyond crop physiology: if canopy structure and surface properties respond dynamically to elevated CO₂, then land–atmosphere coupling in agricultural

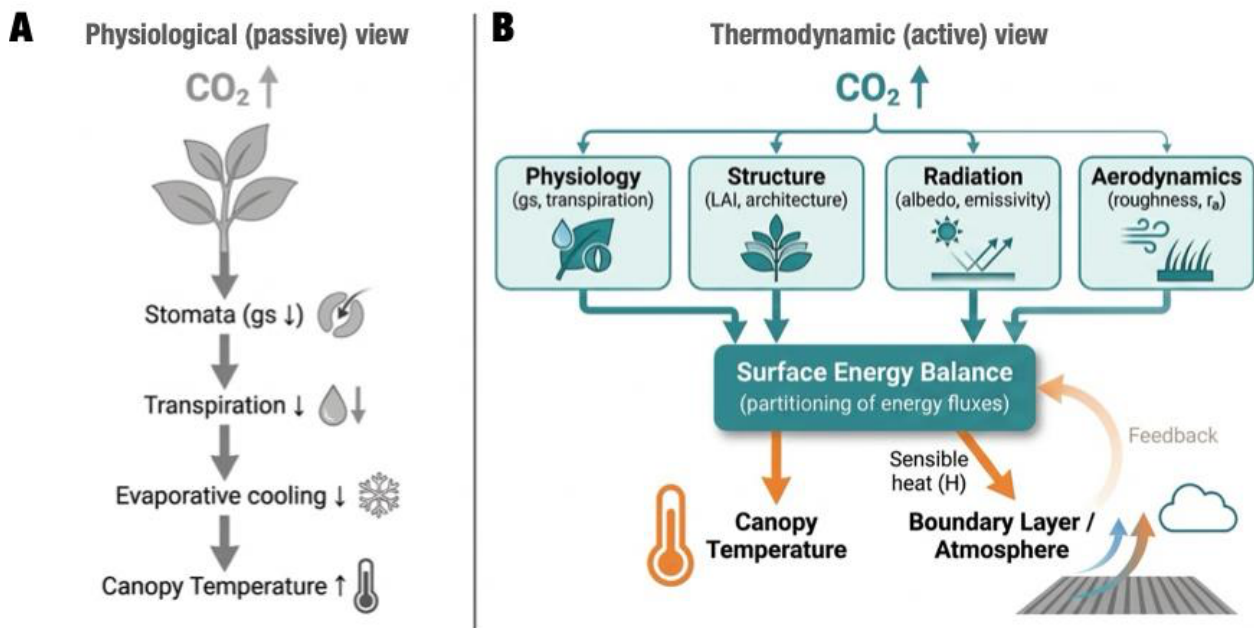
40 regions may be systematically misrepresented, with implications for boundary-layer development
41 and regional climate projections.

42 In Penman–Monteith terms ¹⁶, this implies that while stomatal resistance (r_s) is routinely treated as
43 CO₂-sensitive, aerodynamic resistance (r_a) and radiative terms (net radiation via albedo and
44 emissivity) are often prescribed, weakly dynamic or parameterized through vegetation state
45 variables such as leaf area, rather than explicitly linked to CO₂-driven structural changes in canopy
46 architecture, roughness, albedo or emissivity. This asymmetry reflects a broader imbalance in how
47 crop responses are conceptualized: physiological processes are treated as dynamic and CO₂-
48 responsive, whereas physical processes governing energy exchange are often simplified or assumed
49 invariant.

50 The surface energy balance – the partitioning of incoming radiation into latent, sensible, and stored
51 energy – has rarely been treated as a primary outcome in studies of CO₂ enrichment in crops. Recent
52 field evidence shows that elevated CO₂ can increase leaf temperature by ~1–2 °C independently of
53 stomatal regulation ¹⁷, indicating that additional energy-exchange processes are involved.
54 However, rather than providing a complete mechanistic explanation, such observations highlight a
55 more fundamental gap: the physical pathways linking CO₂, canopy structure, and energy exchange
56 have not been systematically measured or resolved. Because croplands occupy a large fraction of
57 the land surface and are often located in regions of strong land–atmosphere coupling, even modest
58 CO₂-driven shifts in energy partitioning could influence boundary-layer dynamics and near-surface
59 climate.

60 A simple scaling argument illustrates the potential magnitude of this effect. In semi-arid regions,
61 where net radiation often exceeds 400–600 W m⁻² during the growing season, a shift of 10–20%
62 in the partitioning between latent and sensible heat corresponds to changes of ~40–100 W m⁻² in
63 sensible heat flux. Perturbations of this magnitude are comparable to those associated with land-
64 use change and vegetation transitions known to influence regional climate ^{18,19}, suggesting that
65 CO₂-driven crop responses may represent a similarly important, but currently unquantified, forcing.
66 Yet, without direct measurements of energy balance components, it remains unclear whether such
67 shifts occur, through which mechanisms, and under what conditions.

