

Large herbivore effects on phenolics and nutrients of woody species at the Nkuhlu Exclosures (2005-2008): Considerations of species, rainfall and scale

Peter F. Scogings

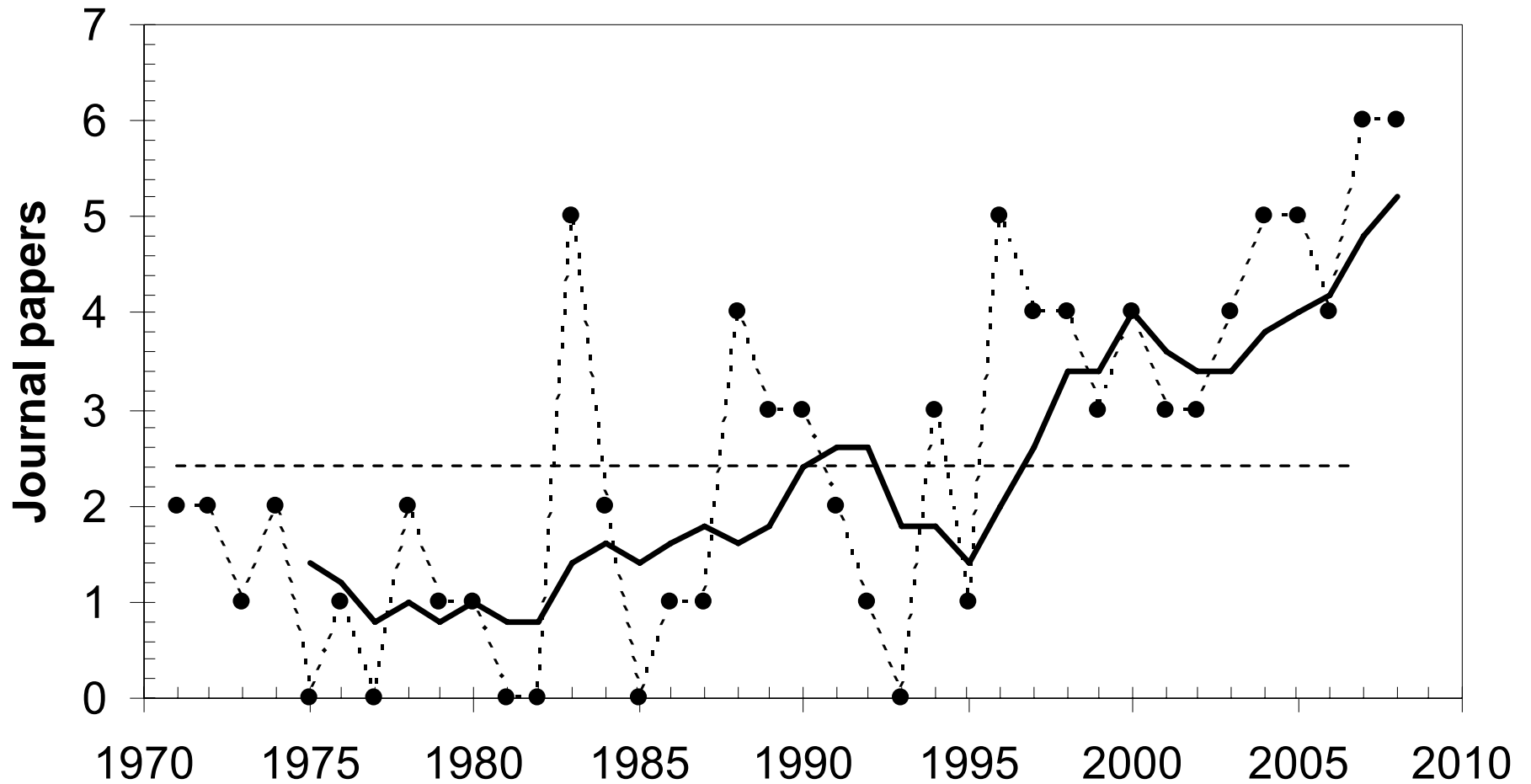
University of Zululand, South Africa

with contributions from

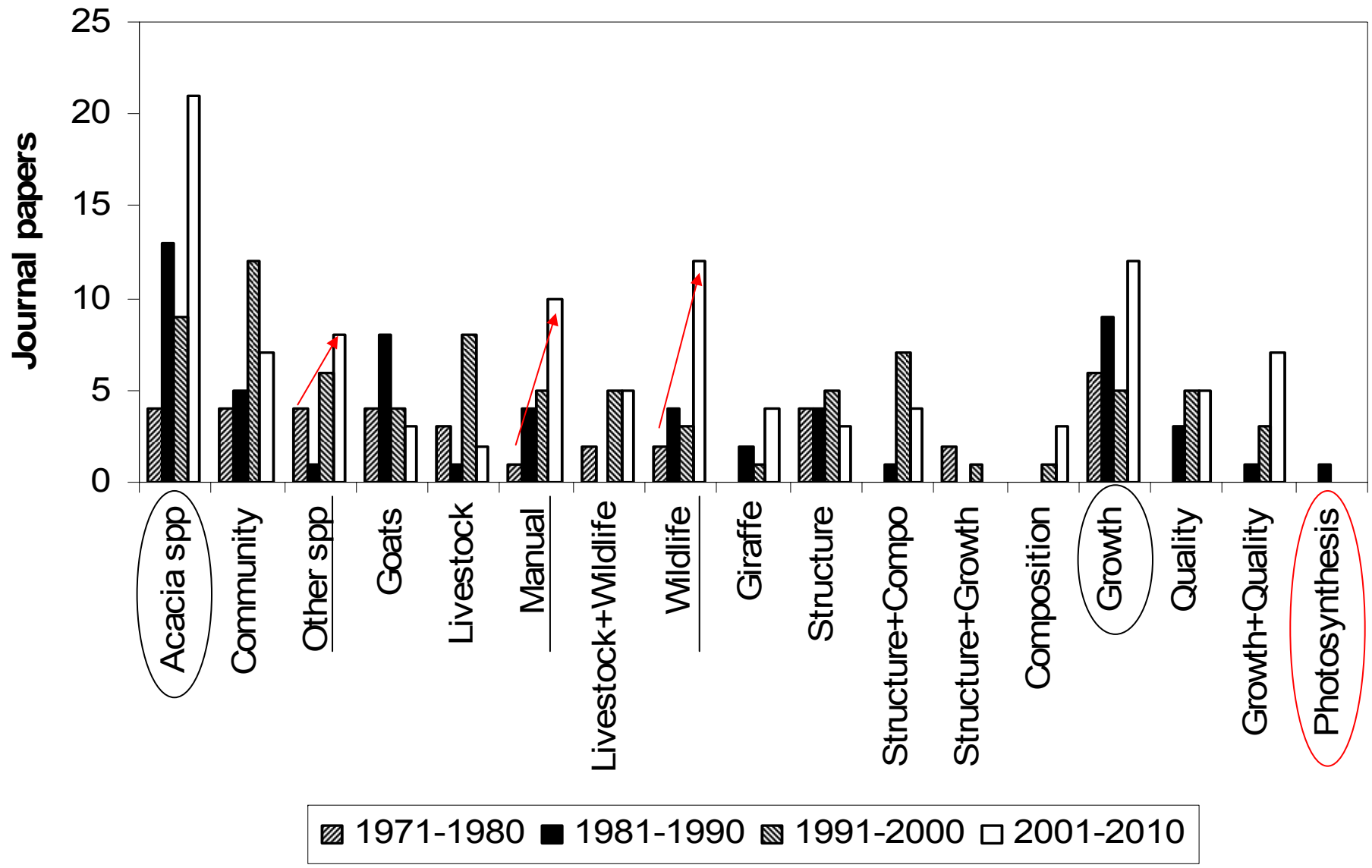
J. Hjältén, C. Skarpe, T. Rooke, D. Hattas, L. Dziba, A. Zobolo, S. Lorentz

Outline

- Brief introduction
- Rapid overview of preliminary results
(skipping the details)
 - trends within 3 wet seasons
(subject to further analysis)
 - exclusion/browsing effects
(completed analysis of Jan. 2008 data)
 - trends over 3 years *(subject to further work)*
- Some *(speculative)* conclusions and generalisations...



Number of peer-reviewed journal papers on ruminant impacts on woody plants in African savannas, 1971-2008. Horizontal dashed line – 38-year mean. Solid bold line – 5-year running mean.



