What limits trees in savannas: The Australian puzzle

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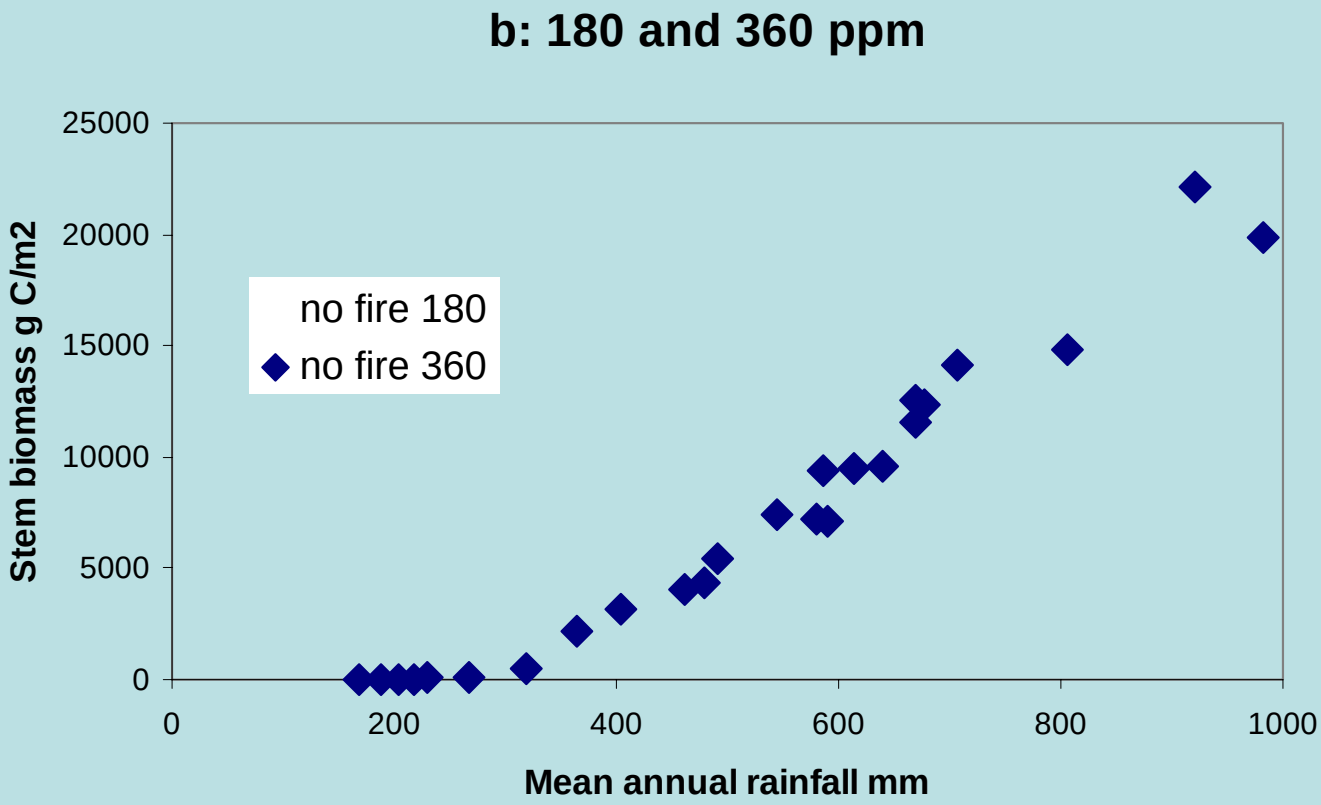
What limits tree cover in tropical grassy ecosystems?

- The root niche (Walter) hypothesis argues trees/grasses at equilibrium with resources
- Resource partitioning by rooting at different soil depths
- tree cover at a site depends on water infiltrating past grasses to deeper soil layers
- Tree cover at equilibrium with resources

The root niche hypothesis predicts:

- Tree cover should increase smoothly with increasing soil moisture
- Differences in tree cover on different soil types

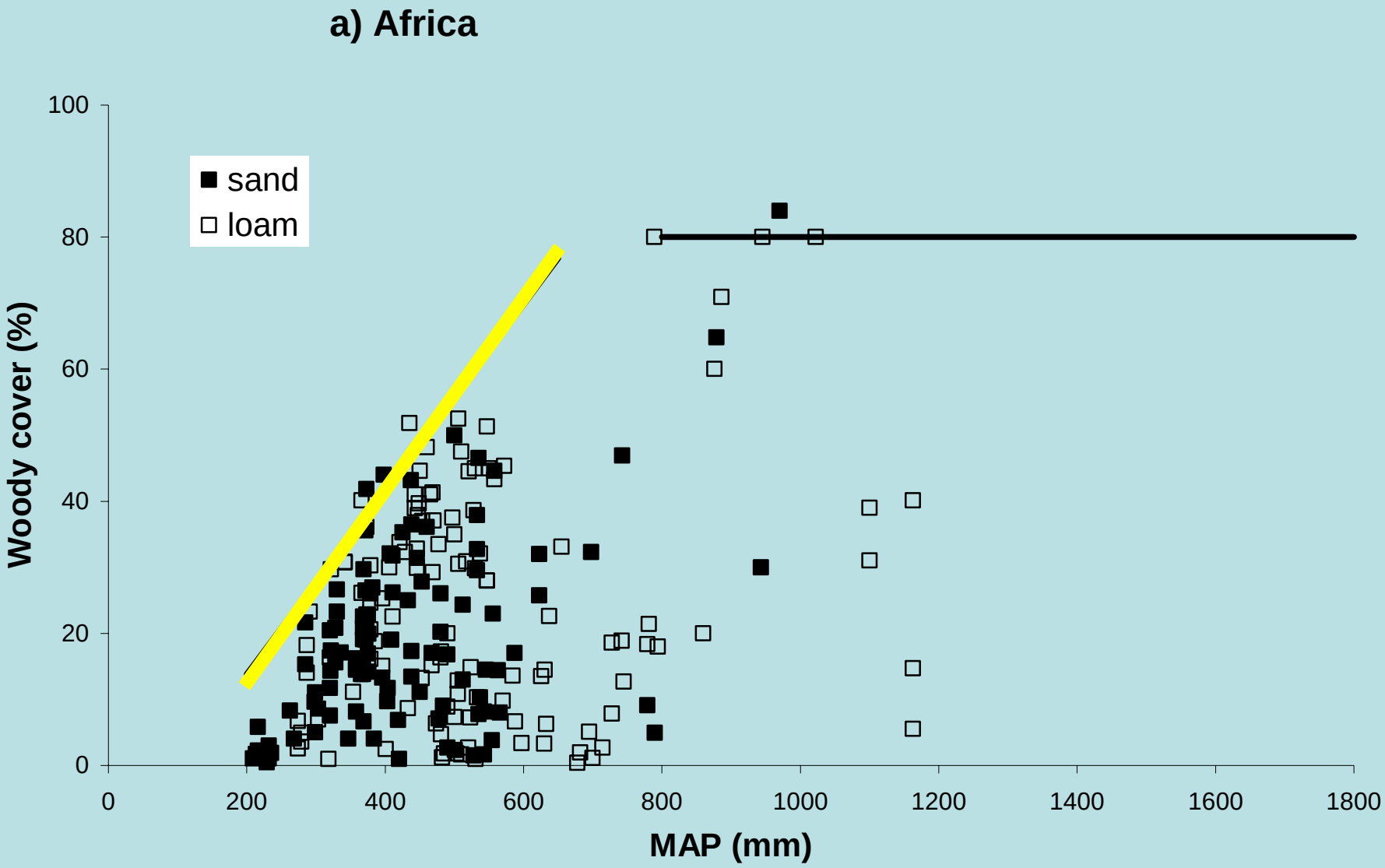
SDGVM simulations of 27.25 S: Climate Potential



What you would expect if tree cover was at equilibrium with resources

What you usually find: variable savanna tree cover, Forest patches, plantations show trees not at equilibrium with their ‘climate potential’.

Tree cover for African savannas vs Mean Annual Precipitation
Sankaran et al Nature 2005



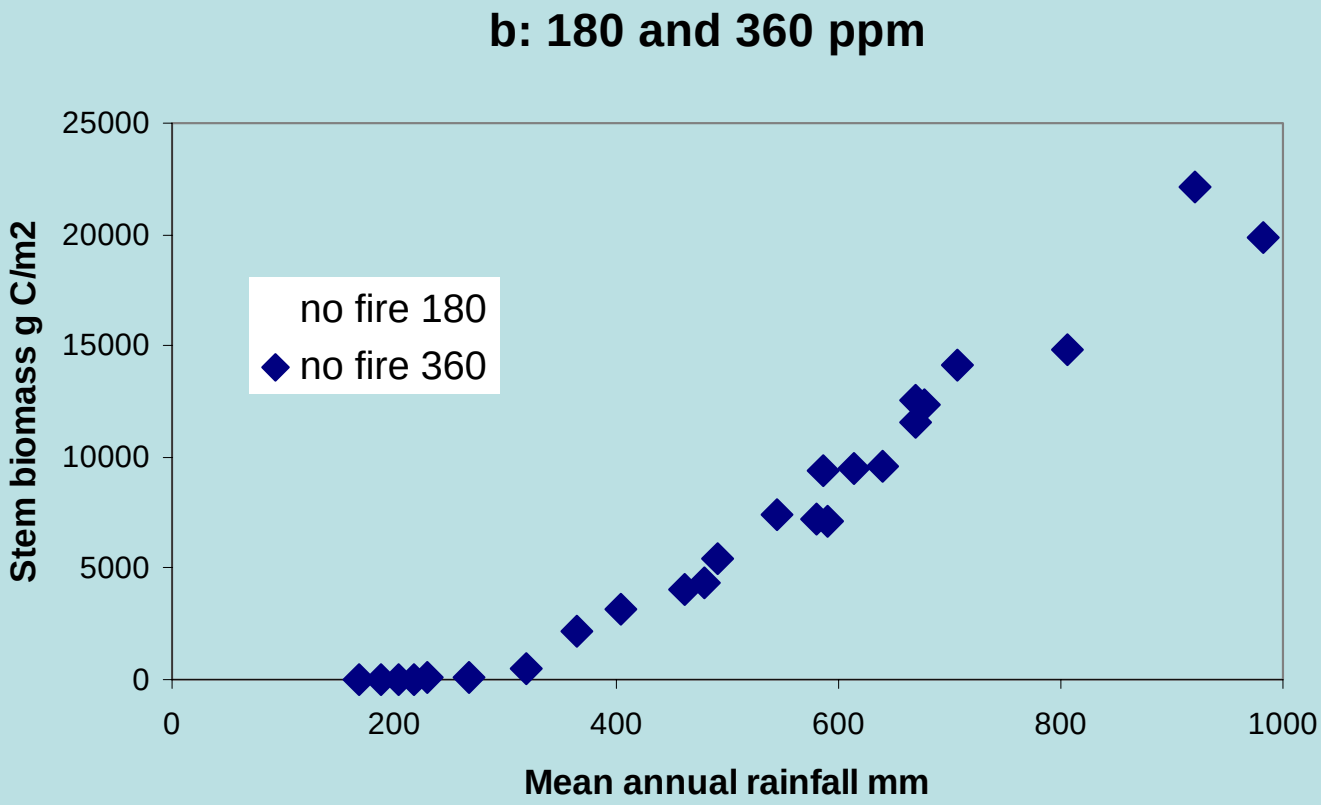
The escape hypothesis: consumer control

- Tree cover is limited by fire/browsing *interacting* with resources
- Juveniles struggle to escape fire/browse trap to become trees
- Fire (and browsing) are patchy in space and time consistent with patchy tree cover
- If saplings escape browse/fire trap, trees grow to climate-limited potential – K_{tree}

The fire trap: below 3m and its tough, above and trees escape fire injury

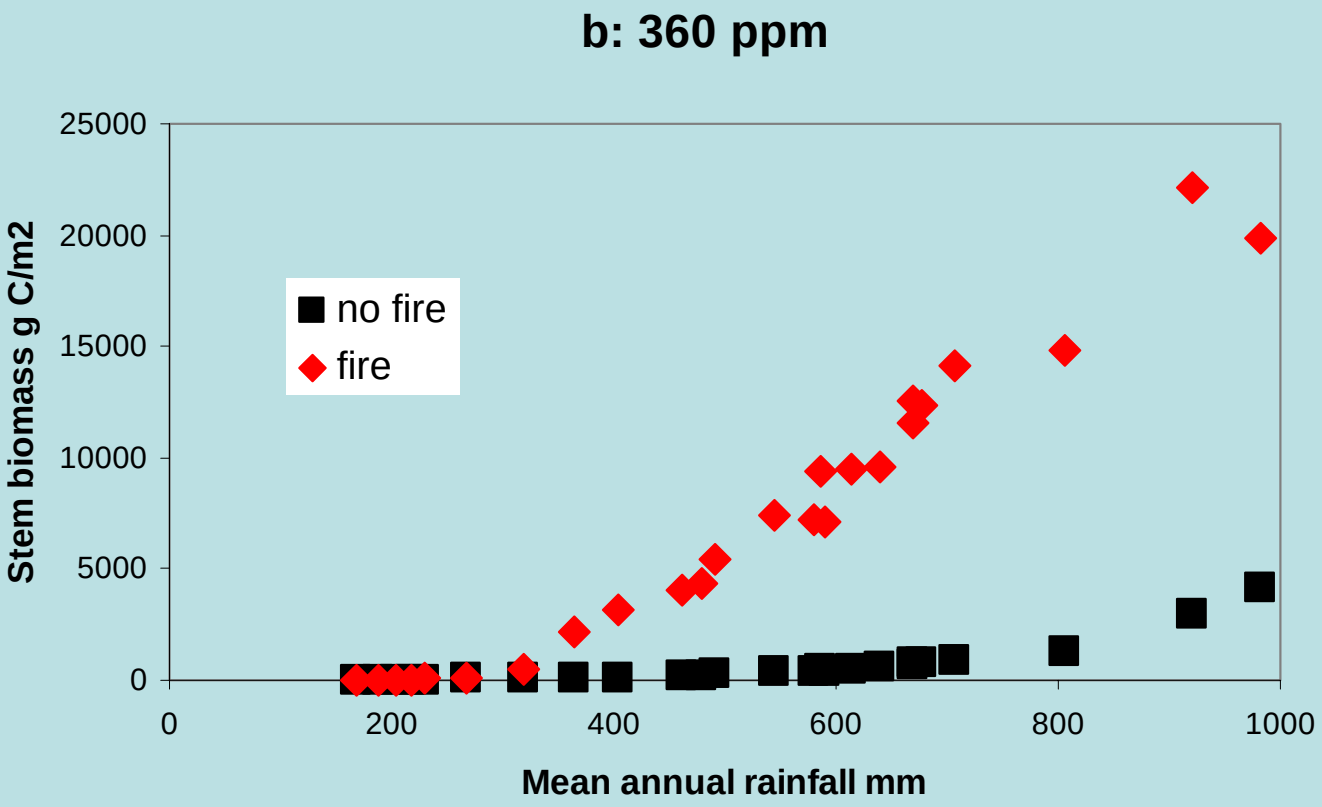
Saplings can spend decades stuck in the fire trap; escape to trees rare, episodic