68 Figure 1 depicts the prevailing physiological view of CO₂'s impact on crops (crops as passive
69 recipients of climate change) versus a more active, thermodynamic view of crops as key agents in
70 climate change, which is not explicitly represented in most current Earth system models.



71

72 **Figure 1 | From physiological to thermodynamic crop responses.** **A.** The prevailing physiological view,
 73 in which elevated CO₂ influences canopy temperature primarily through reduced stomatal conductance and
 74 evaporative cooling. **B.** A thermodynamic, more active view in which CO₂-driven changes in physiology,
 75 canopy structure, radiative exchange and aerodynamic coupling jointly determine surface energy balance,
 76 canopy temperature and atmospheric exchange, with potential feedbacks to boundary-layer processes.

77 **How our current understanding of CO₂ effects on crops emerged**

78 Early experimental efforts relied on growth chambers and open-top chambers²⁰. Although these
 79 systems allowed precise control of atmospheric composition, they altered radiation, turbulence,
 80 humidity, and temperature, introducing artefacts that were particularly problematic for water and
 81 energy exchange^{21–23}. As a result, they were poorly suited to resolving how elevated CO₂ modifies
 82 crop–atmosphere coupling under realistic field conditions.

83 The development of free-air CO₂ enrichment (FACE)²⁴ addressed this limitation by enriching CO₂
 84 directly in the open atmosphere around field-grown crops. FACE preserves natural radiation, wind,
 85 precipitation, and atmospheric variability, and establishes a new standard for studying crop
 86 responses under realistic conditions^{25,26}. This represented a major conceptual advance: it restored
 87 atmospheric realism to crop experimentation, even if the dominant questions remained largely
 88 physiological.

89 Over the past three decades, FACE experiments have transformed crop science, providing the
 90 empirical foundation for understanding CO₂ effects on photosynthesis, stomatal conductance,
 91 evapotranspiration, yield formation, and grain quality^{7,9,27,28}. Much of what is now considered
 92 established knowledge about crop responses to elevated CO₂ is anchored in these experiments. At
 93 the same time, because FACE was primarily mobilized to address physiological and agronomic
 94 questions, it did not systematically resolve crop surface energy balance as a primary outcome.

95 One reason these pathways remain unresolved is that most FACE experiments were not designed
 96 to close the surface energy balance, lacking continuous measurements of net radiation, canopy
 97 temperature and turbulent fluxes at sufficient temporal resolution to resolve coupled
 98 thermodynamic responses.

99 **The structural limits of a physiology-centred view**

100 The general omission of physical processes governing the surface energy balance under elevated
101 CO₂ was recognized early. In the first FACE experiment, conducted in Maricopa, AZ, researchers
102 measured canopy temperature and turbulent fluxes, showing that elevated CO₂ could alter the
103 partitioning of sensible and latent heat even under non-limiting water conditions²⁹. Modelling
104 studies similarly suggested that CO₂-driven changes in canopy structure and physiology could
105 reorganize energy balance and influence canopy temperature³⁰. Yet these efforts remained isolated.
106 The field largely converged on a simplified causal chain: elevated CO₂ reduces stomatal
107 conductance, transpiration declines, and any warming arises from suppressed evaporative cooling
108^{5,31}. This general interpretation has become influential in crop science and modelling^{32–34}, despite
109 rarely being tested directly against full energy-balance measurements under diverse environmental
110 and climatic conditions in FACE.

111 **Croplands as energy-exchanging surfaces**

112 Croplands differ fundamentally from forests in both structure and climatic function. They are short,
113 seasonally transient, and dynamically evolving, with shallow rooting depths and strong contrasts
114 between vegetation and soil. Aerodynamic coupling is therefore weaker and more sensitive to
115 canopy structure, while radiative exchange depends strongly on leaf area, canopy architecture, and
116 soil exposure. These characteristics make croplands particularly sensitive to changes in surface
117 energy partitioning, and therefore potentially important contributors to land–atmosphere exchange.
118 Unlike forests, where aerodynamic coupling is strong and relatively stable, croplands exhibit rapid
119 temporal changes in canopy structure and soil exposure. This dynamism implies that small CO₂-
120 driven shifts in canopy development or architecture could disproportionately affect radiative
121 transfer and turbulent exchange, amplifying their impact on surface energy balance.