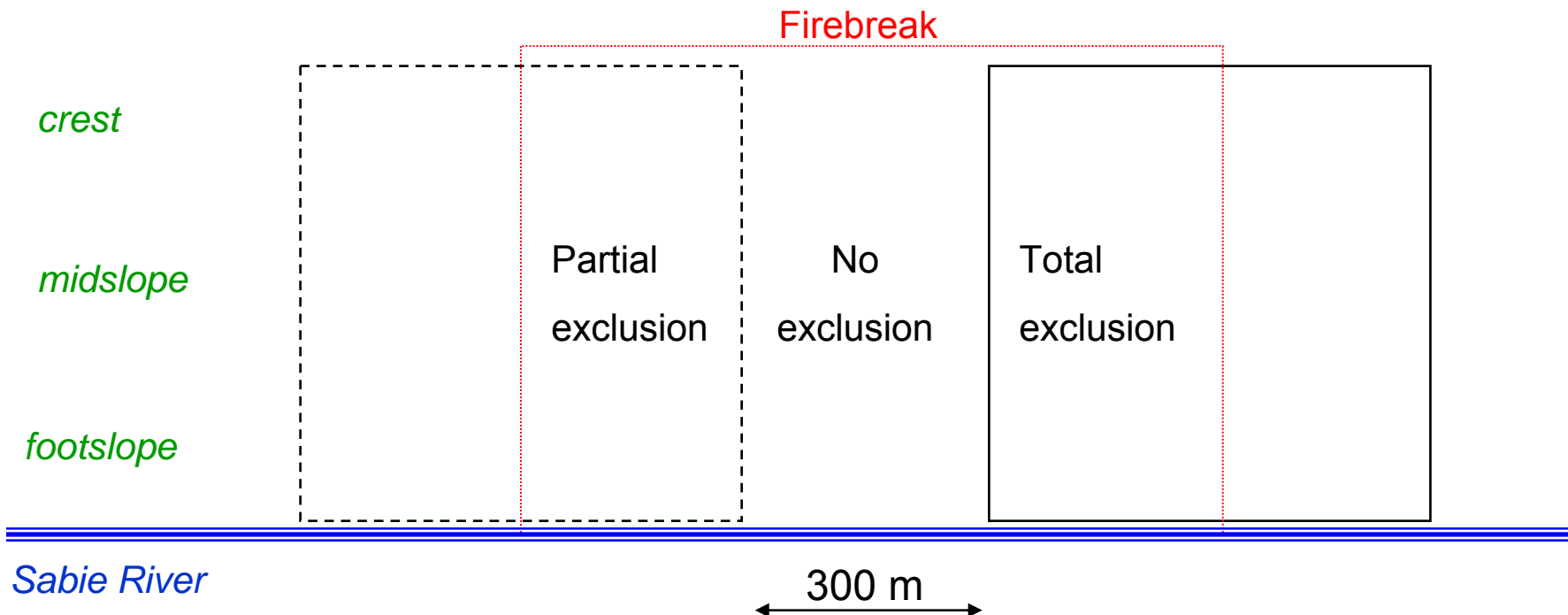
Number of peer-reviewed journal papers on ruminant impacts on woody plants in African savannas, 1971-2008, per decade within three plant categories (far left), six animal categories (left of centre) and eight response categories (right).

Nkuhlu Long-term Exclusion Experiment (est. 2002/2003)

Partial exclusion – excludes elephants (and giraffe)

Total exclusion – excludes all browsers (and grazers)

No exclusion (control) – open to all browsers (and grazers)



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Focus

- Effects of the exclusion treatments on herbivore-related chemical traits of abundant woody species
- Seasonal variations in chemical traits of abundant woody species

Phases

- General trends across two wet seasons (2005/2006 and 2006/2007)
 - 6 species
 - few samples
 - high frequency
- Exclusion effects in the middle of the 2007/2008 wet season
 - 4 species
 - many samples
 - low frequency