We can simulate K_{tree} and compare actual *vs.* potential tree biomass to assess resource vs. consumer control



Simulated K_{tree} for South African transect

Actual veg is grassland with scattered trees



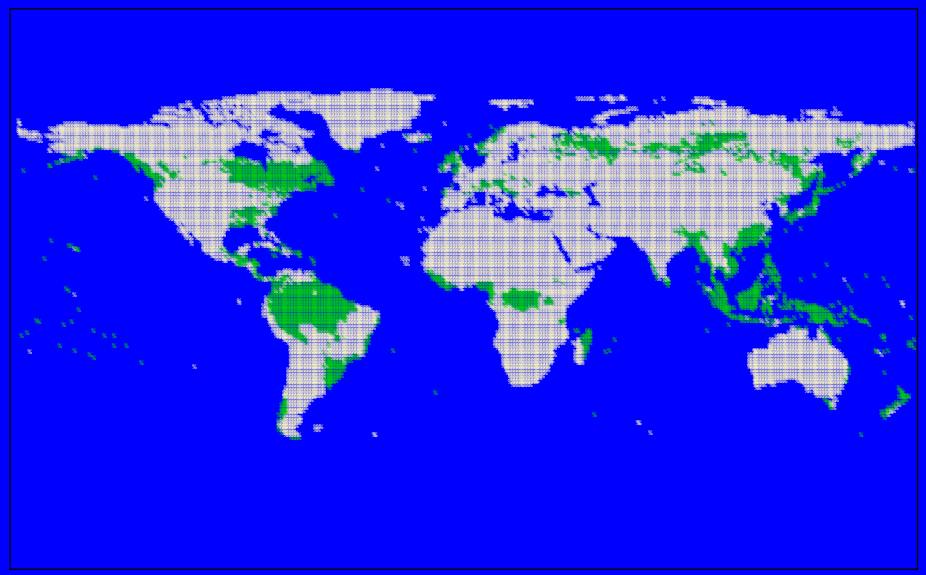
Simulating tree growth AND fire produces realistic vegetation


Cedar Creek, USA: fri 2-3 y for 32 years
Fire exclusion experiments have also shown savanna trees not at equilibrium with resources

Cedar Creek: fire exclusion for 32 years

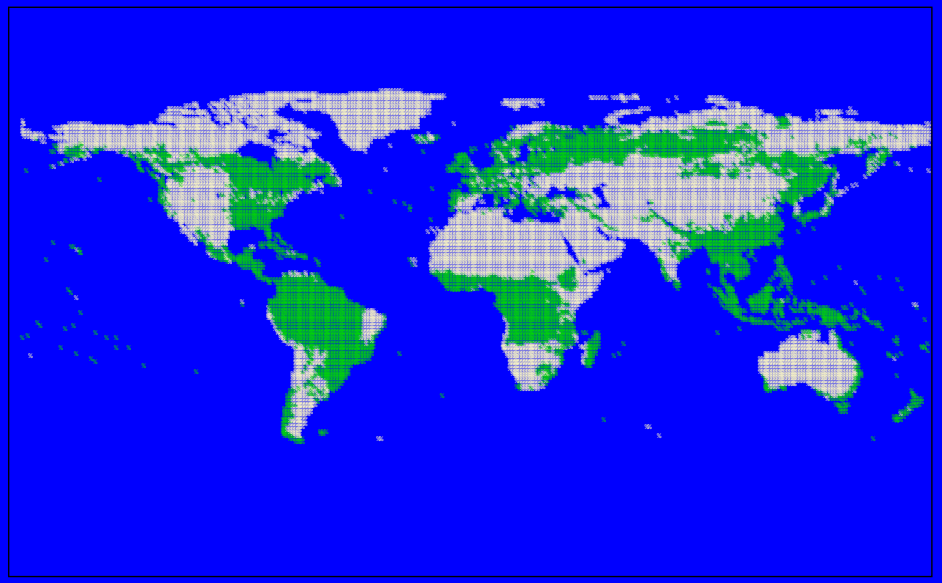
DGVM simulates potential tree cover
Which is much greater than observed

FAO Mapped Forest



Forest = 27% of land

SDGVM Potential forest



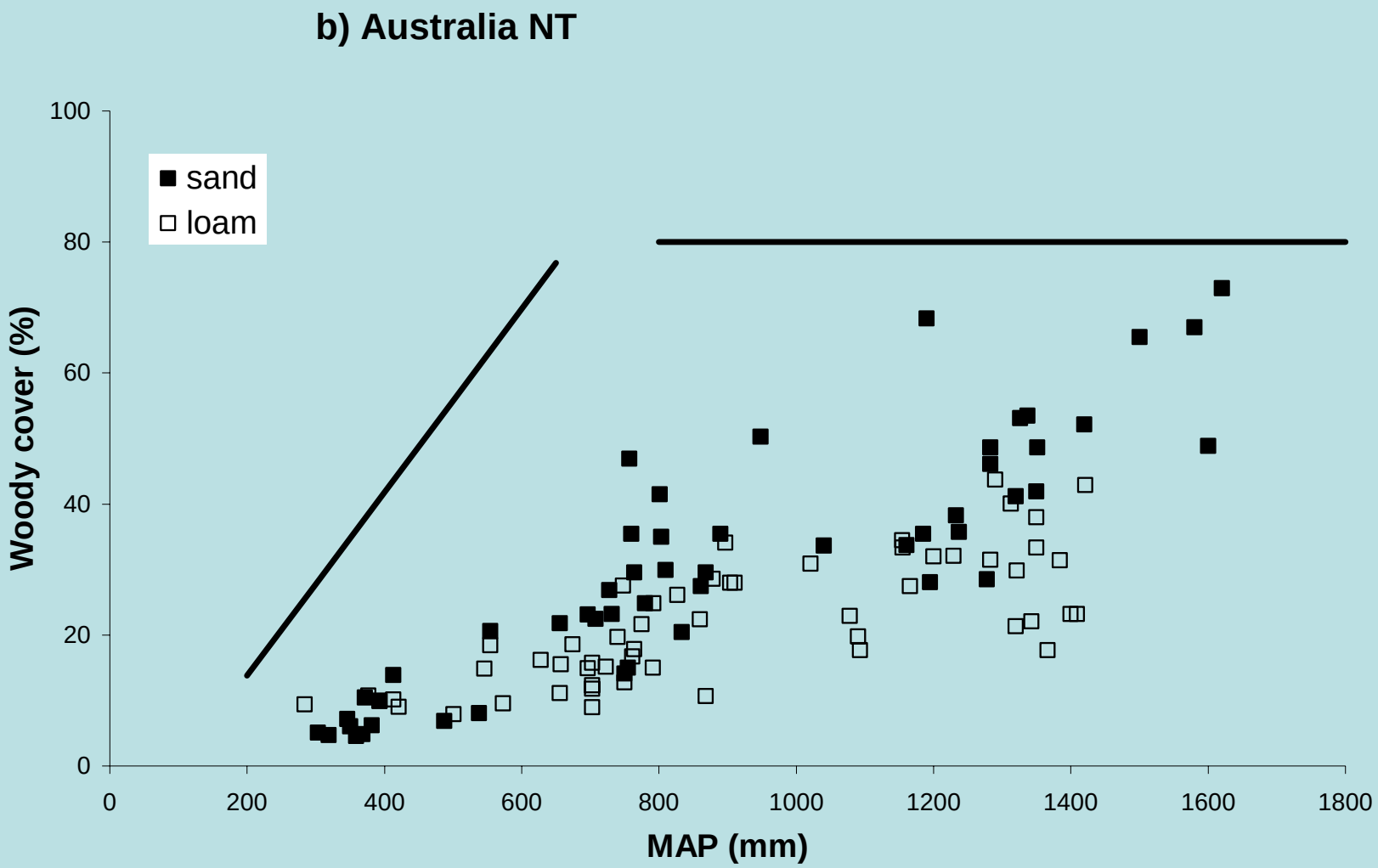
Forest = 56% of land

52% of tropical grassy ecosystems -> forest

41% of cool grassy/shrubby ecosystems -> forest

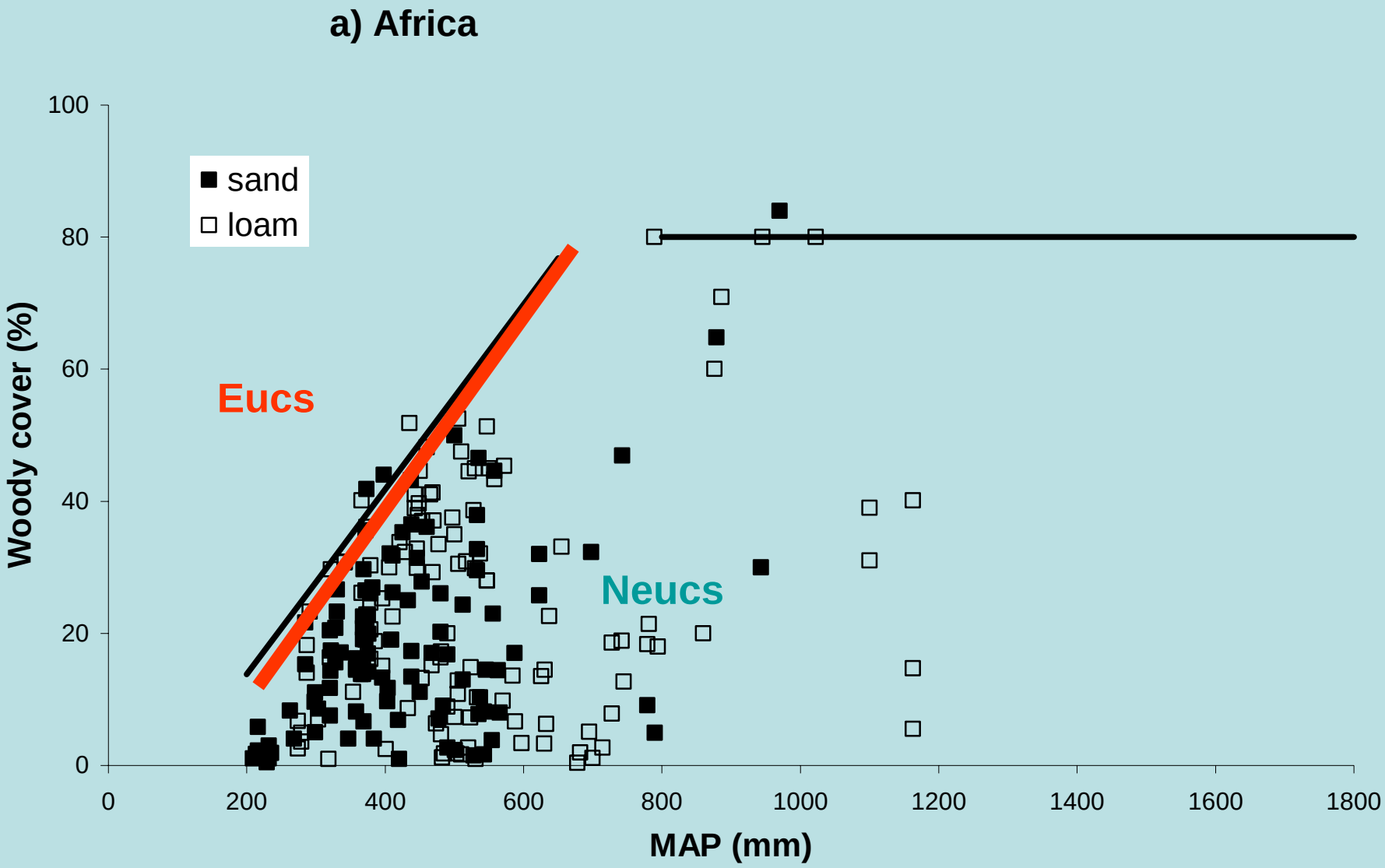
Australian savannas an outlier?

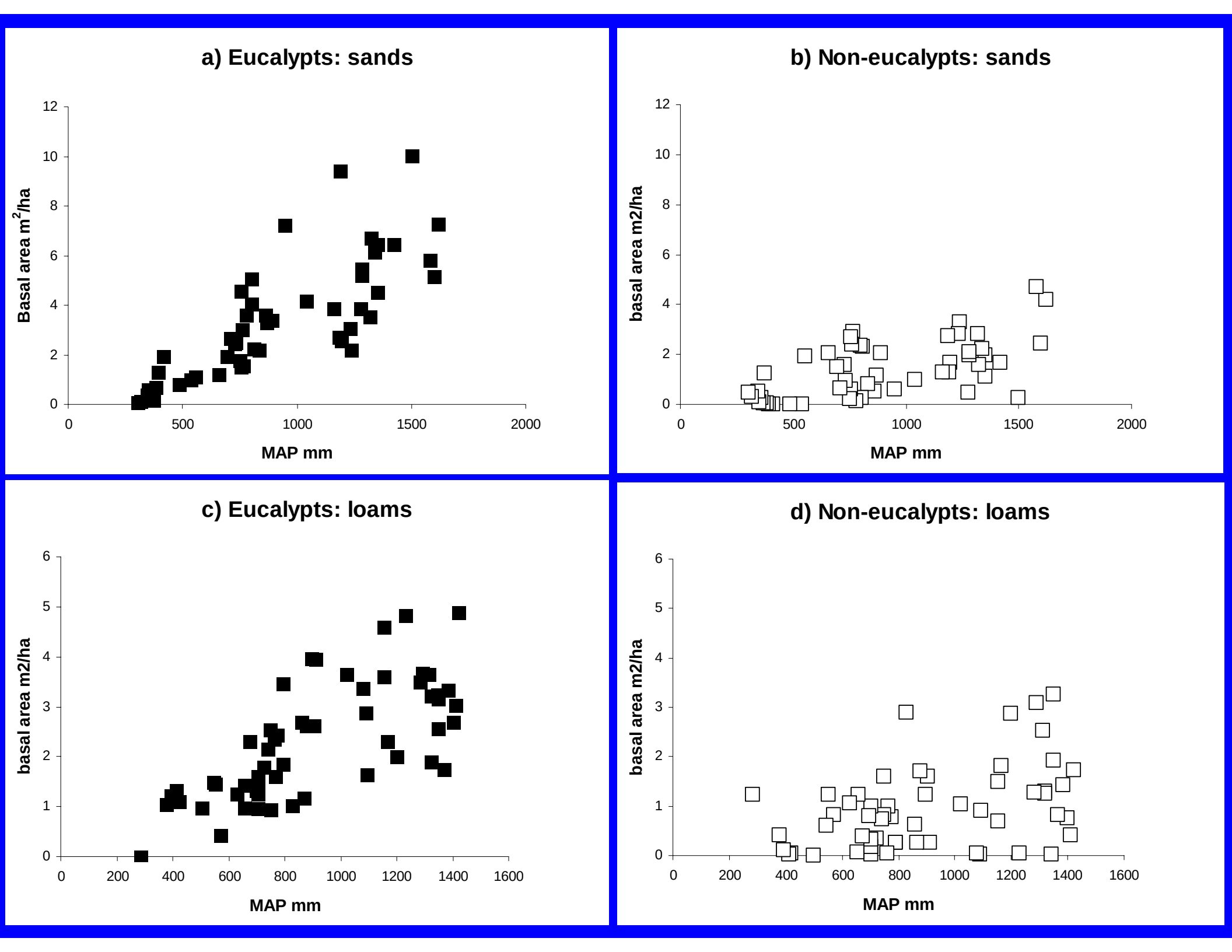
- NT savannas – very uniform tree cover
- But eucalypts account for uniformity
- Strip out eucs and the rest look much like African savannas with small patches of trees, large patches of saplings
- So are Australian savannas ‘different’ because of eucs?
- And if so why?
  - Good at resource uptake and competition?
  - Good at escaping the fire trap?



