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2nd TERRABITES SYMPOSIUM

Tree-grass dynamics in savannas: connecting ecological theory with Dynamic Global Vegetation Models

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Following TERRABITES workshop Madrid November 2010
WG-3 “Modeling Plant Ecology”

DGVMs:

- JSBACH: V. Brovkin and C. Reick, *MPI Hamburg*
- aDGVM: S. Higgins and S. Scheiter, *BIK - Frankfurt University*
- LPJ-GUESS: V. Lehsten *Lund University*
- LPJ: S. Sitch *University of Exeter*

S. Dekker and M. Rietkerk, *Utrecht University;*

B. Cuesta and M.A. Zavala, *University of Alcalà;*

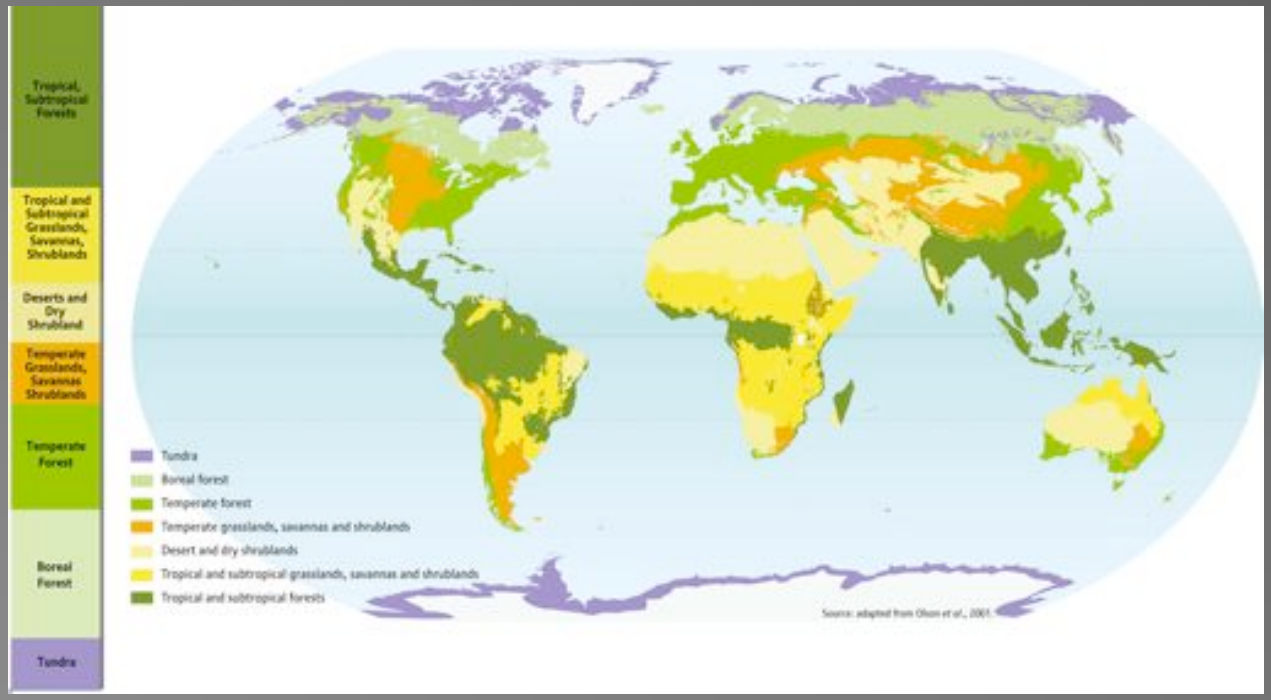
P. van Bodegom, *VU University Amsterdam*;

M. Lyubenova, *University of Sofia*; J. Peñuelas, *CREAF-CEAB-CSIC, Barcelona*; D. Sylvain, *INRA Bordeaux*

Why savannas?

Savannas: co-dominance of grasses and trees

They cover about 20% of the Earth's land surface



The savanna problem

Interesting ecological problem

Trees and grasses in savannas coexist even though they compete mainly for the same limiting resource: water

Savannas and climate

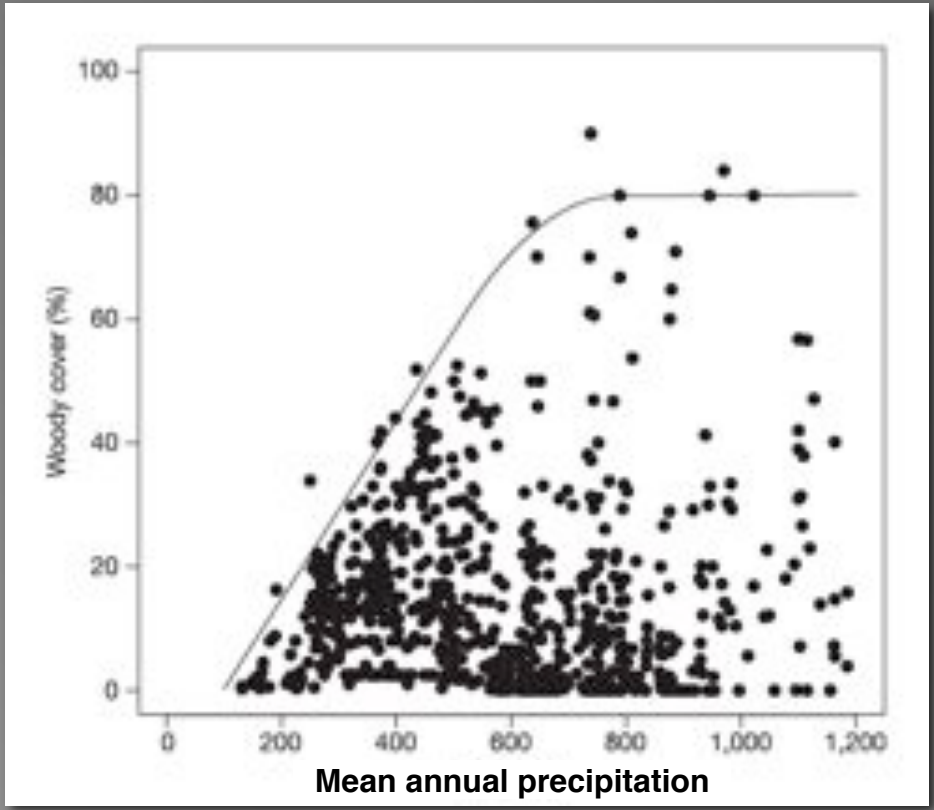
- Savannas are expected to undergo major changes due to increasing temperature and CO_2 concentration, modified rainfall patterns, and subsequently changed variability in fire regimes (IPCC 2007)