Species

- *Acacia exuvialis*
*Acacia grandicornuta**
Dichrostachys cinerea



**Fine leaves, few shoots,
spines**

- *Combretum apiculatum*
*Euclea divinorum** ϵ
Grewia flavescens

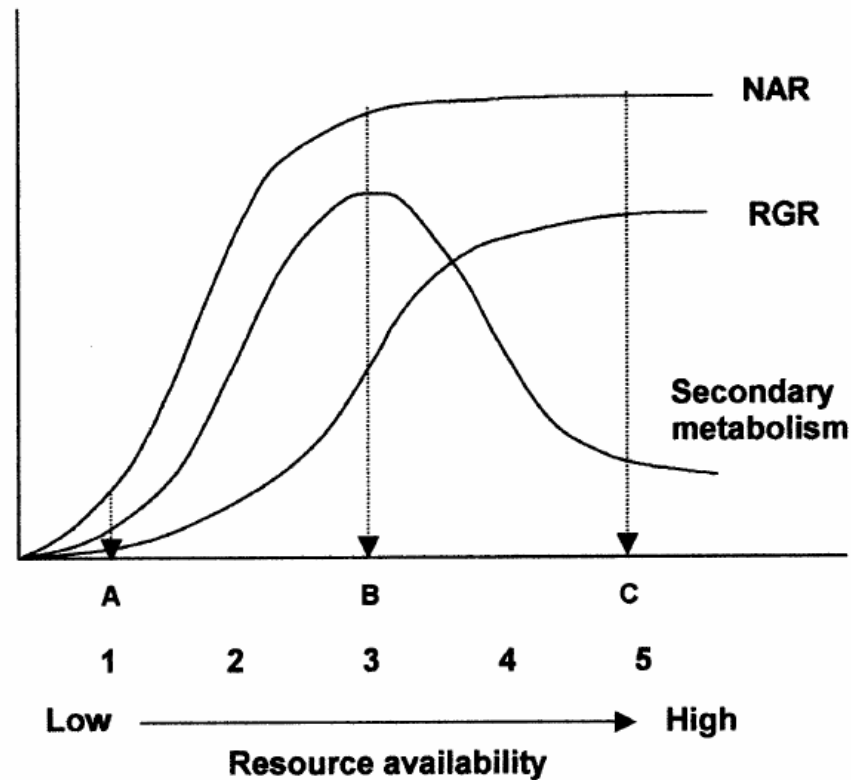


**Broad leaves, many shoots,
no spines**



*sodic footslope; ϵ evergreen

Growth/Differentiation Balance



Relationship of net assimilation rate (NAR), relative growth rate (RGR), and differentiation (specifically secondary metabolism) across a resource gradient, for which the resource affects growth more than it does photosynthesis. **A**: both growth and photosynthesis are constrained by low resource availability. **B**: growth is more constrained than photosynthesis and thus there is more allocation to differentiation (and specifically to secondary metabolism). **C**: growth is less constrained and thus there is more allocation to growth. [Adapted from Herms and Mattson (1992)].