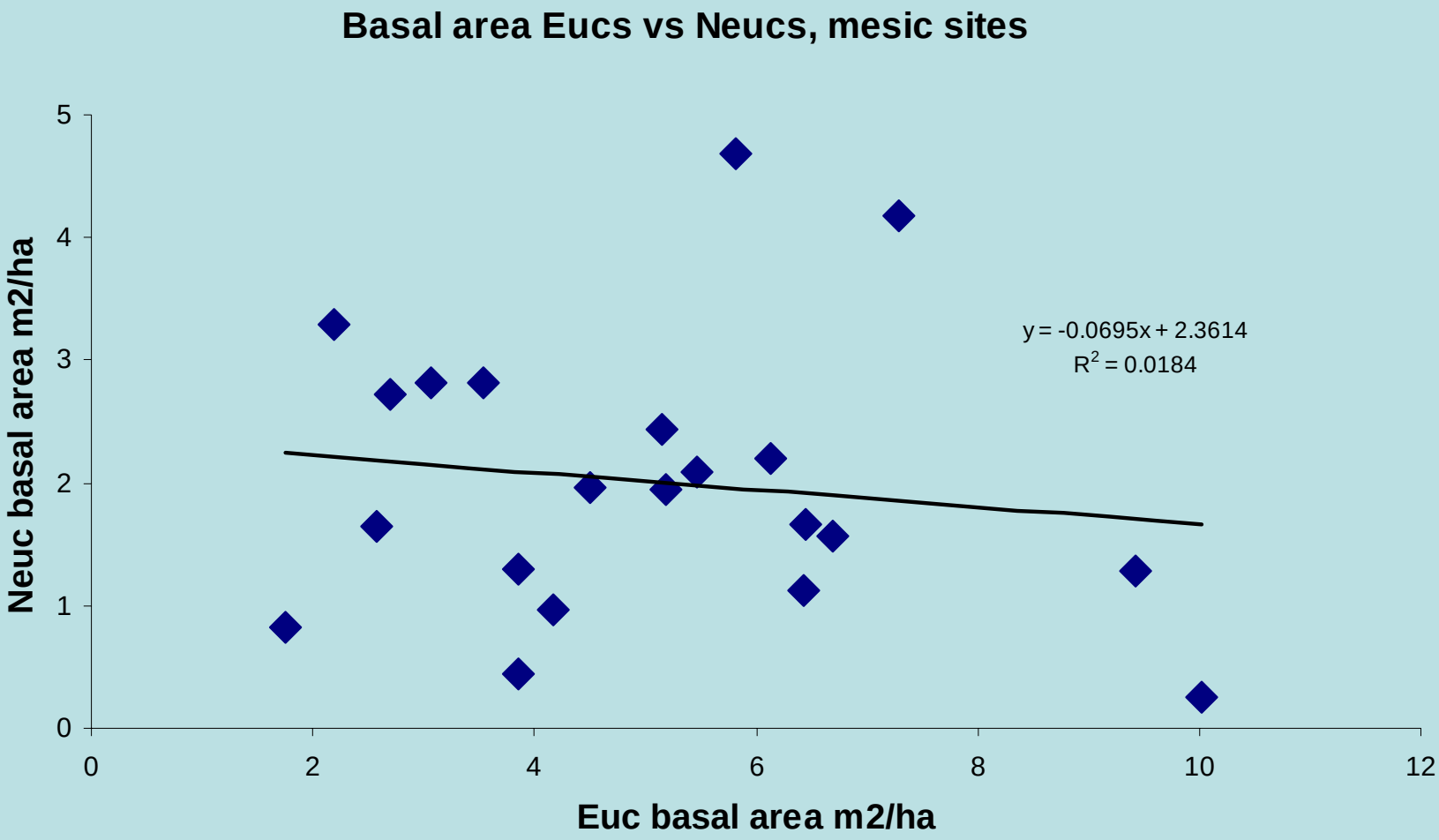
tree biomass increases smoothly with MAP in Oz savannas
FITS Walter idea of trees at equilibrium with resources!

Are Australian savannas different because of eucalypts?
And if so, what is different about eucalypts? Resource use? Or fire adaptive traits




a) Eucalypts: sands
Basal area m2/ha
MAP mm
b) Non-eucalypts: sands
basal area m2/ha
MAP mm
c) Eucalypts: loams
basal area m2/ha
MAP mm
d) Non-eucalypts: loams
basal area m2/ha
MAP mm

Do eucs out-compete neucs?



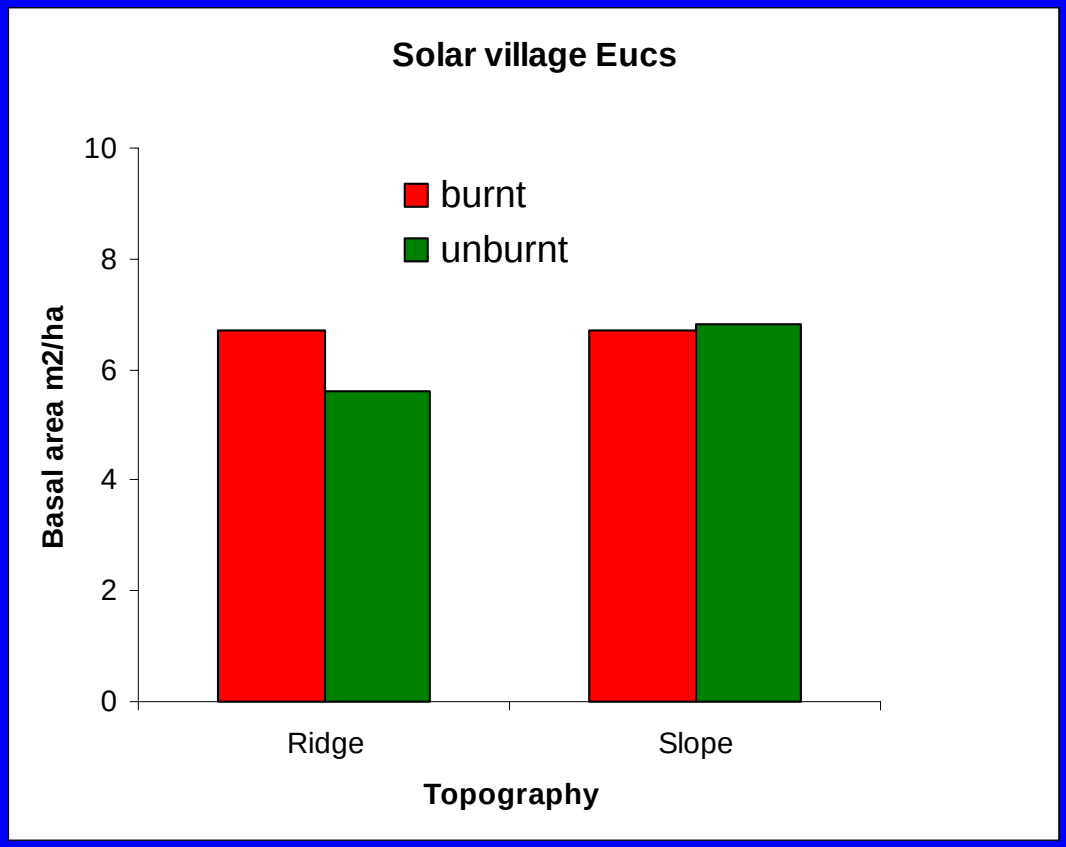
No evidence for negative effects of euc trees on neuc trees

Fire exclusion experiments

- If trees are resource-limited excluding fire will lead to
  - No change in biomass (basal area)

- If trees are fire-limited
  - Increase in biomass until K_{tree}
  - Eucs little change (don't see the fire trap)
  - Neucs large changes as saplings escape