122 Such an effect is especially consequential in semi-arid and transitional regions, where incoming
123 radiation is high and evaporative buffering is limited, making them particularly sensitive to land–
124 atmosphere coupling^{35,36}. If elevated CO₂ alters crop structure, development, or optical properties,
125 as widely observed^{7,28,37,38}, then it may also reorganize surface energy balance through pathways
126 beyond transpiration alone. This is consistent with recent FACE-based observations demonstrating
127 a systematic canopy warming signal that cannot be explained by stomatal regulation alone in a
128 dryland region¹⁷.

129 Elevated CO₂ may influence canopy temperature through three primary physical pathways beyond
130 stomatal regulation. First, changes in canopy structure, including leaf area, architecture, and soil
131 exposure, can alter the interception and distribution of radiation within the canopy³⁹. Second,
132 modifications to surface optical properties, including albedo and emissivity, may influence net
133 radiation and radiative cooling⁴⁰. Third, shifts in canopy structure may affect aerodynamic
134 coupling by altering roughness length, porosity, and boundary-layer resistance, thereby modifying
135 the efficiency of sensible heat exchange with the atmosphere⁴¹. Finally, physiological responses,
136 including changes in stomatal conductance and plant water status, are likely to interact with these
137 structural and physical pathways to influence latent heat flux.

138 These processes are tightly coupled: structural changes influence radiative and aerodynamic
139 properties, while temperature and radiation feed back on physiological responses. Framed this way,
140 crop warming under elevated CO₂ becomes a tractable but unresolved problem in coupled canopy
141 thermodynamics. The relative contribution of these pathways remains uncertain, but each has the

142 potential to modify sensible heat fluxes by tens of $W\ m^{-2}$ under typical growing-season conditions.
 143 Because these pathways operate through distinct physical processes, their combined effects may
 144 be nonlinear and context-dependent, complicating the attribution of canopy warming to any single
 145 mechanism.

146 This framework generates a set of testable hypotheses that define the pathways linking canopy
 147 processes to atmospheric outcomes as described in Box 1 and schematically represented in Fig. 2.

148

149 **Box 1 | Testable hypotheses for thermodynamically resolved crop science**

150 Elevated CO_2 may reorganize crop–atmosphere interactions through coupled physiological and physical
 151 processes, generating four testable hypotheses:

152 **H1 | Non-stomatal warming**

153 Elevated CO_2 increases canopy temperature independently of transpiration through changes in radiative
 154 exchange and aerodynamic coupling.

155 **H2 | Context dependence**

156 The relative importance of physiological and physical pathways should vary systematically with
 157 hydroclimatic context, canopy structure, soil exposure and phenology.

158 **H3 | Atmospheric propagation**

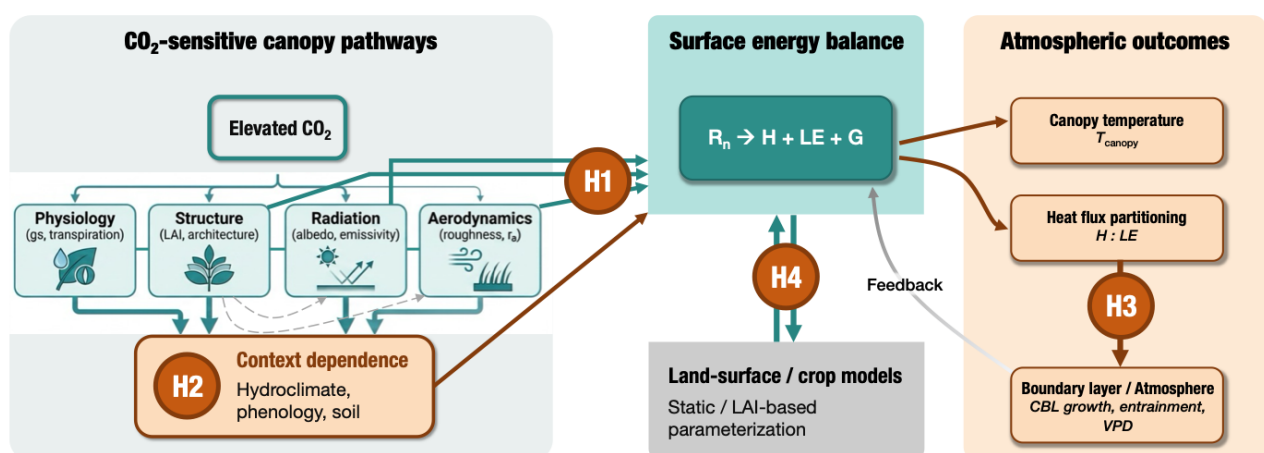
159 CO_2 -driven increases in sensible heat flux from croplands enhance boundary-layer growth and atmospheric
 160 drying under water-limited conditions.