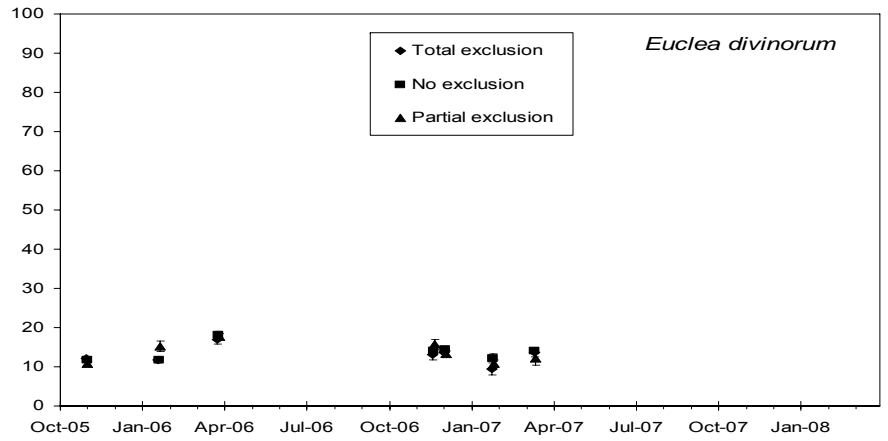
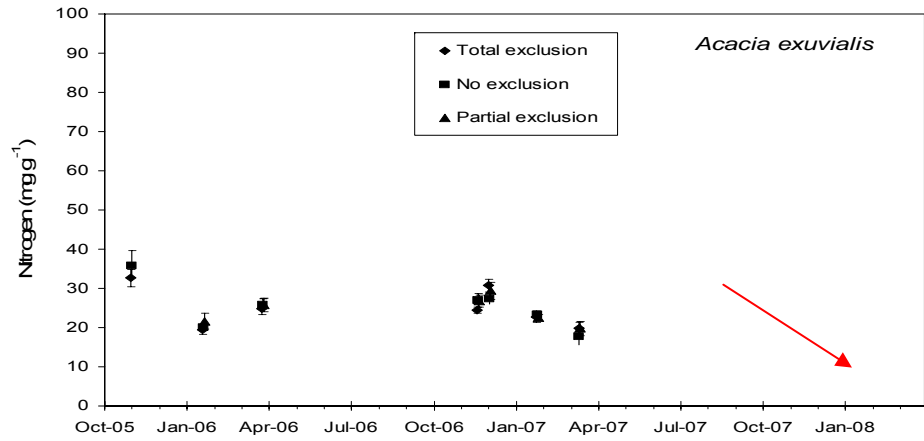
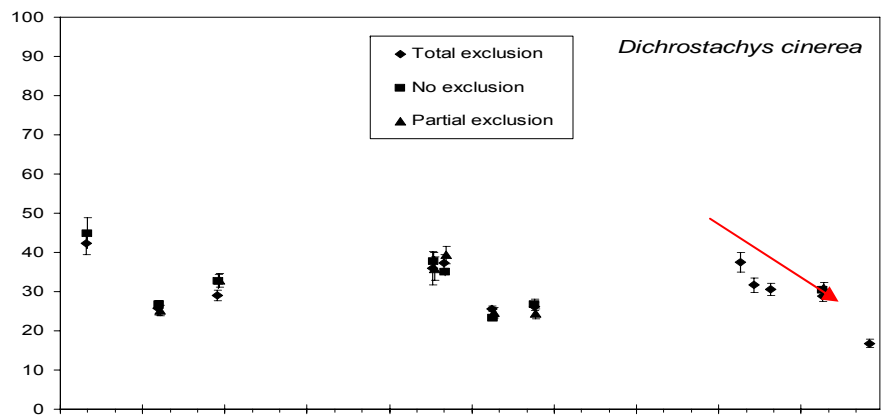
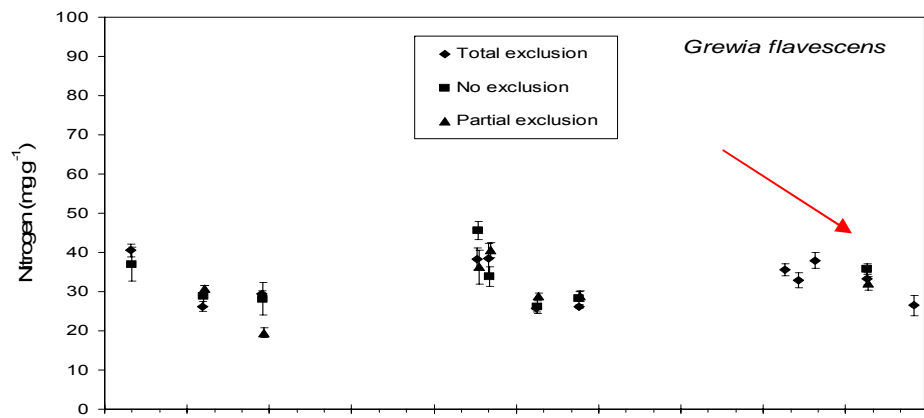
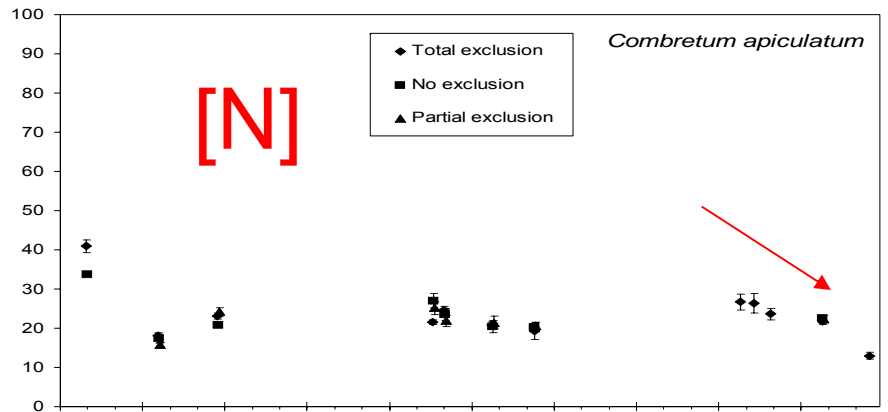
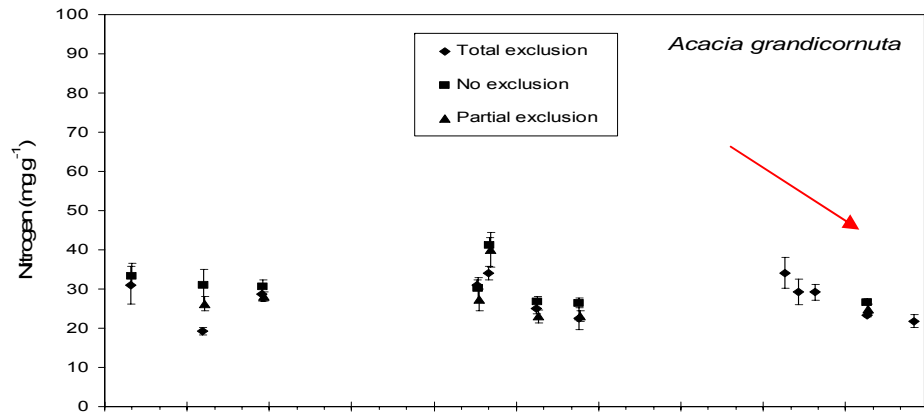
Some predictions...