Woinarski et al 2004. Austral Ecology. **~ annual burn vs. unburnt for 23 y**



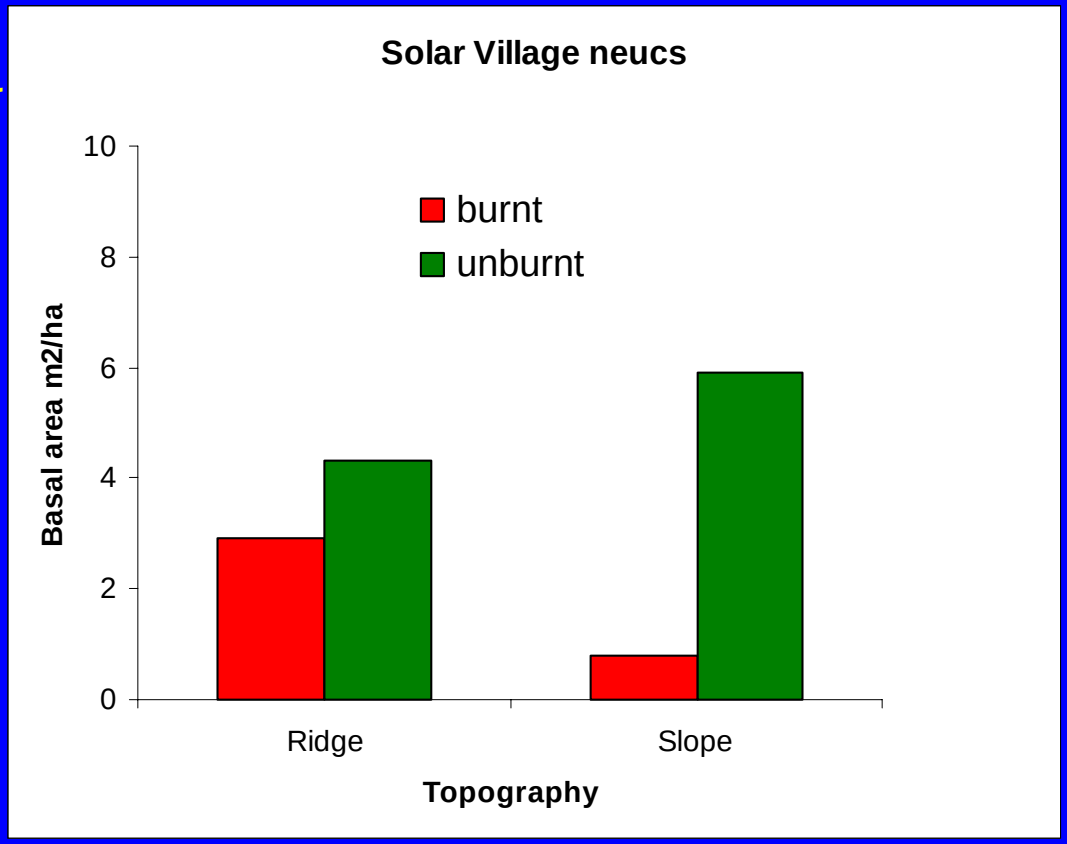
Eucs – no change in basal area

RESOURCE LIMITED

Woinarski et al 2004. Austral Ecology. **~ annual burn vs. unburnt for 23 y**

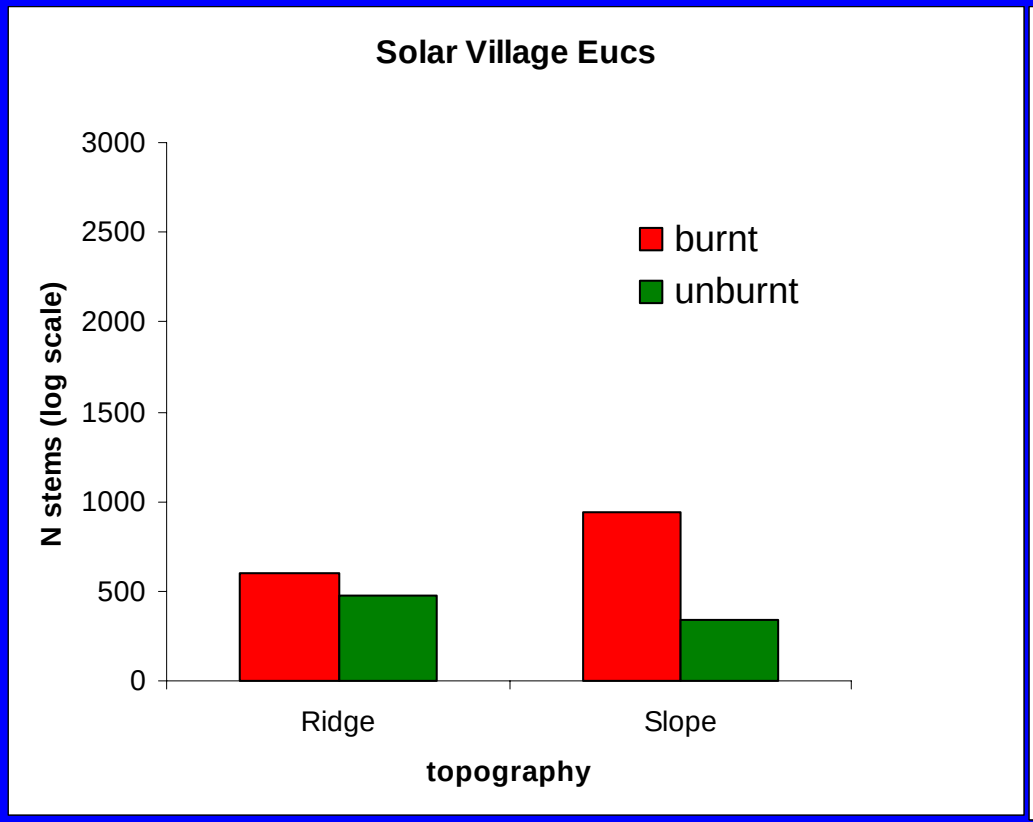
Neucs – *increase* in basal area

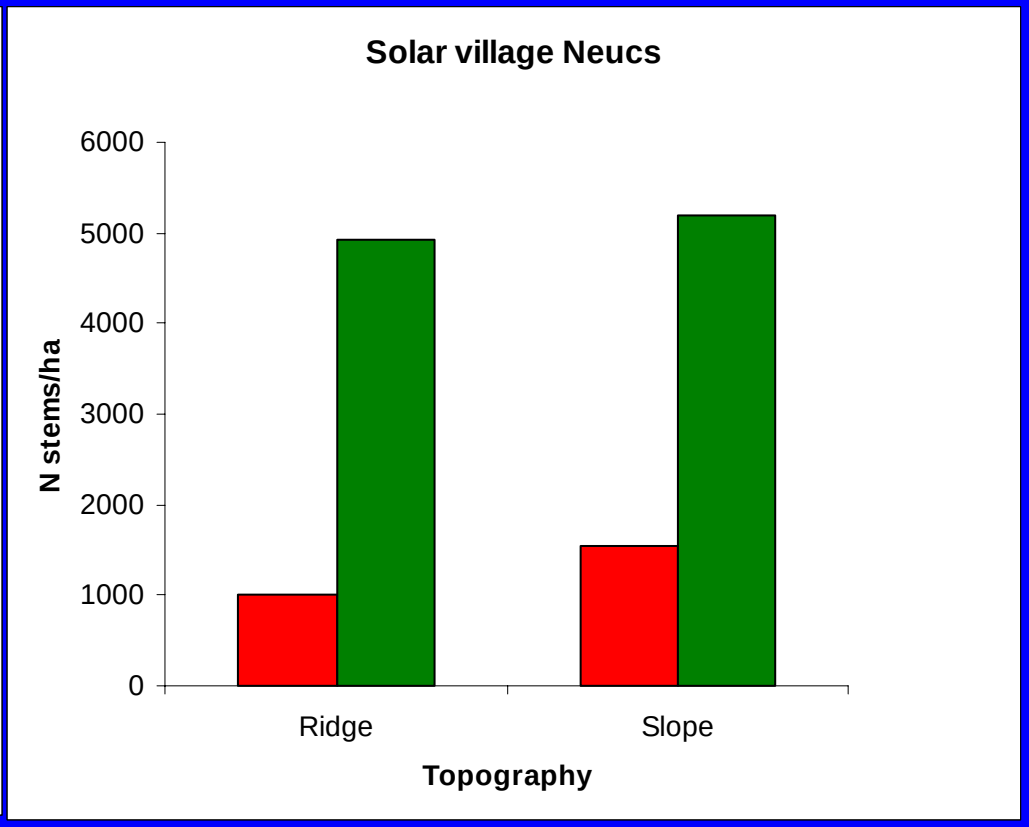
FIRE LIMITED



'Neucs' are savanna broad-leaved spp
forest species also invading the site

Stem densities show massive increase for neucs = escaping fire trap?





eucs

neucs

Woinarski et al 2004. Austral Ecology. **~ annual burn vs. unburnt for 23 y**

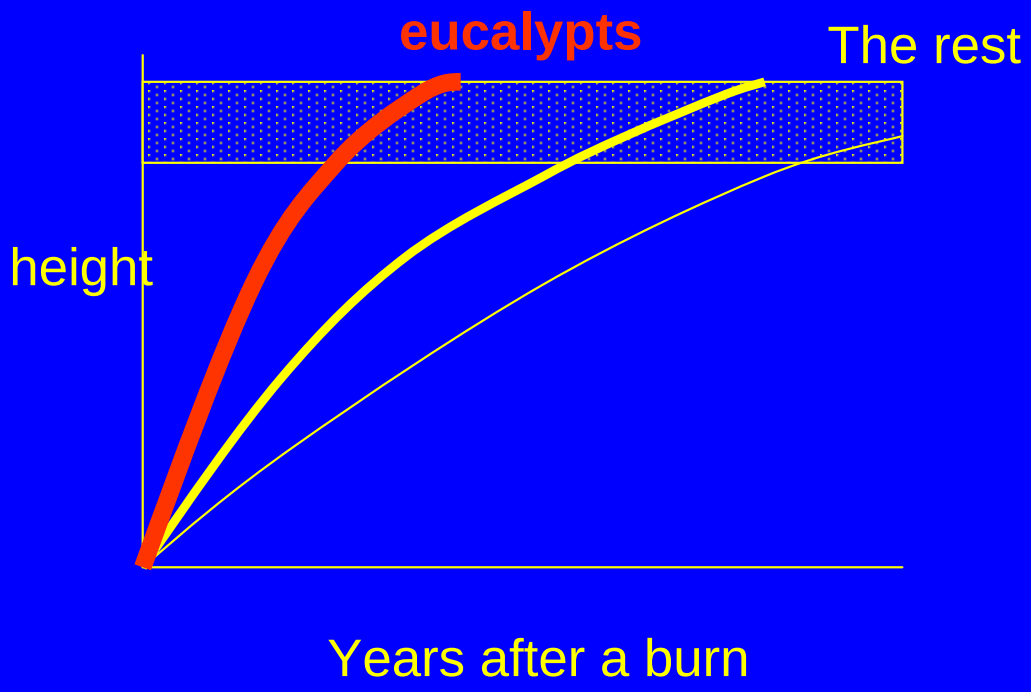
Why do eucs escape more easily?

- Saplings better able to tolerate injury (thicker bark, bark replacement etc)
- Saplings faster at growing out of the fire trap

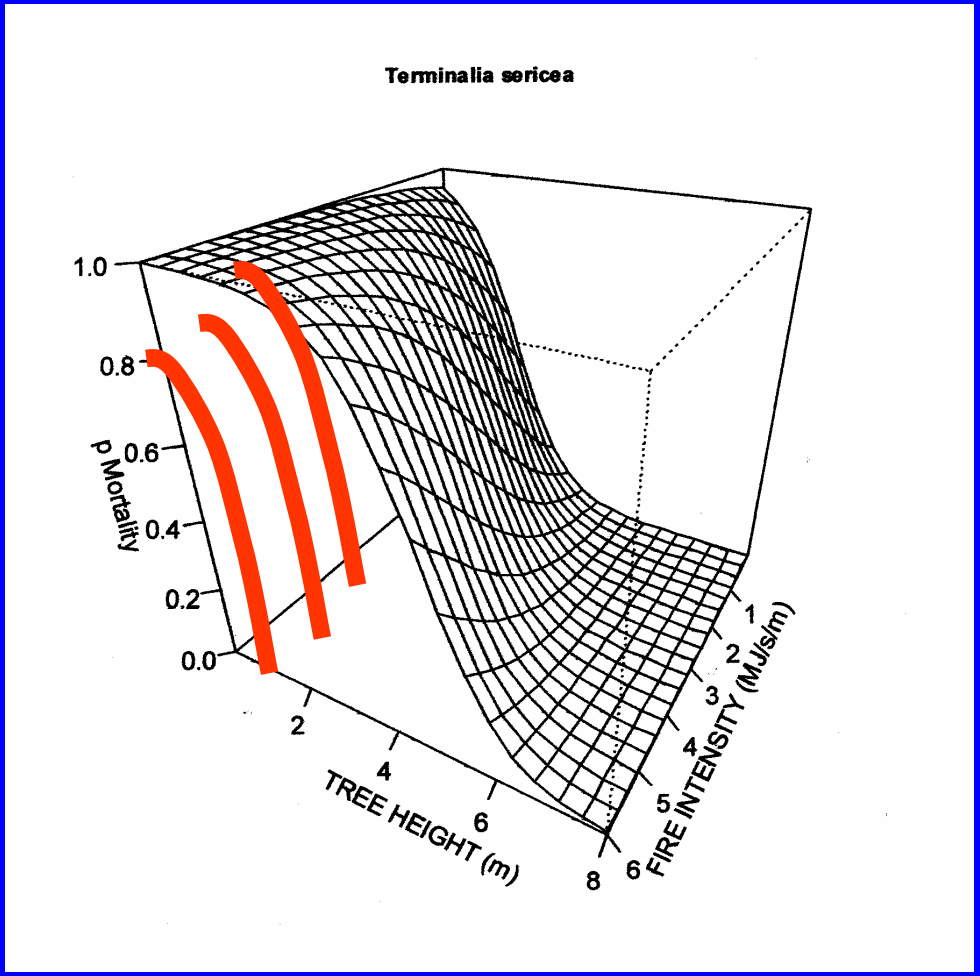
– **Sapling release: Rapid sapling growth?**

– Or **better able to tolerate fire?**

Post-burn sapling growth rates



Top-kill and fire intensity



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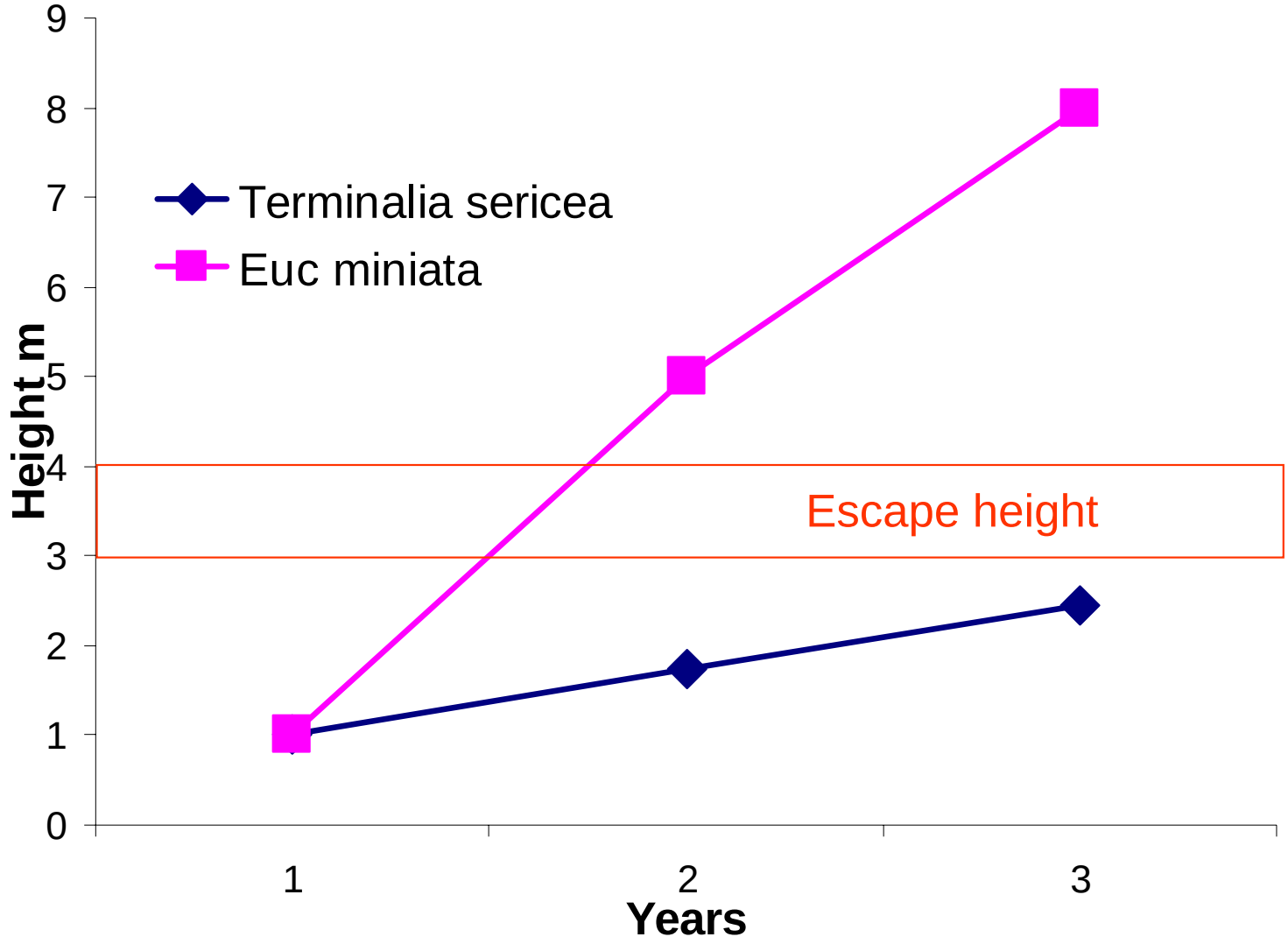
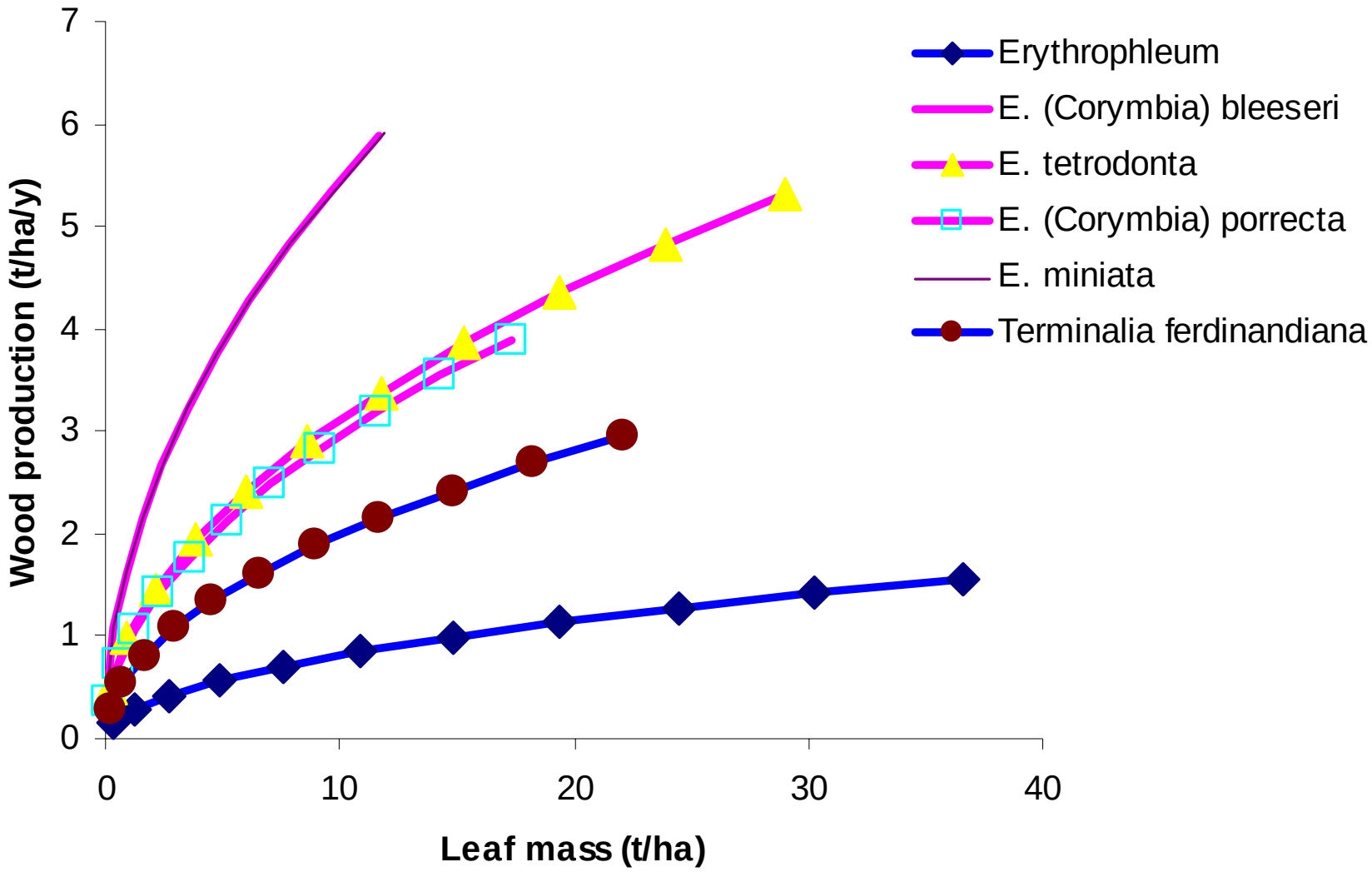
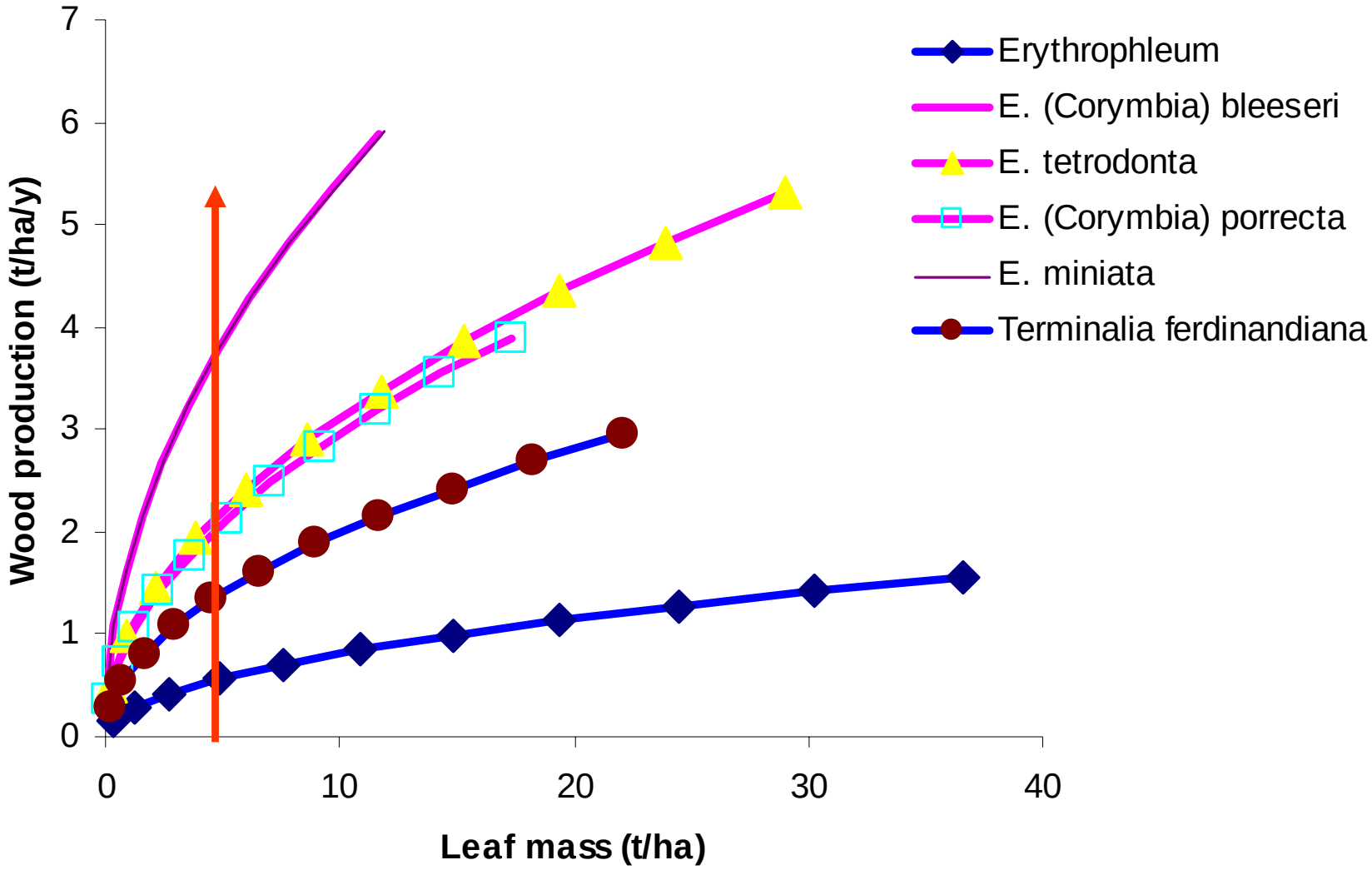