161 **H4 | Model bias**

162 If these processes are not explicitly represented, current land-surface and crop models may exhibit
 163 systematic biases in projections of land–atmosphere coupling and regional climate.

164 These hypotheses define a structured set of pathways linking canopy-scale processes to atmospheric
 165 outcomes, as illustrated in Fig. 2.

166



167

168 **Figure 2 | Hypothesized pathways linking elevated CO_2 to canopy thermodynamics and atmospheric**
 169 **feedbacks.** Elevated CO_2 may alter canopy temperature through interacting physiological, structural,
 170 radiative and aerodynamic pathways that determine surface energy balance ($R_n \rightarrow H + LE + G$). These
 171 processes are coupled and context dependent, with canopy structure influencing both radiative exchange
 172 and aerodynamic coupling. The resulting changes in sensible and latent heat partitioning can propagate to
 173 the boundary layer, affecting convective boundary-layer (CBL) growth, entrainment and atmospheric

174 drying. **H1–H4** correspond to the testable hypotheses defined in Box 1: non-stomatal warming (**H1**), context
175 dependence (**H2**), atmospheric propagation (**H3**), and model bias (**H4**).

176 Among these pathways, changes in aerodynamic coupling – via shifts in canopy roughness and
177 porosity – and changes in radiative exchange – via altered leaf angle distribution and surface optical
178 properties – are likely to be particularly important candidates for explaining canopy warming
179 independent of transpiration, although their relative contributions remain unresolved.

180 **Unresolved aspects of crop–atmosphere coupling**

181 This perspective points to three agenda-setting questions for crop–atmosphere interactions under
182 elevated CO₂. First, the magnitude and seasonal evolution of CO₂-driven changes in crop surface
183 energy balance remain poorly constrained. Second, the physical pathways underlying canopy
184 warming are not well resolved. Third, the atmospheric relevance of cropland thermodynamic
185 responses remains largely unexplored. Together, these questions define a focused research agenda
186 linking canopy-scale processes to atmospheric outcomes.

187 **Observational requirements for resolving crop energy balance**

188 Addressing these gaps requires an observational strategy that treats surface energy balance as a
189 primary outcome of CO₂ enrichment rather than a secondary by-product. FACE remains uniquely
190 suited to this task, but must be extended to include measurements of radiation, temperature, and
191 turbulent exchange under open-air conditions. These measurements are essential for testing the
192 empirical hypotheses outlined in Box 1 and for constraining model representations of crop–
193 atmosphere coupling.

194 An energy-resolved FACE design would require co-located measurements of four-component
195 radiation, high-frequency canopy and soil temperature, turbulent fluxes, soil heat flux, canopy
196 structure and aerodynamic state. These measurements should be repeated across phenological
197 stages and soil water regimes to distinguish transient physiological responses from structural and
198 radiative reorganization.

199 **Linking field-scale processes to atmospheric effects**

200 Surface fluxes of sensible and latent heat regulate boundary-layer growth and atmospheric moisture
201 by controlling buoyancy production and turbulent mixing. Given the spatial extent of croplands,
202 CO₂-driven shifts in energy partitioning could contribute to land–atmosphere feedbacks that
203 influence heat extremes and hydroclimatic stress⁴². In this context, croplands should be viewed
204 not only as recipients of climate change but also as active contributors to regional climate
205 dynamics.

206 The extent to which such thermodynamic shifts influence the atmosphere depends on spatial
207 coherence and scale. At the field scale, changes in canopy energy partitioning primarily affect local
208 temperature and fluxes. However, over large, contiguous agricultural regions, coherent increases
209 in sensible heat flux may alter convective boundary-layer (CBL) development, enhance
210 entrainment of warm, dry air, and contribute to atmospheric drying. In such cases, croplands may
211 not only respond to climate forcing but also participate in feedback loops that amplify near-surface
212 warming and vapor pressure deficit^{43–45}.

213 Although the magnitude of the thermodynamic contribution remains uncertain due to a lack of
214 empirical observations, even small systematic increases in canopy temperature can shift crops
215 beyond critical thermal thresholds during sensitive developmental stages. This suggests that
216 neglecting non-physiological pathways may introduce disproportionately large biases in
217 projections of heat stress risk and future climate change.

218 **Reframing crop responses to elevated CO₂**

219 Croplands represent one of the most extensive managed interfaces between the biosphere and
220 atmosphere, yet their thermodynamic role under elevated CO₂ remains poorly constrained. This
221 perspective introduces the concept of a “thermodynamic ideotype” for crops under elevated CO₂,
222 in which canopy traits that enhance heat dissipation, such as architecture, reflectance, and
223 aerodynamic roughness, are considered alongside physiological efficiency. This framing implies a
224 shift in crop design and evaluation, from maximizing carbon gain alone to jointly optimizing carbon
225 assimilation and thermal regulation under future atmospheric conditions. FACE experiments
226 restored atmospheric realism to the study of crop responses to elevated CO₂; the next step is to
227 fully account for the physical consequences of that realism.