- Concentrations of condensed tannins (CT) and total phenols (TP) are lowest early in the wet season (and increase)
(GDB prediction? or simply an age effect?)
- Browsed plants have (vs unbrowsed):
 - lower [CT] or [TP] early in the wet season
 - higher [CT] or [TP] late in the wet season

Will come back to this later...

Questioning some assumptions...

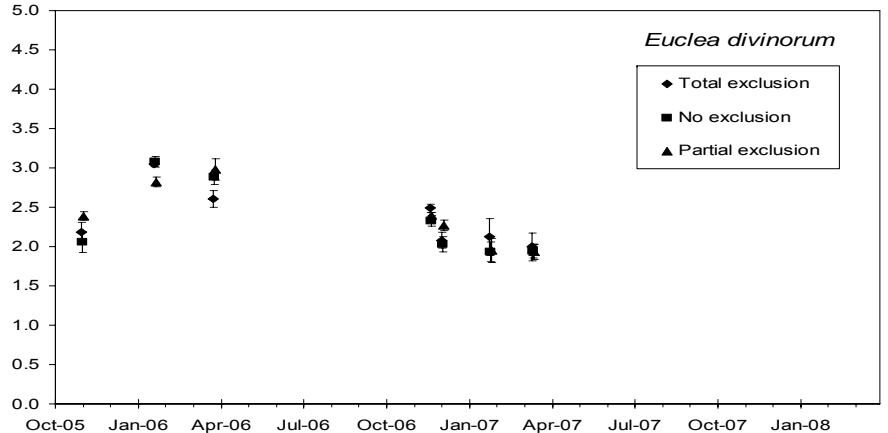
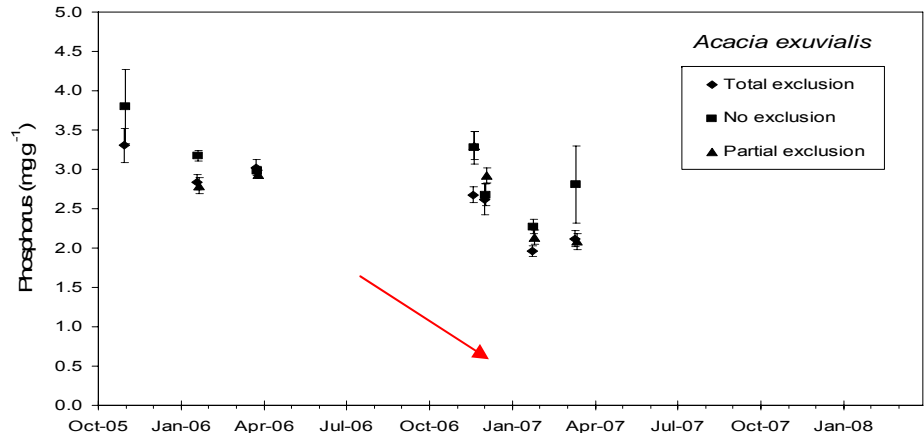