Terminalia no grass, no fires
Euc sapling, grass, 2 fires in 3 years!!

Fensham, bowman 1992

What are euc saplings doing differently to grow more rapidly than neucs?


Wood production (t/ha/y)
0
1
2
3
4
5
6
7
0
10
20
30
40
Leaf mass (t/ha)
Erythrophleum
E. (Corymbia) bleeseri
E. tetrodonta
E. (Corymbia) porrecta
E. miniata
Terminalia ferdinandiana



Eucalypts grow 1.5 to > 7 times more wood than neucs for same mass of leaf

How do they do it?

- Suggestions please

How do they do it?

- Carbon gain
  - Similar A_{max} to neucs
  - Similar leaf lifespan
  - Photosynthetic bark + for eucs
- Carbon allocation
  - Similar root:shoot ratios
  - Both eucs and neucs store below-ground TNC to subsidise sapling pole growth
- So why are eucs super-trees?

Summary

- Australian savannas seem to be outliers: too many trees, too uniform in space and time *vs* other savannas
- Outliers because of eucalypts
- Fire escape attributes, not resource acquisition best explanation?
- **So euc tree cover at equilibrium with resources? But neucs fire, not resource limited**

Conclusion

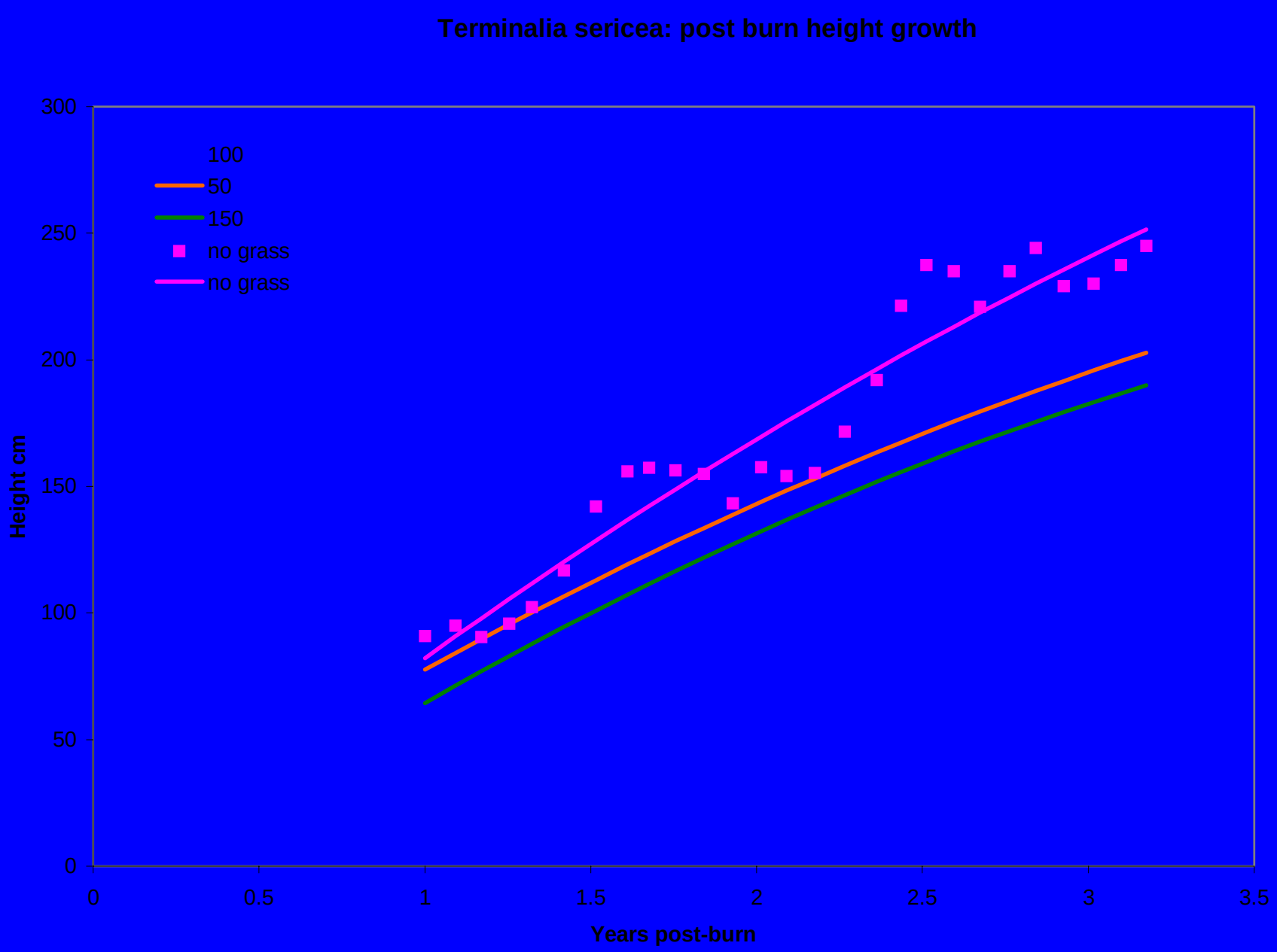
- Eucalypts first clade in the world to crack the savanna grass fire problem
- Understanding how they do it can give insights into what limits tree cover in savannas elsewhere
- And insights into what limits whole tree carbon gain?

Many thanks to:

- Alan Andersen and the Darwin CSIRO lab
- Lynda Prior, Dave Bowman, Caroline Lehman, Lyndsey Hutley and others from CDU
- Ed February, Carla Staver, Diane Southey from UCT field trip to Oz
- Guy Midgley, Ian Woodward, and others for ecophys discussions

Implications

- Modelling savannas requires mix of ecosystem physiology, demography?
- Do we need different PFT to get trees into savannas in DGVMs with realistic C_4 grass fire regimes?
- Very little empirical work on fire/sapling growth interactions in context of escape
- Very little known on tree longevity in these systems


Terminalia sericea: post burn height growth
300
250
200
150
100
50
0
Height cm
100
50
150
no grass
no grass
0
0.5
1
1.5
2
2.5
3
3.5
Years post-burn

Why so few trees in tropical grassy ecosystems?

- Because grassy biomes are very hostile places for tree recruitment
  - Grasses out-compete young trees
  - Grasses burn
  - Grasses attract grazers/browsers

Why so few trees? A demographic problem

- Demographic bottleneck models
  - Trees limited by
    - Rare conditions for seedling establishment
    - Rare sapling release from fire/browse trap

    - (Higgins, Bond, Trollope 2001. J. Ecol)

For saplings to escape and become trees

- Need a break from fire/herbivory
- Or faster growth to escape height under same fire/herbivory
- Or a combination