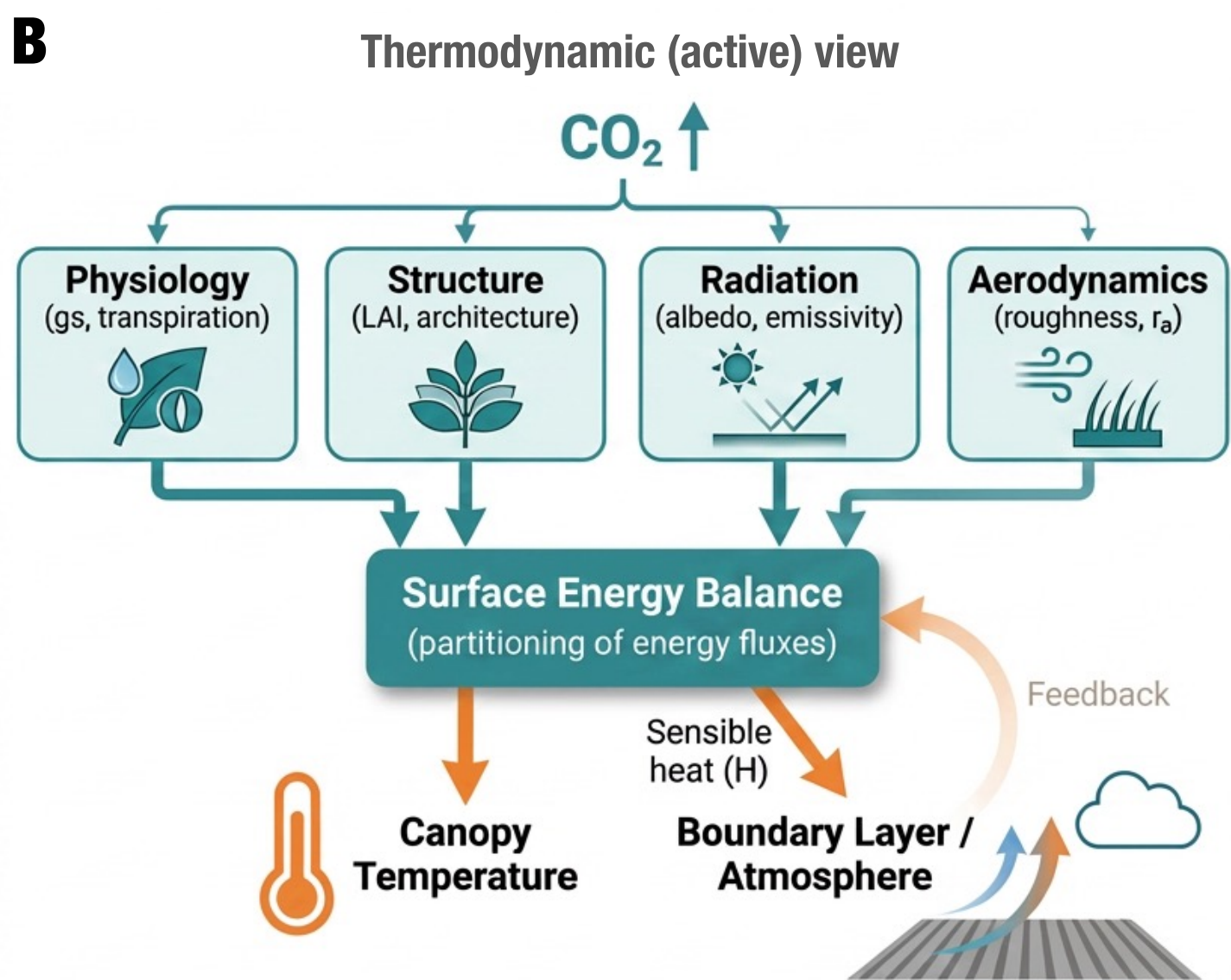
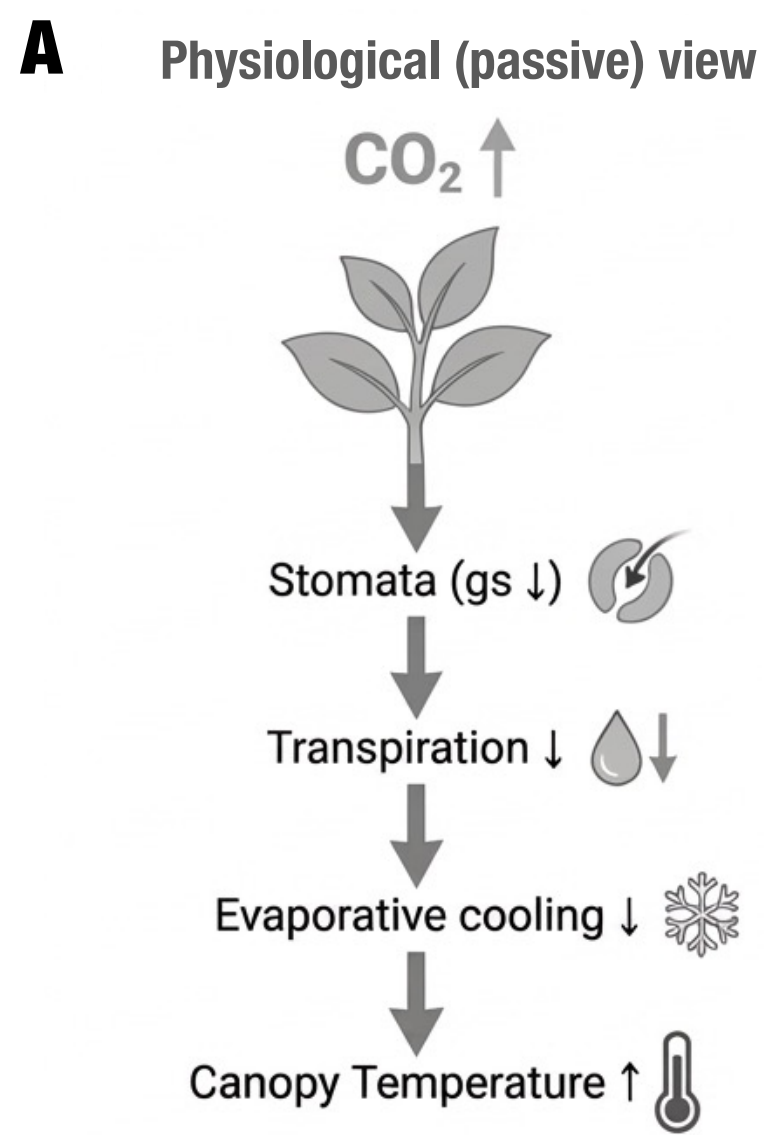
228 Given the vast spatial extent of croplands and their concentration in regions of strong land–
229 atmosphere coupling, even modest shifts in surface energy partitioning, on the order of tens of W
230 m⁻² in sensible heat flux, could influence boundary-layer development and near-surface climate.
231 In agricultural regions already vulnerable to heat stress, such changes may exacerbate thermal
232 extremes, with consequences for crop productivity, labor capacity, and food security, particularly
233 in semi-arid environments. In this context, croplands should be viewed not only as recipients of
234 climate forcing but as dynamic regulators of energy exchange that can modulate regional climate.
235 Explicitly representing these processes is therefore essential for improving projections of land–
236 atmosphere coupling and agricultural climate risk within Earth system frameworks, including those
237 used by the IPCC.