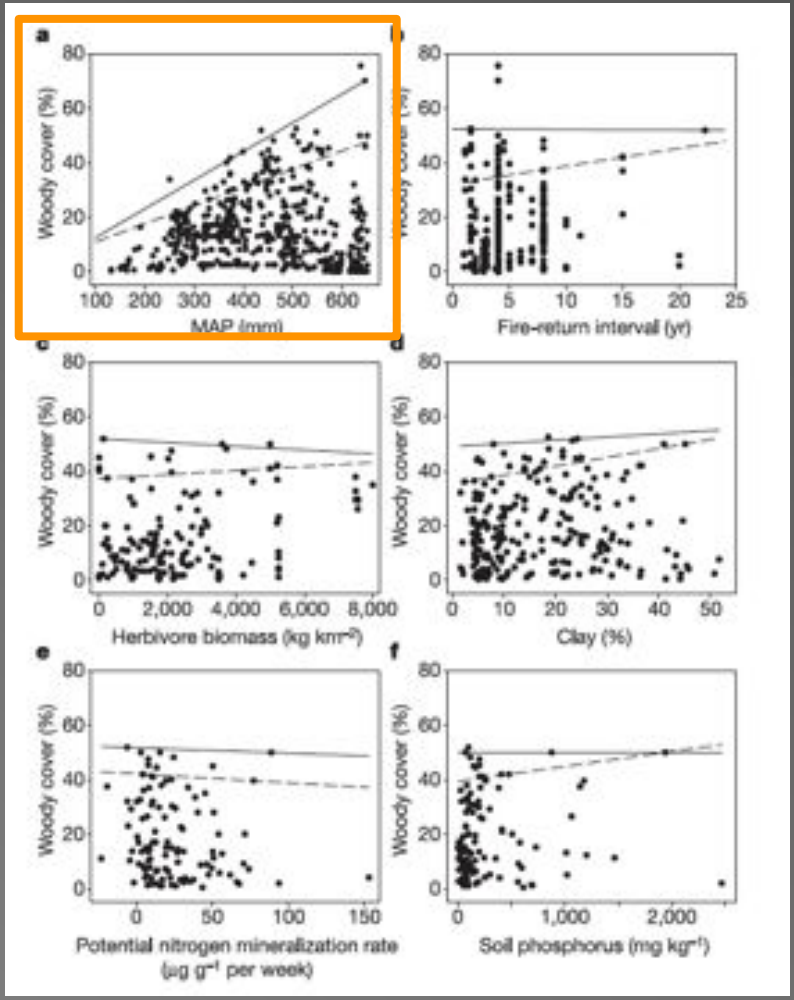
- For example, in African savannas, paleo-ecological evidence of the last glacial, as well as observations of the last 50-100 years, suggest that increasing CO_2 coincide with increase of savanna tree growth (Bond et al., 2003, Scheiter and Higgins 2009)

Which are the relevant mechanisms determining savanna existence?