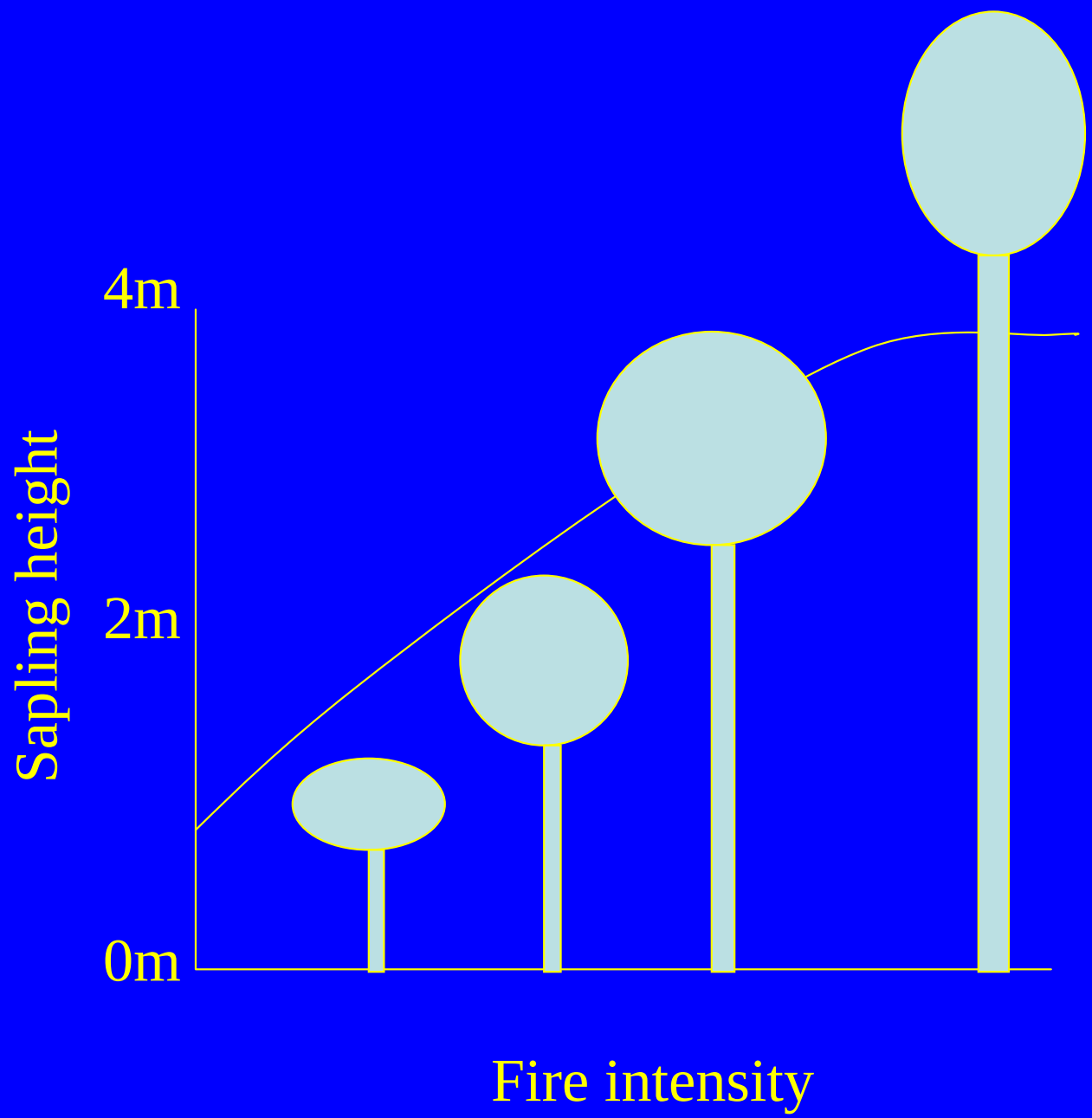
Key prediction

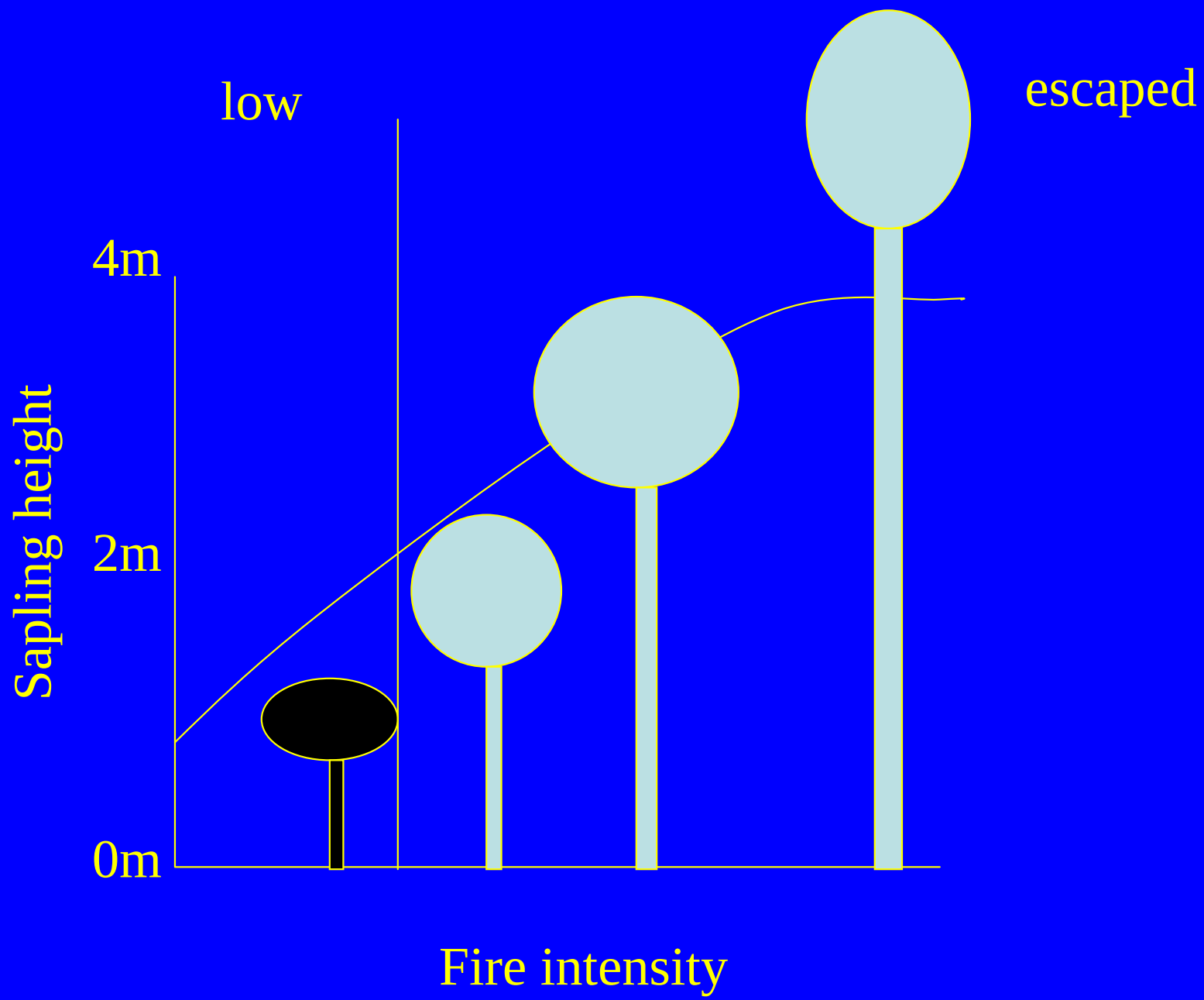
- Remove the consumer, fire or herbivory, and tree cover will increase to K (‘climate potential)

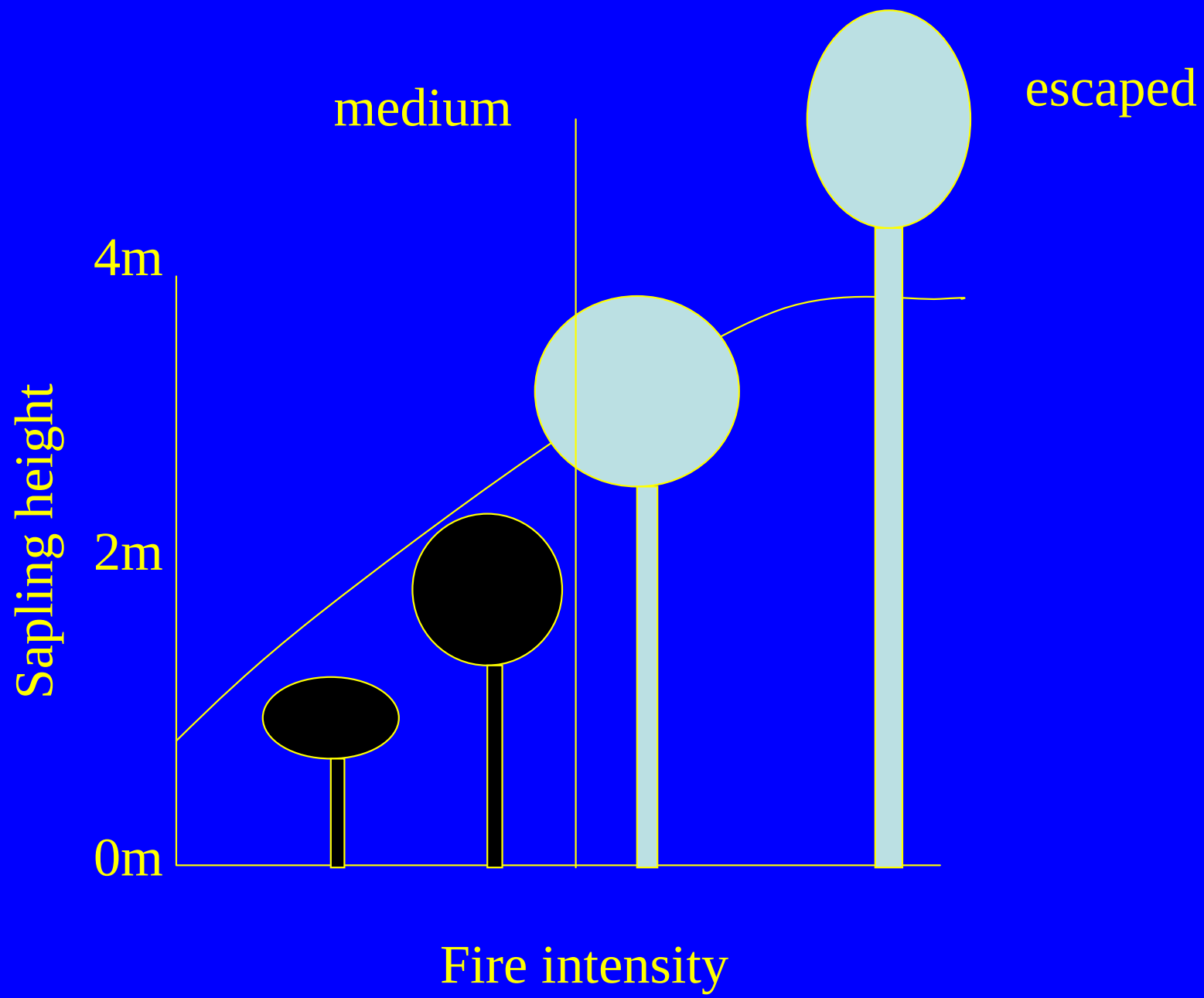
What prevents saplings escaping?

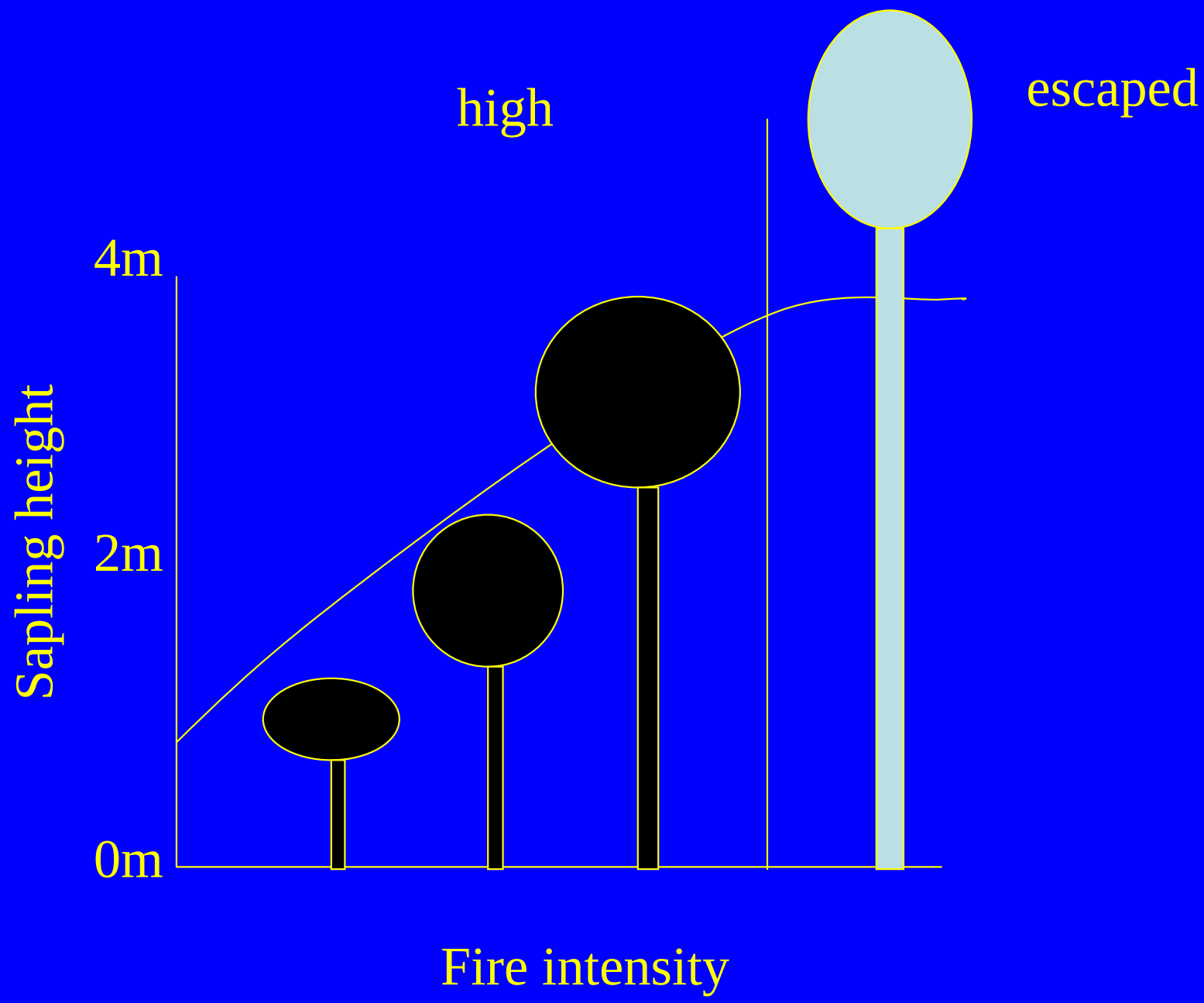
- Very few spp (none?) killed by fire.
- But all are “top-killed” (shoots killed) if small enough
- Probability of topkill increases with fire intensity (heat released by a fire)
- P topkill decreases with height of plant