238 **References**

- 239 1. Allen, L. H., Kakani, V. G., Vu, J. C. V & Boote, K. J. Elevated CO₂ increases water use efficiency by
240 sustaining photosynthesis of water-limited maize and sorghum. *J. Plant Physiol.* **168**, 1909–1918 (2011).
- 241 2. Kimball, B. A. Crop responses to elevated CO₂ and interactions with H₂O, N, and temperature. *Curr. Opin.*
242 *Plant Biol.* **31**, 36–43 (2016).
- 243 3. Bishop, K. A. *et al.* Similar photosynthetic response to elevated carbon dioxide concentration in species with
244 different phloem loading strategies. *Photosynth. Res.* **137**, 453–464 (2018).
- 245 4. Toreti, A. *et al.* Narrowing uncertainties in the effects of elevated CO₂ on crops. *Nat. Food* **1**, 775–782 (2020).
- 246 5. Ainsworth, E. A. & Rogers, A. The response of photosynthesis and stomatal conductance to rising [CO₂]:
247 mechanisms and environmental interactions. *Plant. Cell Environ.* **30**, 258–270 (2007).
- 248 6. Kimball, B. A. *et al.* Free-air CO₂ enrichment and soil nitrogen effects on energy balance and
249 evapotranspiration of wheat. *Water Resour. Res.* **35**, 1179–1190 (1999).
- 250 7. Ainsworth, E. A. & Long, S. P. 30 years of free-air carbon dioxide enrichment (FACE): What have we learned
251 about future crop productivity and its potential for adaptation? *Glob. Chang. Biol.* **27**, 27–49 (2021).
- 252 8. Myers, S. S. *et al.* Increasing CO₂ threatens human nutrition. *Nature* **510**, 139–142 (2014).
- 253 9. Wang, D. *et al.* Impact of rising CO₂ on food security and human health risks and potential adaptation
254 strategies. *Glob. Chang. Biol.* **31**, 1–16 (2025).
- 255 10. Gojon, A., Cassan, O., Bach, L., Lejay, L. & Martin, A. The decline of plant mineral nutrition under rising
256 CO₂: physiological and molecular aspects of a bad deal. *Trends Plant Sci.* **28**, 185–198 (2023).