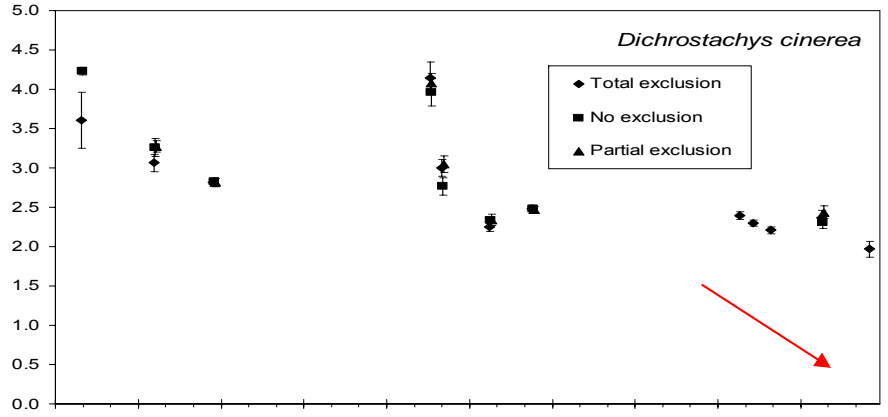
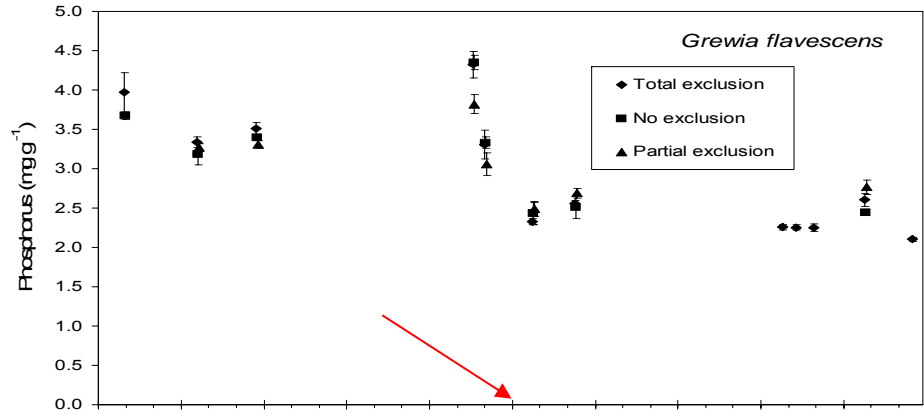
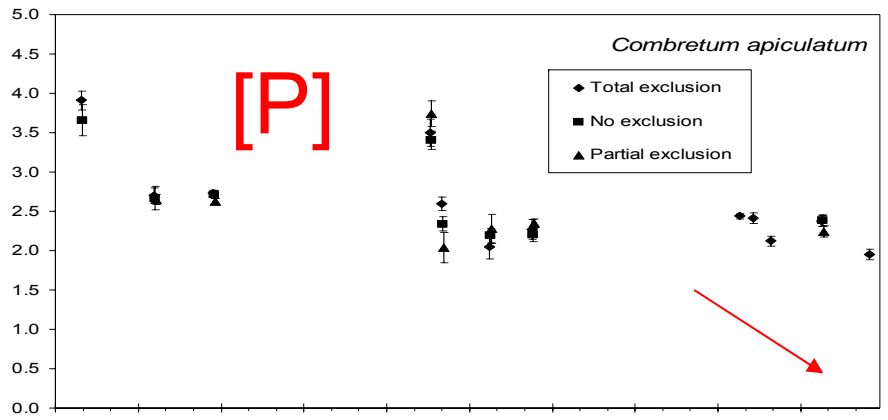
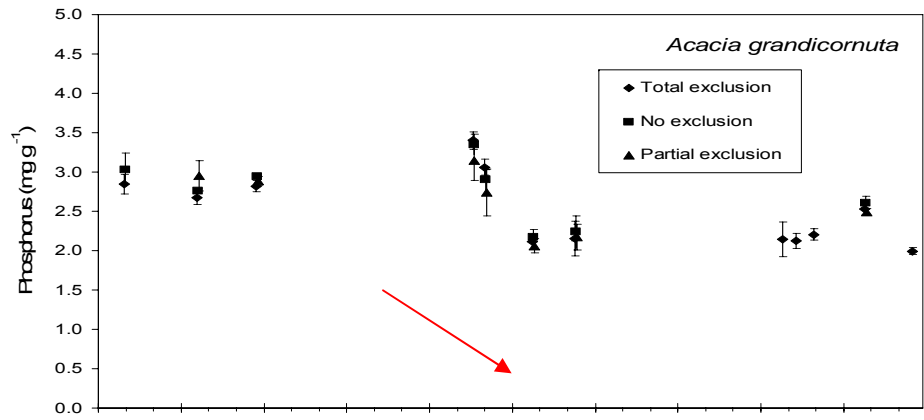
- Are nutrient concentrations (e.g., N & P) and growth rate highest early in the wet season?
- Do [N], [P] and growth rate decrease during the wet season?
- Is photosynthesis rate highest early in the wet season?
- Is high photosynthesis rate maintained during the wet season?