4m
2m
0m
Sapling height
Fire intensity


4m
2m
0m
Sapling height
Fire intensity

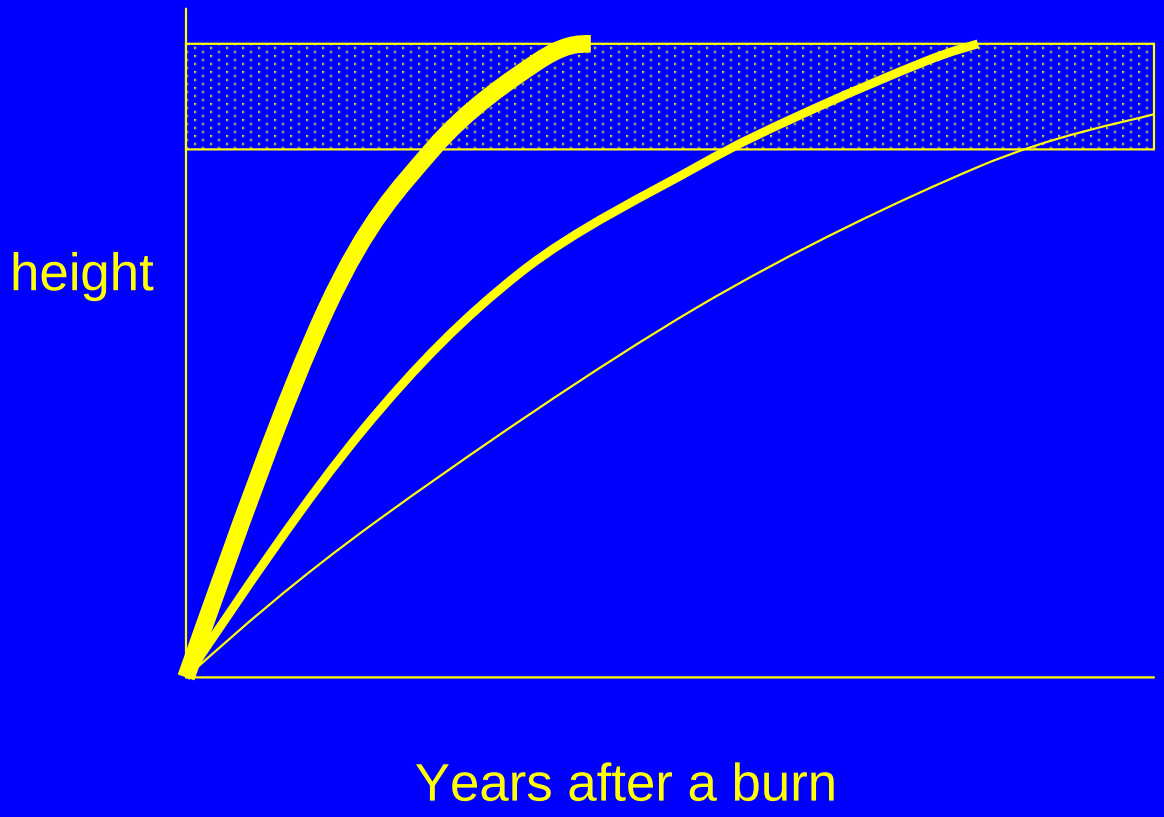

low
escaped
4m
2m
0m
Sapling height
Fire intensity


medium
escaped
4m
2m
0m
Sapling height
Fire intensity

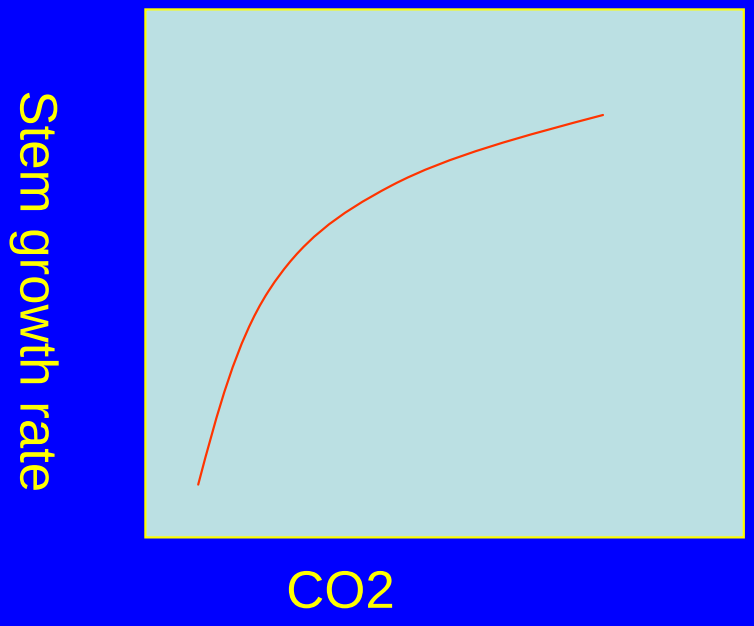

high
escaped
4m
2m
0m
Sapling height
Fire intensity

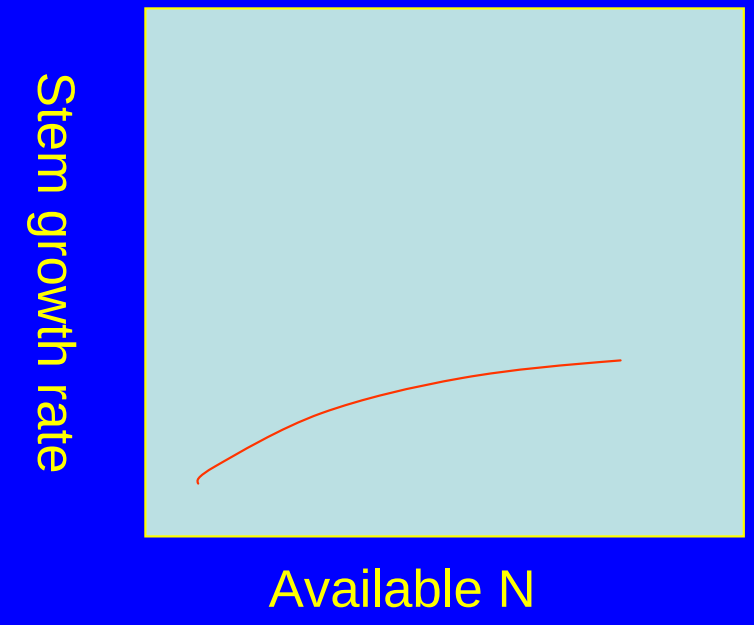
The plant factor: How frequently do we need intense burns?

Growth rates to escape height are important but poorly known



Likely to vary among species, sites and soils, high vs. low rain years and changing CO2



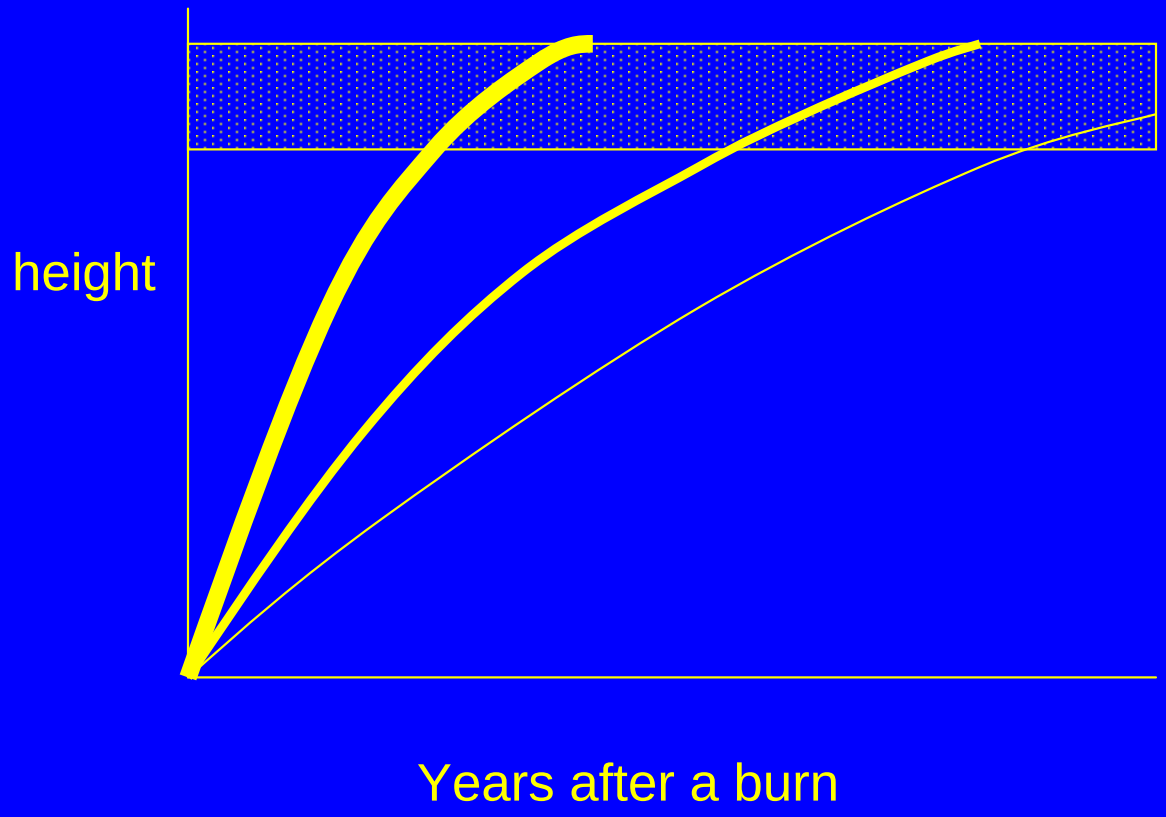


We are looking at response curves
To different environmental factors

Are eucs better at escaping fires?

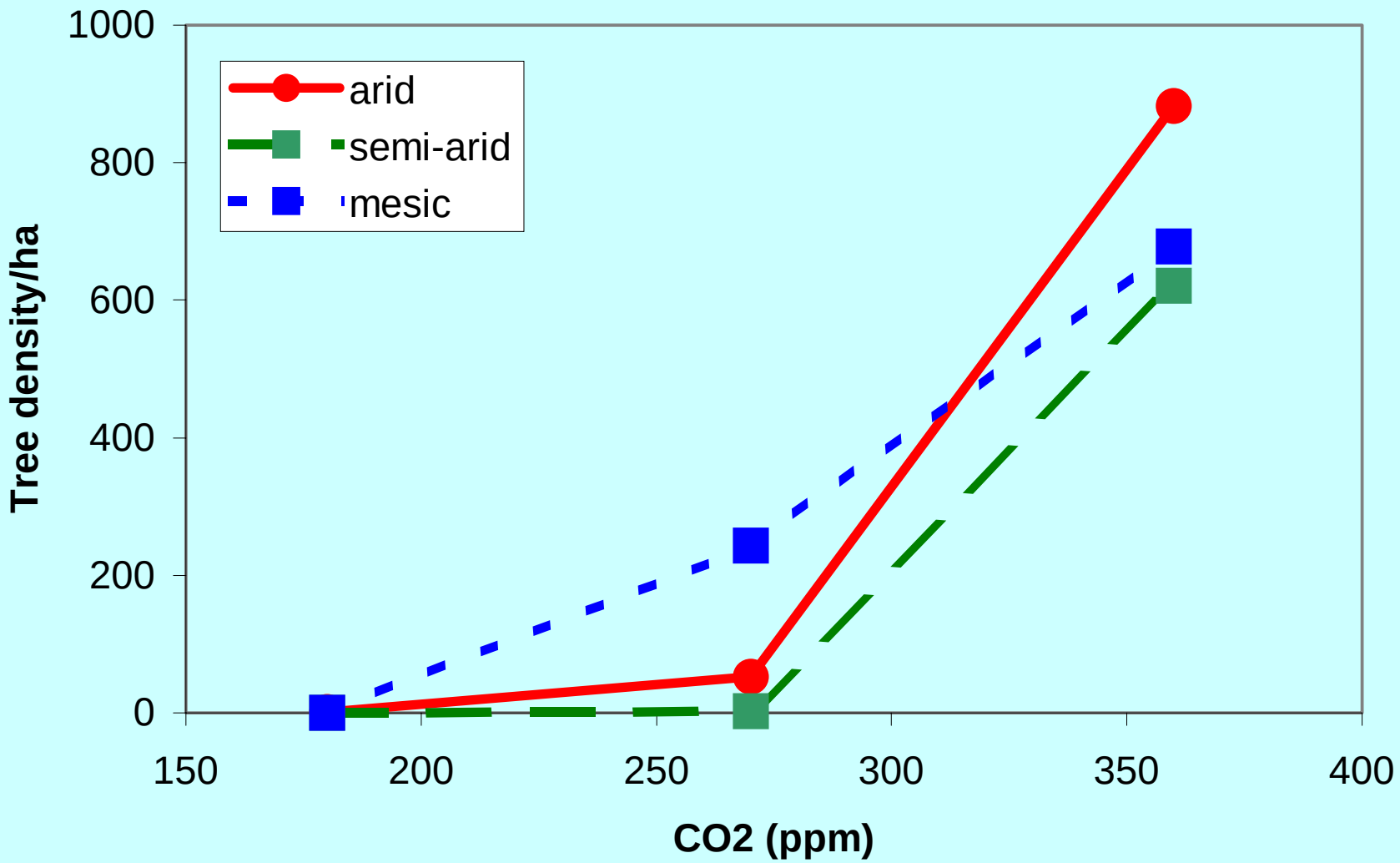
- Fire exclusion expts: Large changes in neucs as fire-suppressed saplings grow to trees, no change in eucs (saplings already escaped)
- Demographic studies: neucs stuck in fire trap, euc saplings escape easily