- 257 11. Gray, S. B. *et al.* Intensifying drought eliminates the expected benefits of elevated carbon dioxide for soybean.
258 *Nat. Plants* **2**, (2016).
- 259 12. Yang, Y., Roderick, M. L., Zhang, S., McVicar, T. R. & Donohue, R. J. Hydrologic implications of vegetation
260 response to elevated CO₂ in climate projections. *Nat. Clim. Chang.* **9**, 44–48 (2019).
- 261 13. Forzieri, G. *et al.* Increased control of vegetation on global terrestrial energy fluxes. *Nat. Clim. Chang.* **10**,
262 356–362 (2020).
- 263 14. Vanuytrecht, E. & Thorburn, P. J. Responses to atmospheric CO₂ concentrations in crop simulation models: a
264 review of current simple and semicomplex representations and options for model development. *Glob. Chang.*
265 *Biol.* **23**, 1806–1820 (2017).
- 266 15. Knauer, J. *et al.* Effects of mesophyll conductance on vegetation responses to elevated CO₂ concentrations in
267 a land surface model. *Glob. Chang. Biol.* **25**, 1820–1838 (2019).
- 268 16. Monteith, J. L. Evaporation and environment. (1965).
- 269 17. Helman, D., Mulero, G. & Tamata, E. Elevated CO₂ increases leaf temperature independently of stomatal
270 regulation. *Res. Sq.* (2026) doi:10.21203/rs.3.rs-9493050/v1.
- 271 18. Behrendt, A. *et al.* Observation of sensible and latent heat flux profiles with lidar. *Atmos. Meas. Tech.* **13**,
272 3221–3233 (2020).
- 273 19. Stull, R. B. *An Introduction to Boundary Layer Meteorology.* (Springer Dordrecht, 1988).
274 doi:https://doi.org/10.1007/978-94-009-3027-8.
- 275 20. Bishop, K. A., Leakey, A. D. B. & Ainsworth, E. A. How seasonal temperature or water inputs affect the
276 relative response of C₃ crops to elevated [CO₂]: A global analysis of open top chamber and free air CO₂
277 enrichment studies. *Food Energy Secur.* **3**, (2014).
- 278 21. Cunningham, P., Linn, R. R., Koo, E. & Wilson, C. J. Large-Eddy Simulations of Air Flow and Turbulence
279 within and around Low-Aspect-Ratio Cylindrical Open-Top Chambers. *J. Appl. Meteorol. Climatol.* **52**, 1716–
280 1737 (2013).
- 281 22. Yu, X. *et al.* Biophysical warming patterns of an open-top chamber and its short-term influence on a
282 Phragmites wetland ecosystem in China. *China Geol.* **6**, 594–610 (2023).
- 283 23. Hollister, R. D. *et al.* A review of open top chamber (OTC) performance across the ITEX Network. *Arct. Sci.*
284 **9**, 331–344 (2022).
- 285 24. Miglietta, F., Lanini, M., Bindi, M. & Magliulo, V. Free Air CO₂ Enrichment of potato (*Solanum tuberosum*,
286 L.): design and performance of the CO₂-fumigation system. *Glob. Chang. Biol.* **3**, 417–427 (1997).
- 287 25. Mollah, M., Norton, R. & Huzzey, J. Australian grains free-air carbon dioxide enrichment (AGFACE) facility:
288 design and performance. *Crop Pasture Sci.* **60**, 697–707 (2009).
- 289 26. Kottmann, L., Kretschmer, L., Carotenuto, F., Zaldei, A. & Brilli, L. Experimental Design and Performance
290 of a Free Air Carbon Dioxide Enrichment Facility in Northern Germany. *J. Agron. Crop Sci.* **211**, e70034
291 (2025).
- 292 27. Long, S. P., Ainsworth, E. A., Rogers, A. & Ort, D. R. Rising Atmospheric Carbon Dioxide: Plants FACE the
293 future. *Annu. Rev. Plant Biol.* **55**, 591–628 (2004).
- 294 28. Ainsworth, E. A. & Long, S. P. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A
295 meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂.
296 *New Phytol.* **165**, 351–372 (2005).
- 297 29. Frumau, K. F. A. & Vugts, H. F. Energy balance of a wheat canopy under elevated and ambient CO₂
298 concentrations. *Phys. Chem. Earth* **21**, 131–134 (1996).
- 299 30. Grossman, S. *et al.* Simulated Responses of Energy and Water Fluxes to Ambient Atmosphere and Free-Air
300 Carbon Dioxide Enrichment in Wheat. *J. Biogeogr.* **22**, 601 (1995).
- 301 31. Burkart, S., Manderscheid, R., Wittich, K.-P., Löpmeier, F. J. & Weigel, H.-J. Elevated CO₂ effects on canopy
302 and soil water flux parameters measured using a large chamber in crops grown with free-air CO₂ enrichment.
303 *Plant Biol.* **13**, 258–269 (2011).
- 304 32. Swann, A. L. S., Hoffman, F. M., Koven, C. D. & Randerson, J. T. Plant responses to increasing CO₂ reduce
305 estimates of climate impacts on drought severity. *Proc. Natl. Acad. Sci. U. S. A.* **113**, 10019–10024 (2016).
- 306 33. Ryder, J. *et al.* A multi-layer land surface energy budget model for implicit coupling with global atmospheric