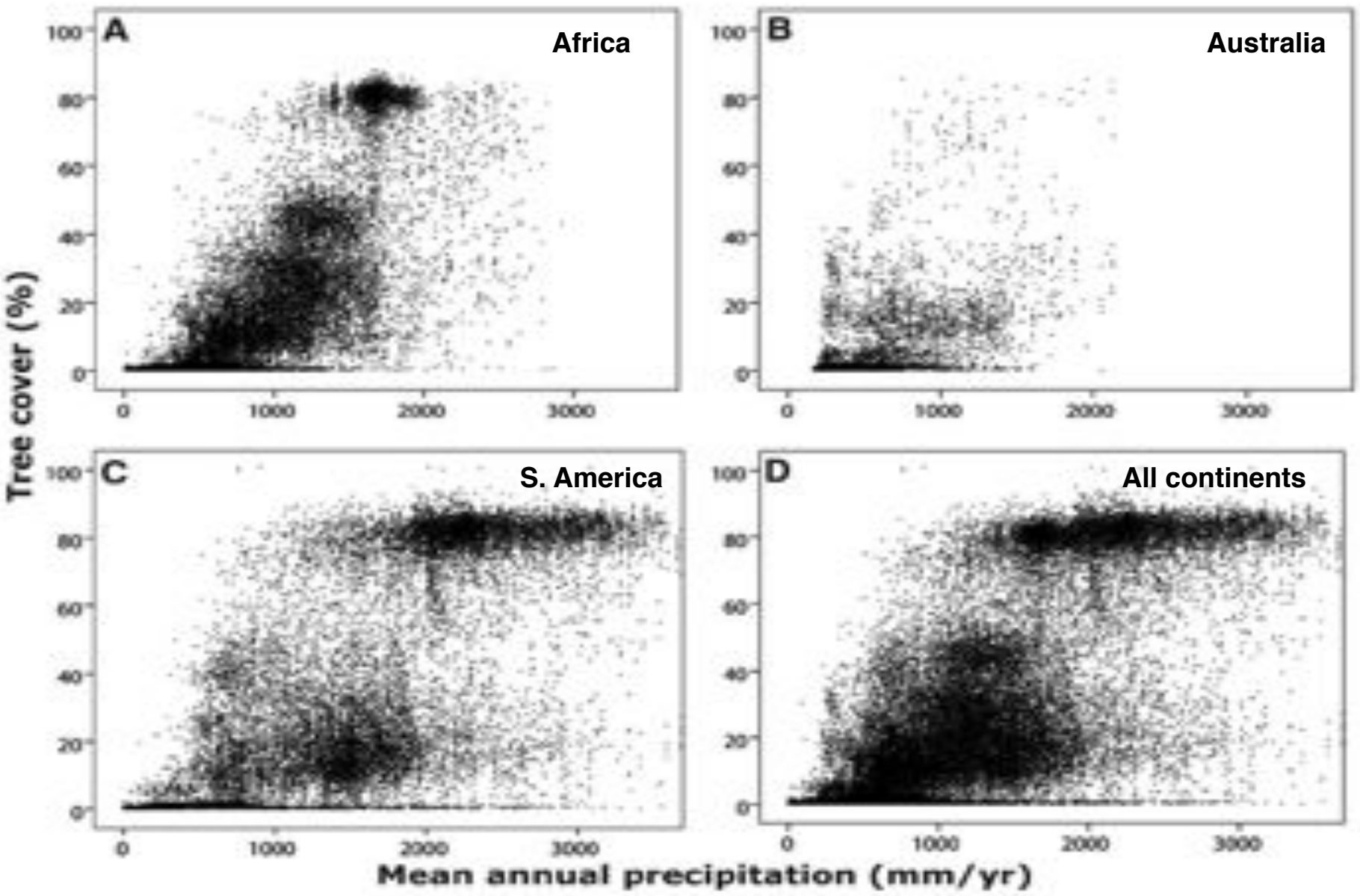
Are they included into DGVMs?