Growth responses all evaluated relative to escaping fire/browsers



Consequences for trees using DB model

Bond, Midgley, Woodward GCB 2003

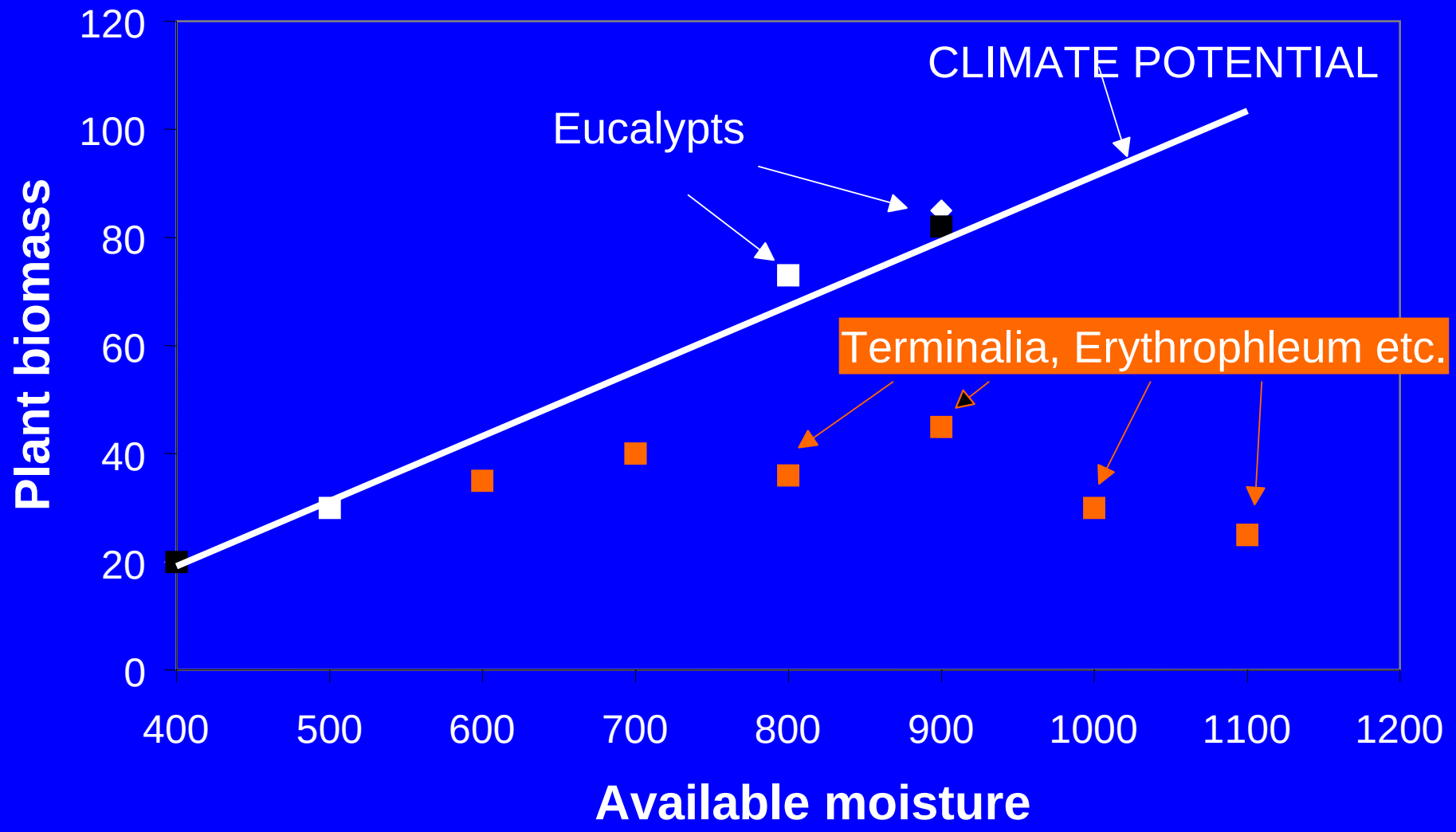


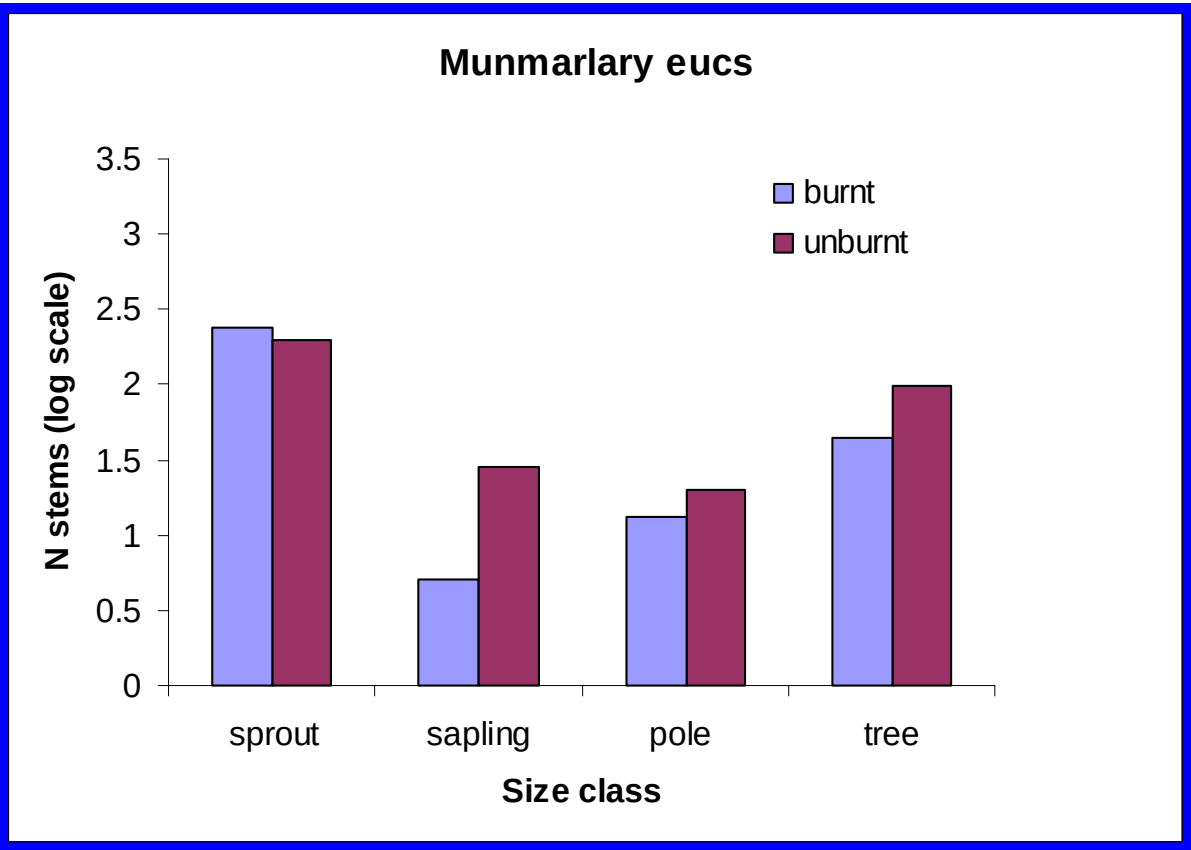
Are Australian savannas too woody?

- Africa/Australia comparison (Nth/Sth America?)
  - Data sources
    - Mahesh Sankaran Africa (and/or Kalahari transect)
    - Dick Williams Australia (and/or Australian transect)

Are eucalypts the key contributor to woodiness?

- Dick Williams data set?

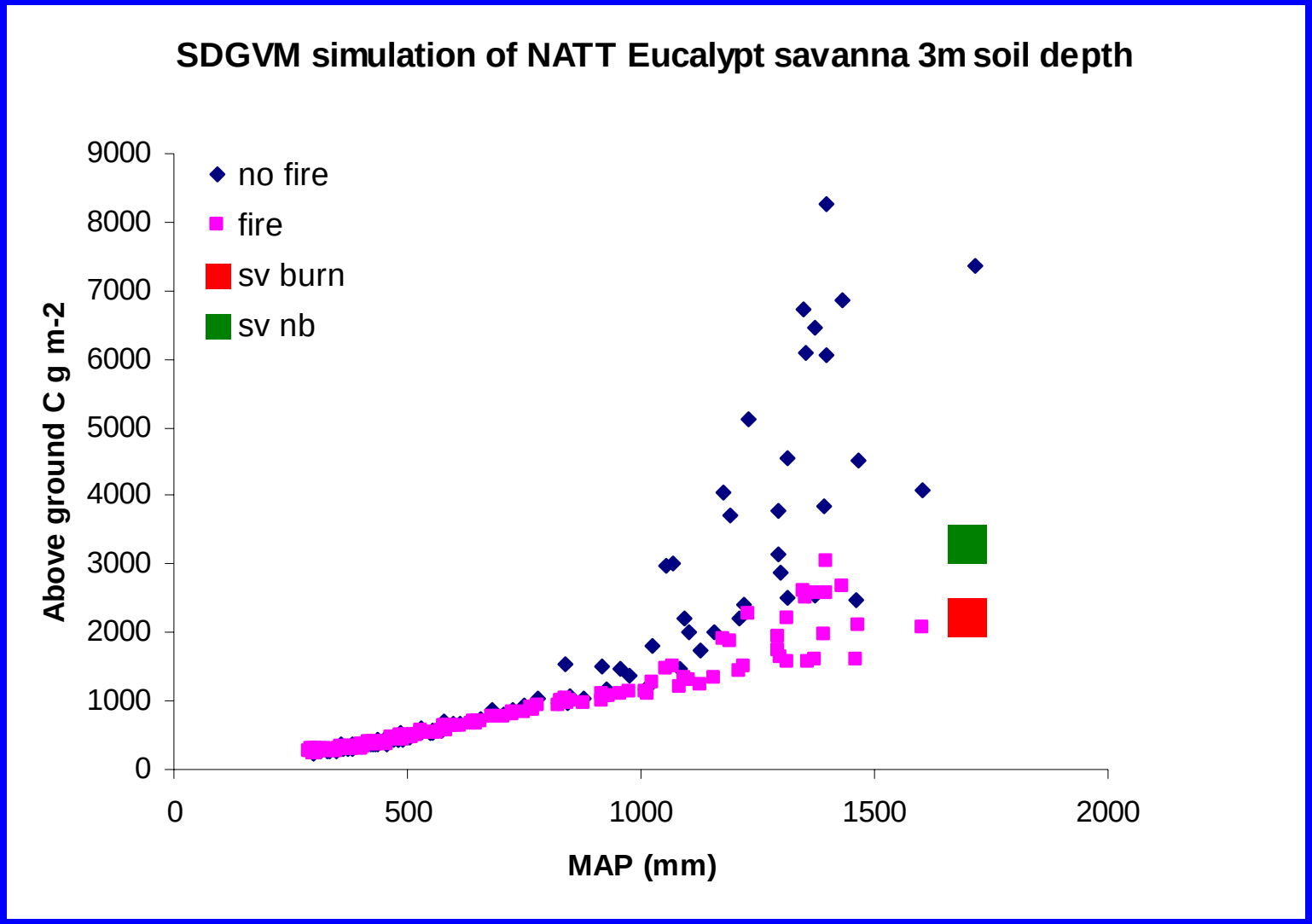




Bowman and Panton 1995
Aust. J. Ecol

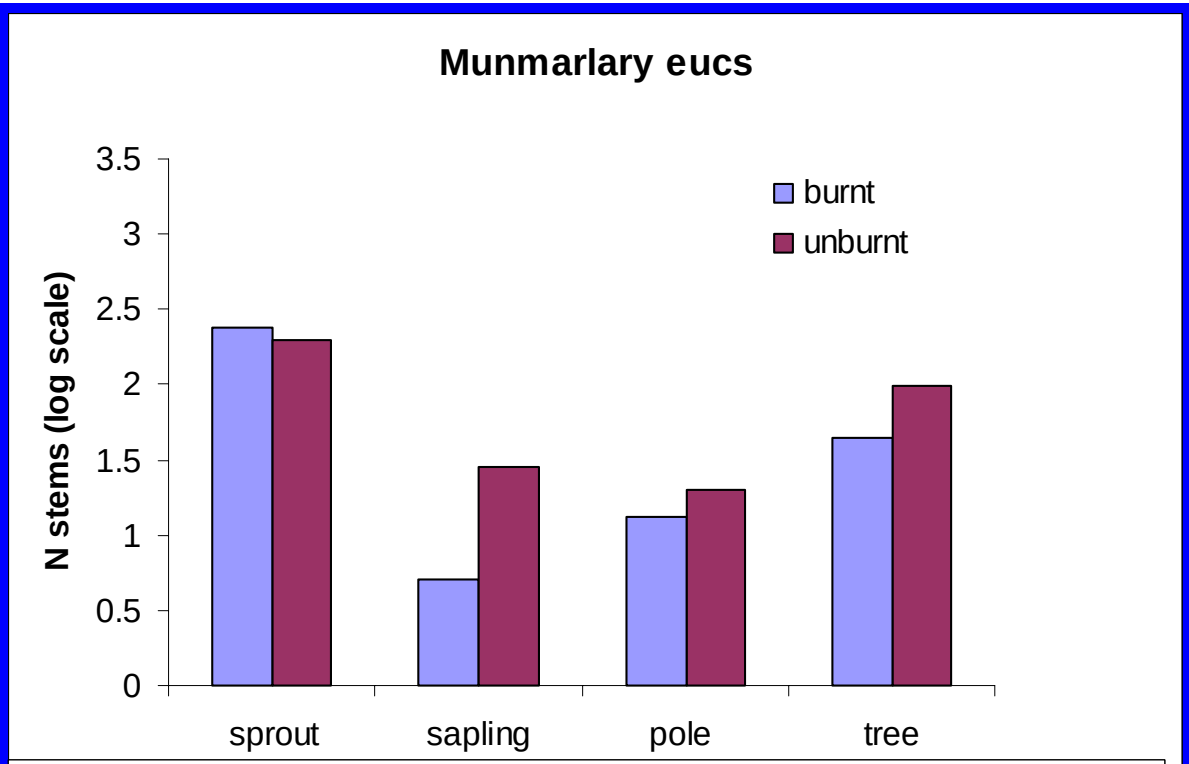
After 20 years fire exclusion

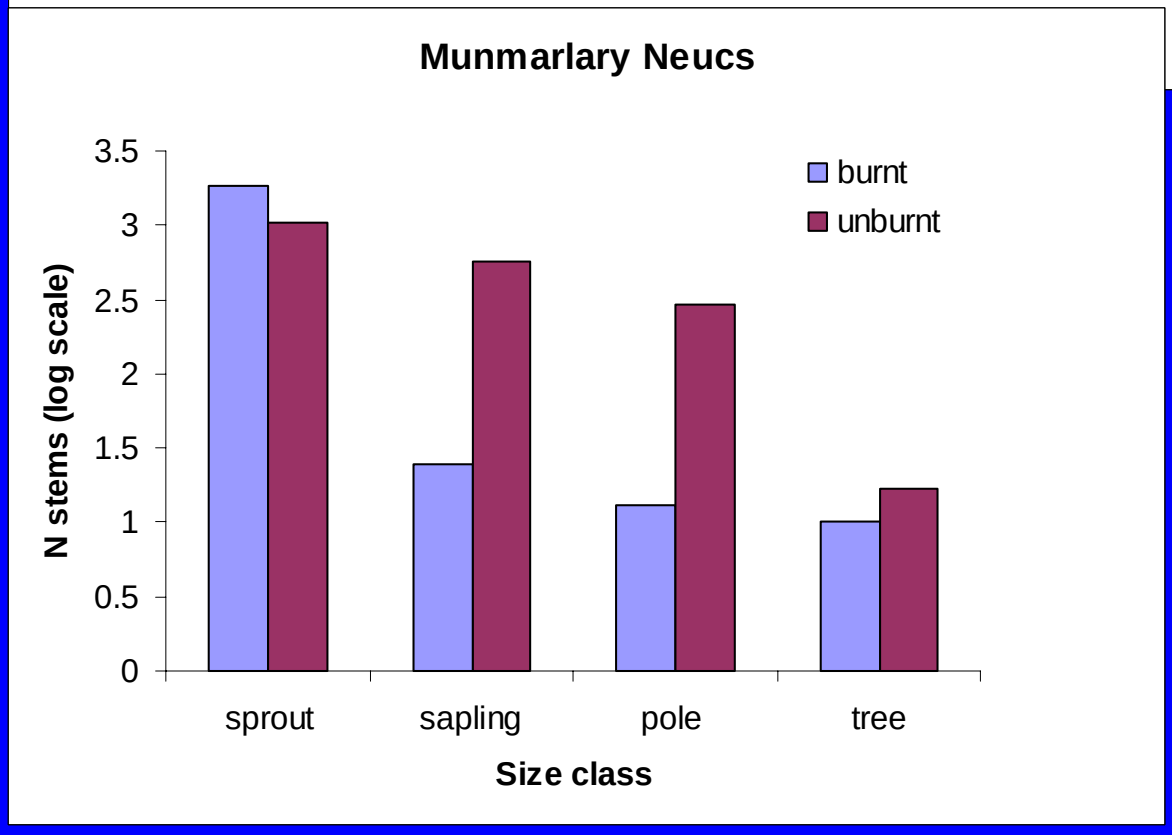
Expt vs DGVM simulation



Increasing but still a long way to go to reach K_{tree}
A FOREST!

Is woodiness determined by resource acquisition or fire and demographic bottlenecks?





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