- 307 simulations. *Geosci. Model Dev.* **9**, 223–245 (2014).
- 308 34. Chitsaz, N., Guan, H., Shanafield, M. & Batelaan, O. Evaluating CO₂ effects on semi-empirical and empirical
309 stomatal conductance simulation in land surface models. *J. Hydrol.* **620**, 129385 (2023).
- 310 35. Tian, L., Yang, Y., Feng, J., Li, Y. & Zhang, B. Energy-mediated feedbacks of vegetation greening enhance
311 precipitation efficiency and sustain water yield in global semi-arid regions. *Nat. Water* (2026)
312 doi:10.1038/s44221-026-00631-y.
- 313 36. Chen, C. *et al.* Biophysical effects of croplands on land surface temperature. *Nat. Commun.* **15**, 10901 (2024).
- 314 37. Long, S. P., Ainsworth, E. A., Leakey, A. D. B., Nöbsrger, J. & Ort, D. R. Food for thought: Lower-than-
315 expected crop yield stimulation with rising CO₂ concentrations. *Science (80-.)*. **312**, 1918–1921 (2006).
- 316 38. Leakey, A. D. B. *et al.* Elevated CO₂ effects on plant carbon, nitrogen, and water relations: Six important
317 lessons from FACE. *J. Exp. Bot.* **60**, 2859–2876 (2009).
- 318 39. Campbell, G. S. & Norman, J. *An Introduction to Environmental Biophysics*. (Springer New York, 1998).
- 319 40. Bonan, G. *Climate change and terrestrial ecosystem modeling*. (Cambridge university press, 2019).
- 320 41. Raupach, M. R. Simplified expressions for vegetation roughness length and zero-plane displacement as
321 functions of canopy height and area index. *Boundary-Layer Meteorol.* **71**, 211–216 (1994).
- 322 42. Cao, L., Bala, G., Caldeira, K., Nemani, R. & Ban-Weiss, G. Importance of carbon dioxide physiological
323 forcing to future climate change. *Proc. Natl. Acad. Sci.* **107**, 9513–9518 (2010).
- 324 43. Miralles, D. G., Vilà-Guerau de Arellano, J., McVicar, T. R. & Mahecha, M. D. Vegetation–climate feedbacks
325 across scales. *Ann. N. Y. Acad. Sci.* **1544**, 27–41 (2025).
- 326 44. Skinner, C., Poulsen, C. & Mankin, J. Amplification of heat extremes by plant CO₂ physiological forcing. *Nat.*
327 *Commun.* **9**, (2018).
- 328 45. Zhang, Z. *et al.* US Corn Belt enhances regional precipitation recycling. *Proc. Natl. Acad. Sci.* **122**,
329 e2402656121 (2025).
- 330



CO₂-sensitive canopy pathways

Elevated CO₂

Physiology
(gs, transpiration)

Structure
(LAI, architecture)

Radiation
(albedo, emissivity)

Aerodynamics
(roughness, r_a)

H2 Context dependence
Hydroclimate,
phenology, soil

H1

Surface energy balance

$$R_n \rightarrow H + LE + G$$

H4

Land-surface / crop models
Static / LAI-based
parameterization

Atmospheric outcomes

Canopy temperature
 T_{canopy}

Heat flux partitioning
 $H : LE$

H3

Boundary layer / Atmosphere
CBL growth, entrainment,
VPD

Feedback