Tree cover and rainfall



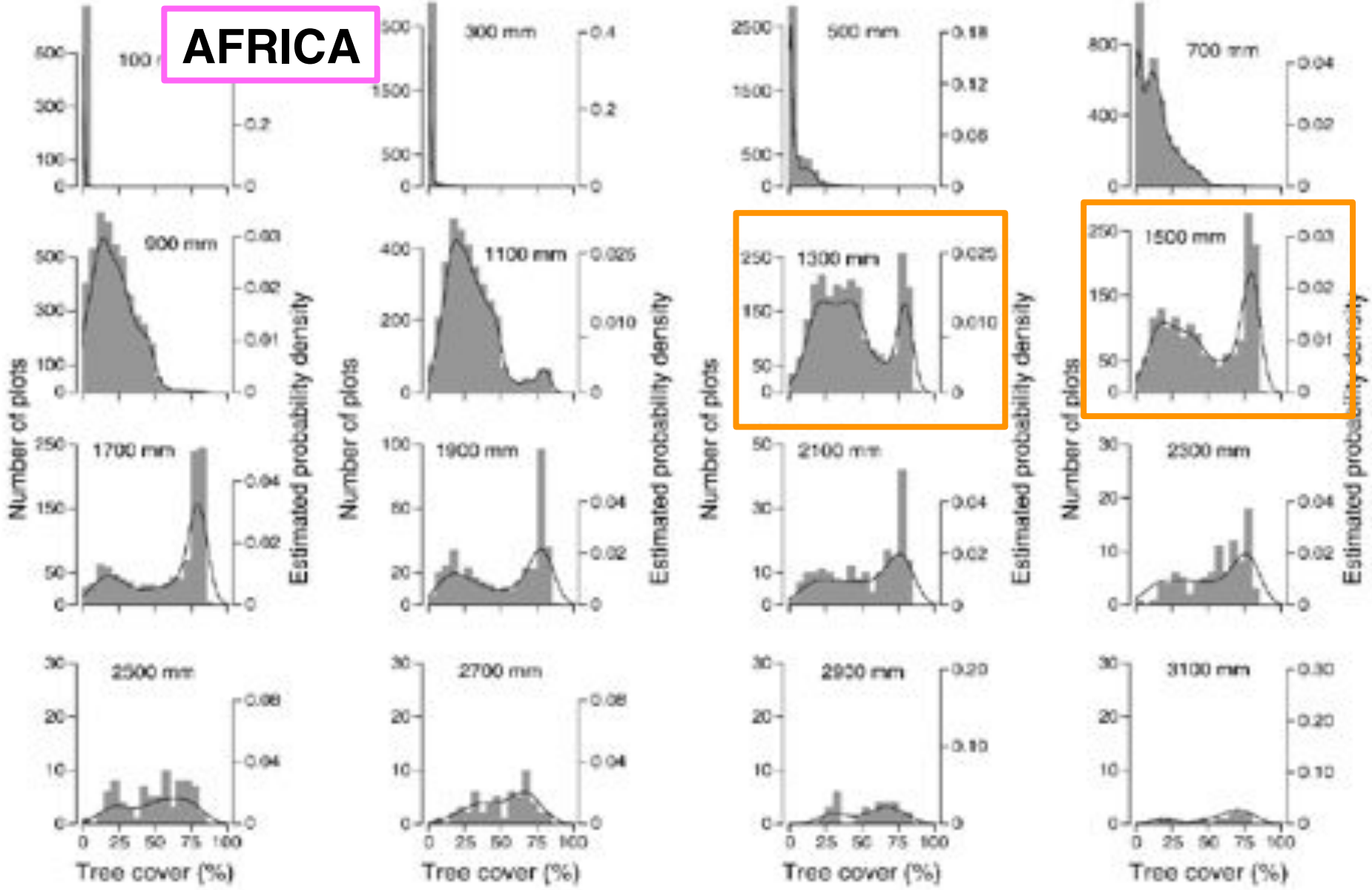


Sankaran et al., 2005, Nature

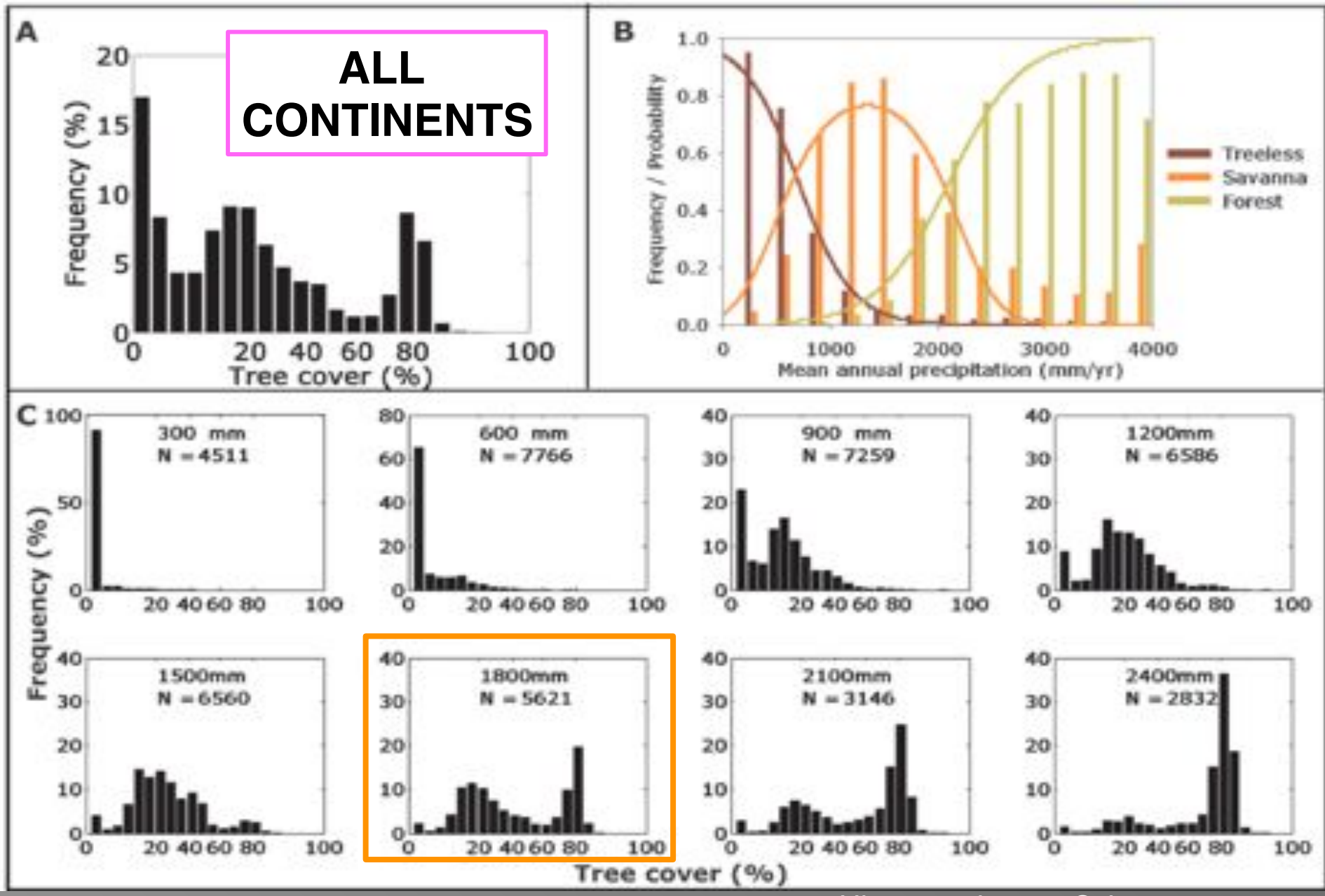


Hirota et al. 2011 Science

AFRICA

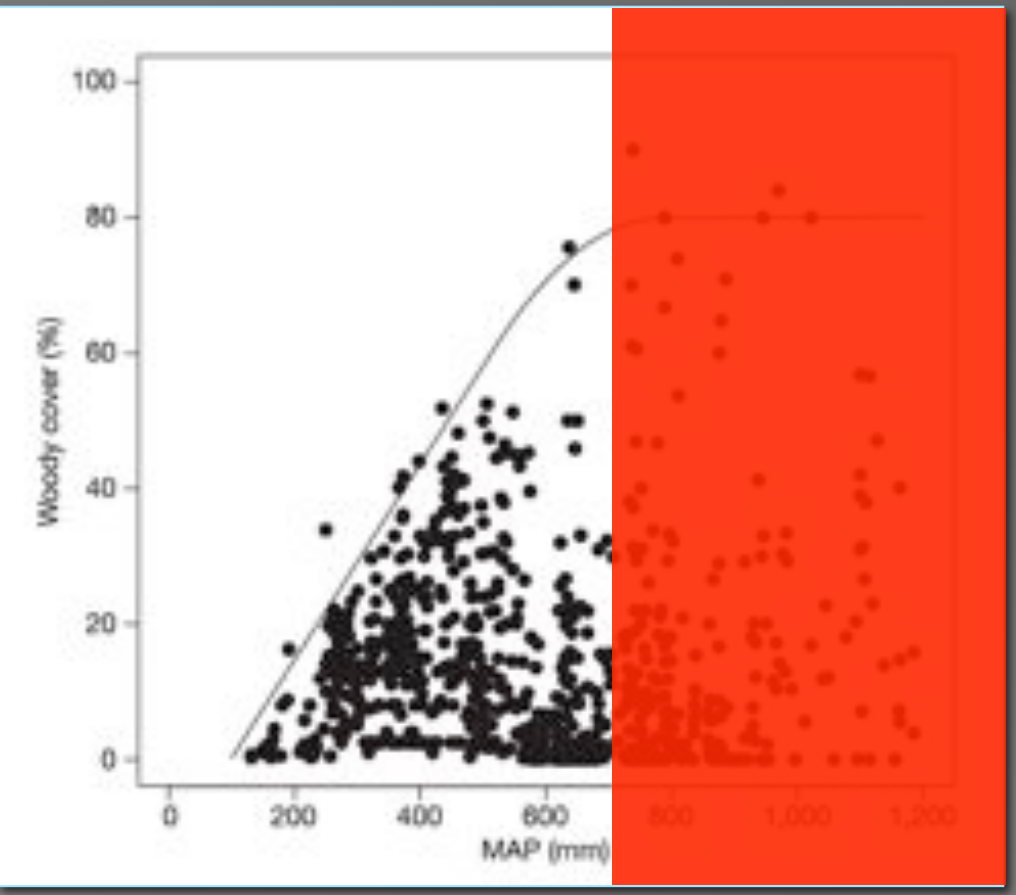


Staver et al. 2011 Ecology



Hirota et al. 2011 Science

Dry savannas



Sankaran et al., 2005, Nature

In the driest savannas (up to 650-1000 mm per year of rainfall):

Tree cover displays a maximum value increasing almost linearly with mean annual rainfall.

Tree-grass coexistence

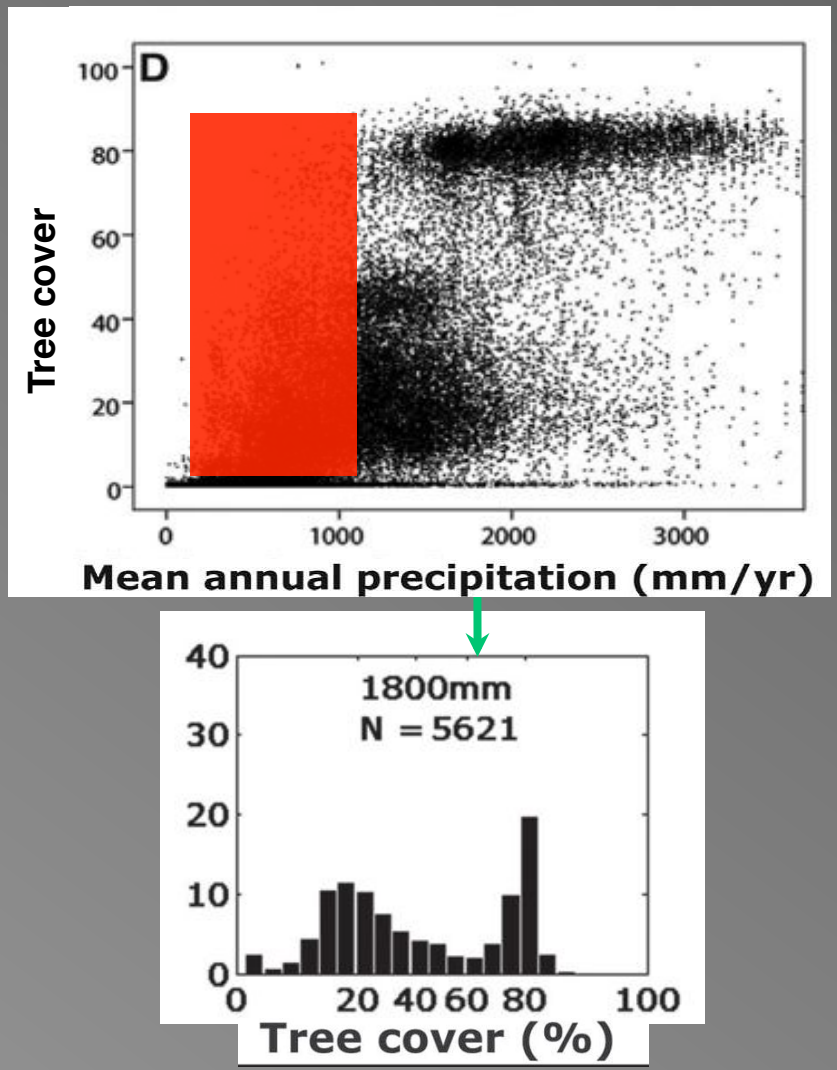
- connected to competition for water
- fires may further limit tree expansion

Dry savannas

What determines the limit to tree cover? Dry savannas have a “deterministic” stable equilibrium connected to water limitation to tree growth. Different hypothesis:

- root-depth separation, e.g. Walter 1971 (not always the case)
- tree demography: tree seedlings compete with grasses (e.g. Baudena et al. 2010)
- roots and shoots separate competition (Scheiter and Higgins 2007)

Humid savannas



Hirota et al. 2011 Science

Humid savannas:

No dependence on rainfall rate

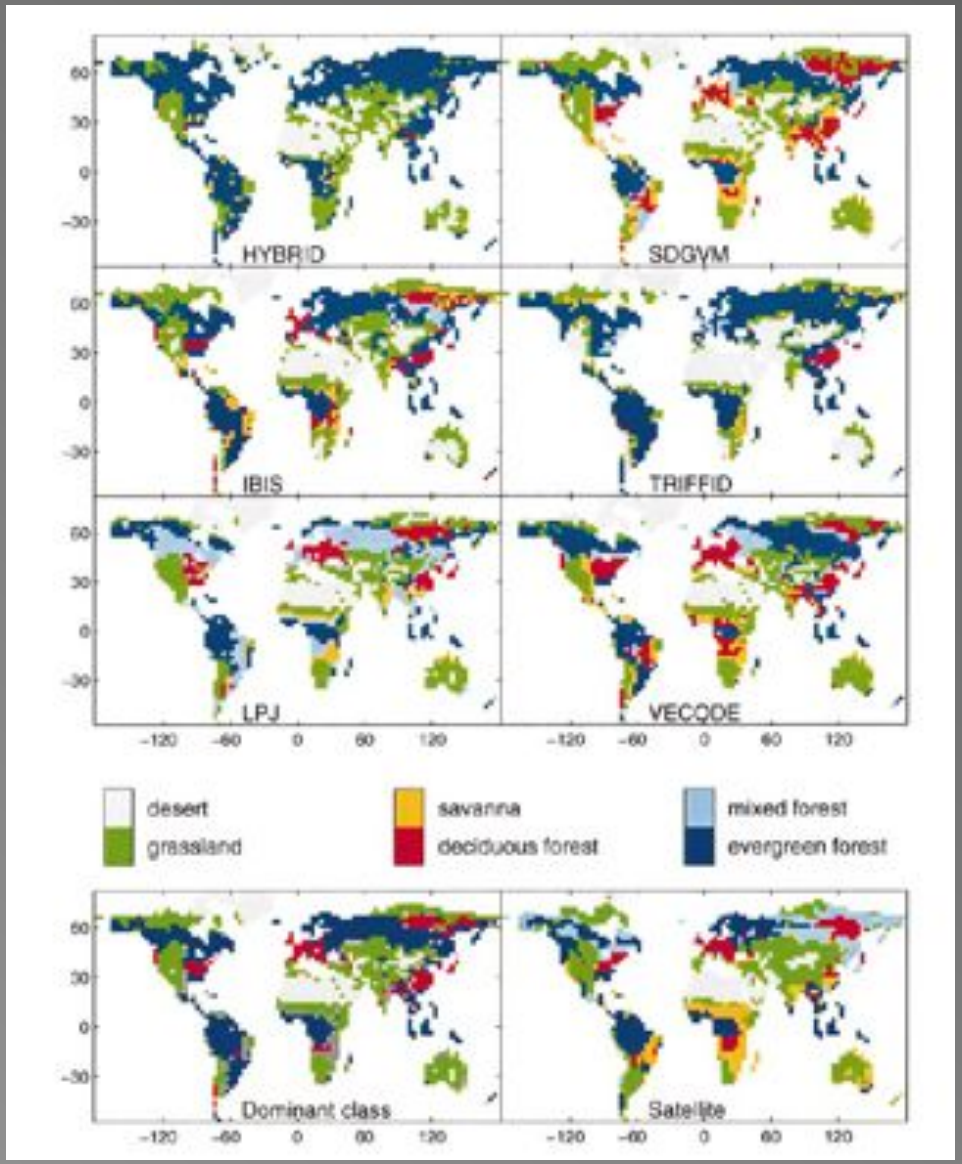
Bimodality of forest and savanna (while intermediate tree cover ~60% does not occur)

Wet savannas are not due to internal tree-grass dynamics (e.g. competition for resources) but to "disturbances", i.e. fires

Fires driving savanna-forest bistability

- C4-grasses are highly flammable: they enhance fire occurrence.
- Grasses also benefit from fire: they regenerate faster than trees
- Fire prevents trees from establishing, and differentiates high and low tree cover
- Forests may replace savannas in case of fire exclusion

Savannas and DGVMs



- Most DGVMs underestimate savanna extent
- DGVMs were not specifically tested for tropical tree-grass systems.
- Improving the current representation of savanna dynamics for present climatic conditions is essential for projecting biome and climate changes into the future

Cramer et al. 2001

Are these ecological mechanisms included in the DGVMs?

Analysis of different DGVMs

- JSBACH

Land surface component of the MPI Earth system model (Raddatz et al., 2007)

- aDGVM

Specifically designed for tree-grass tropical systems – not part of a ESM (Scheiter and Higgins 2009)

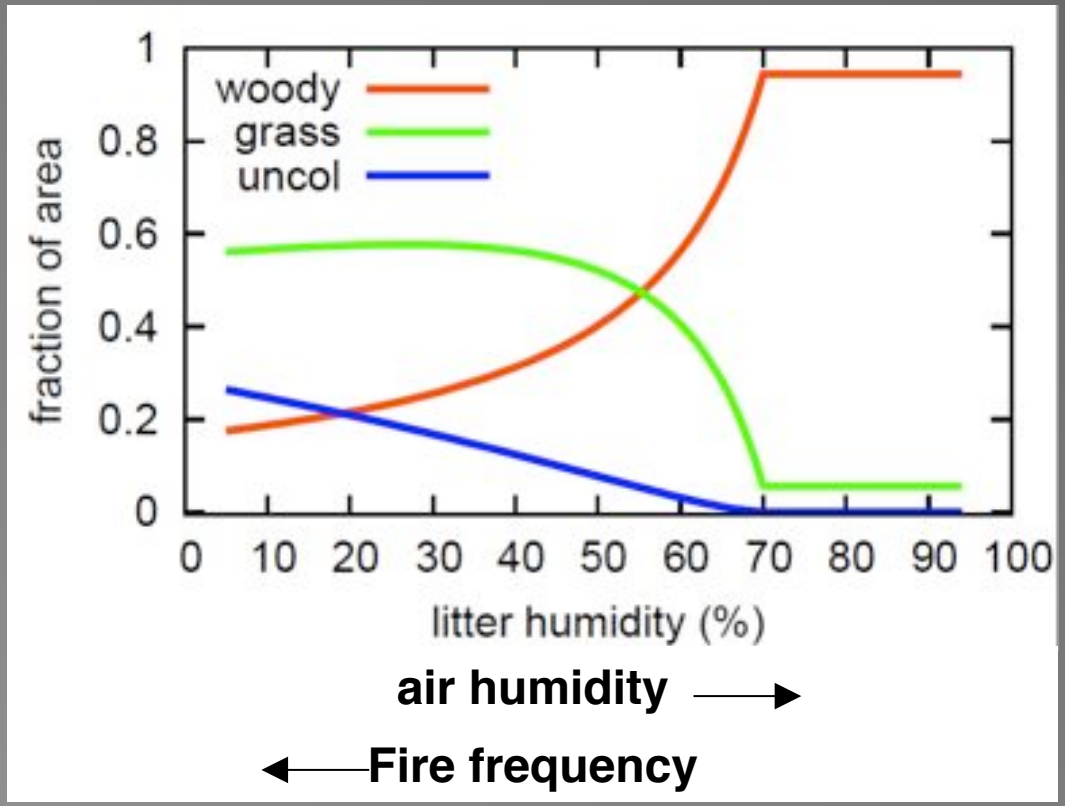
JSBACH

Tree-grass ecology:

- Two classes: woody types (trees, shrubs) and grass types (C_3 and C_4 grasses).
- Within the woody and grass classes: vegetation cover driven by resource availability (i.e. water)
- Tree-grass competition: Trees outcompete grasses in general. Competition for space, not dependent on resource levels.

JSBACH-DYNVEG

- Coexistence is driven by fire only
- Fire frequency depends only on litter humidity



$$\frac{dw}{dt} = \frac{\Theta(u)}{\tau^{(w)}} - \frac{w}{\gamma^{(w)}} - wD^{(w)}$$

$$\frac{dg}{dt} = \frac{u}{\tau^{(g)}} - \frac{g}{\gamma^{(g)}} - gD^{(g)}$$

$$u = 1 - w - g$$

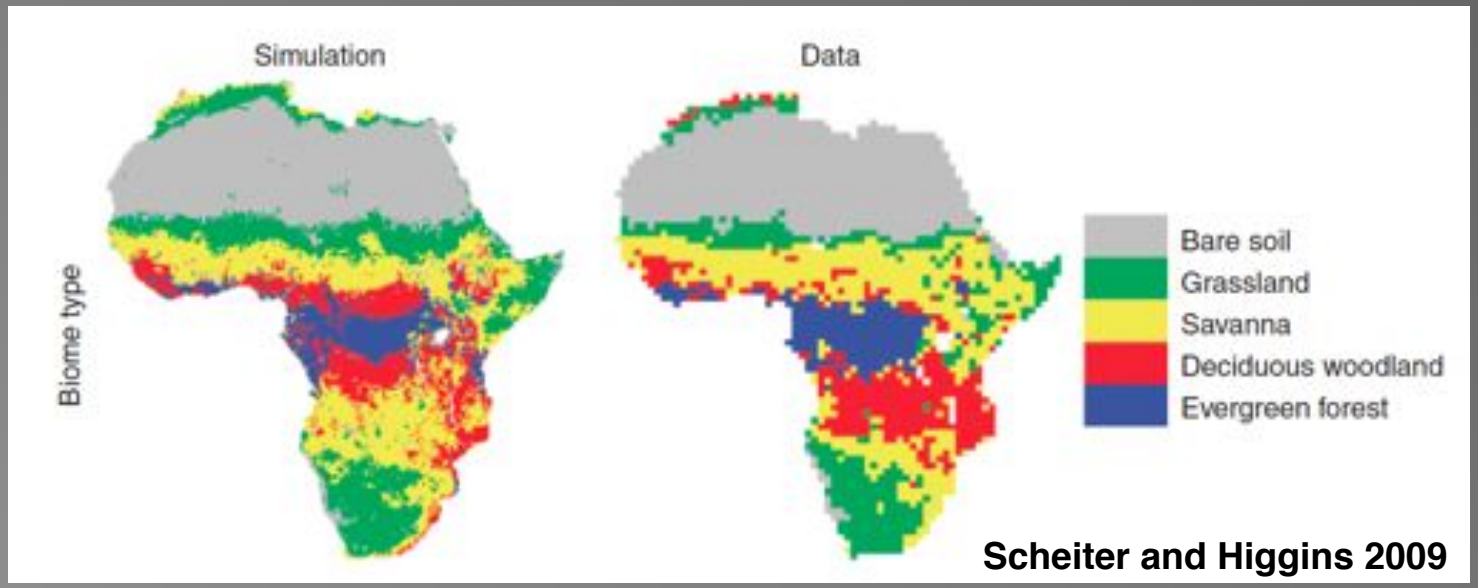
aDGVM

- Developed for tropical vegetation
- Individual based structure for trees, super-individual for grasses

- Trees and grasses extract water from (potentially) different depths.

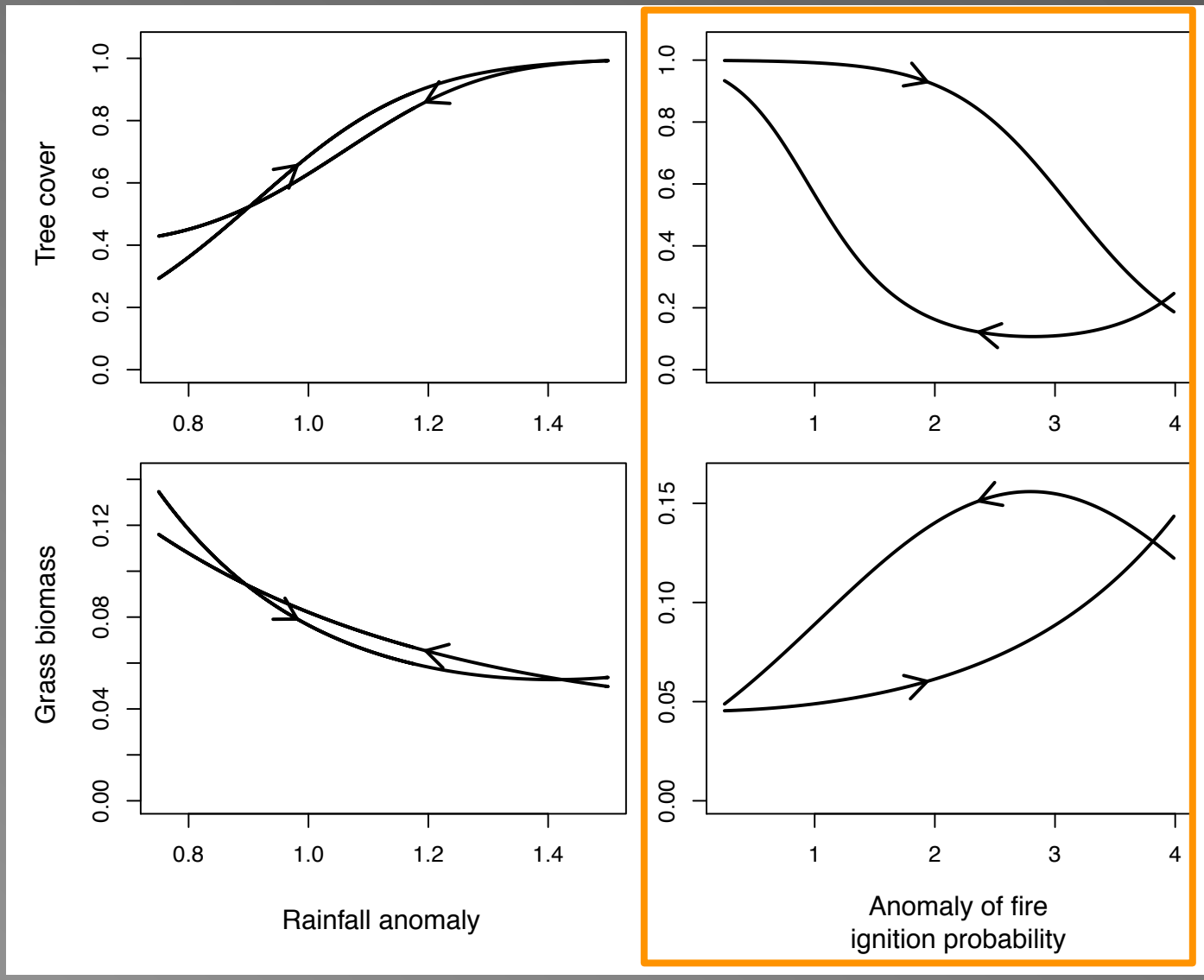
aDGVM: Fire

- Fire intensity is a function of the grass fuel load and its moisture content
- Tree stems damaged by fire can resprout from roots.
- Either trees remain trapped in a cycle of top-kill and resprouting, or they can attain larger, fire-resistant sizes



Scheiter and Higgins 2009

aDGVM



Bistability of savanna and forest corresponding to the same fire regimes.

Skukuza, Kruger Park,
570mm MAP
550ppm CO2

Conclusions

- Dry savannas:

  There is a deterministic limit to tree cover connected to water availability

  Disturbances (e.g. fires) enhance coexistence but are not the only driver

- Wet savannas:

  Fire feedback leads to bistable savanna/ forest.

  It may be the explanation for the observed bimodal distribution of tree cover.

Conclusions

- Necessary to include into DGVMs both water limitation to tree growth and fire effects (or disturbances in general, e.g. grazing)
- Even if the models catch the present distribution of vegetation, they may not include the appropriate main mechanisms
- This could lead to wrong predictions under future climate scenarios

Thank you!

The savanna problem

How do tree and grass coexist using the same limiting resource (water)?
Most of the ecological models predicting savannas as deterministic stable equilibria assume that trees and grasses have differential ability to acquire and partition water
But: root-depth separation is not supported by observations
Other theories suggest that tree demographic structure is important (tree seedlings and grasses compete, while adult trees are competitively superior)

Or: savannas occur because of temporal and/or spatial disturbances and variations in environmental conditions, e.g. fire, grazing, browsing.

The savanna problem

Tree-grass coexistence: stable or unstable?

Stable: coexistence is observed because of the internal tree-grass dynamics.

Unstable: savannas are intermediate stages between forests and grasslands, which we observe only as a result of factors “external” to the dynamics (fire, grazers etc)

LPJ-GUESS

- Woody individuals, grass superindividuals
- Different root depths for trees and grasses
- Tree age structure

LPJ-GUESS

- Savannas are observed, in absence of disturbances, for a relatively small precipitation range, otherwise forest or grassland are the stable states
- Forests occur in absence of disturbances given sufficient precipitation, while grasslands appear at high frequency of fire occurrence, or low precipitation.

LPJ-GUESS-SPITFIRE

- size selective fire mortality
- Frequent fires lead to a high mortality of young (small) age cohorts, they even have a positive effect on large trees by reducing the competition with younger age cohorts.