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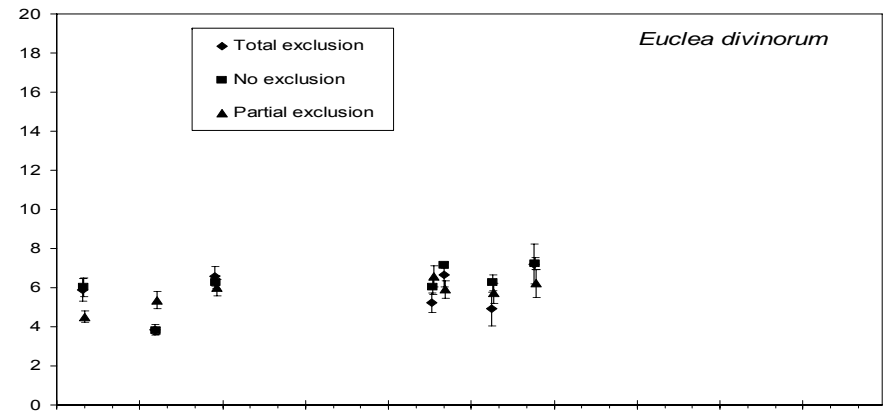
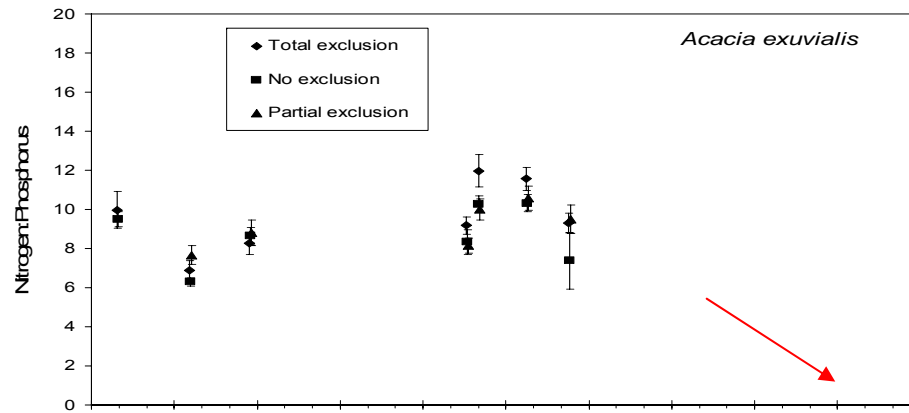
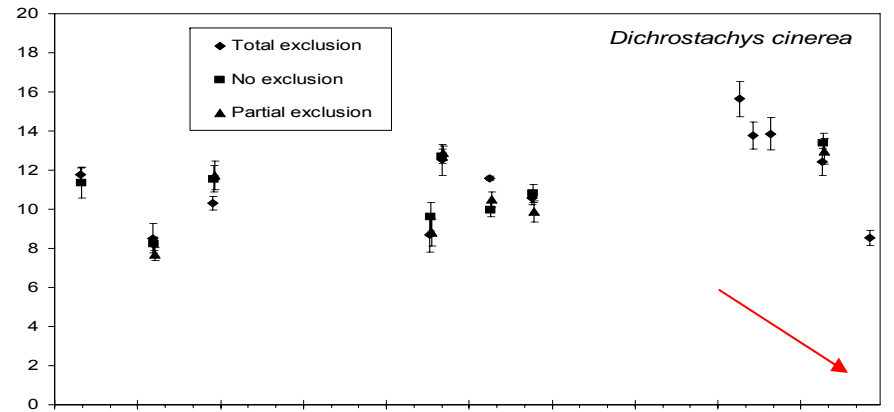
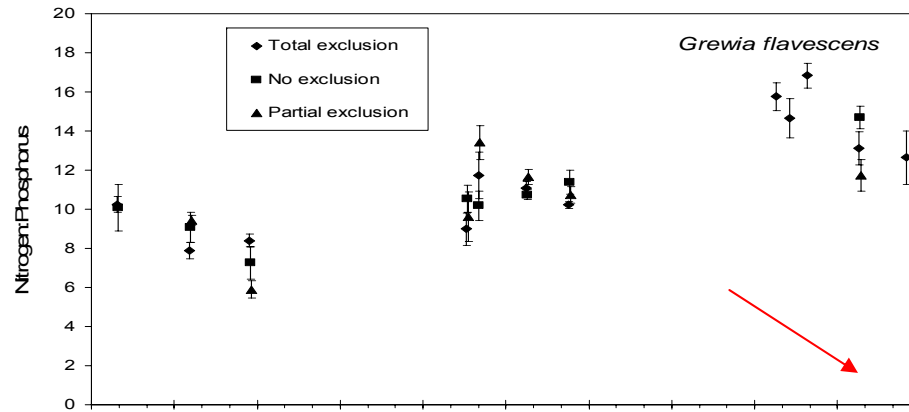
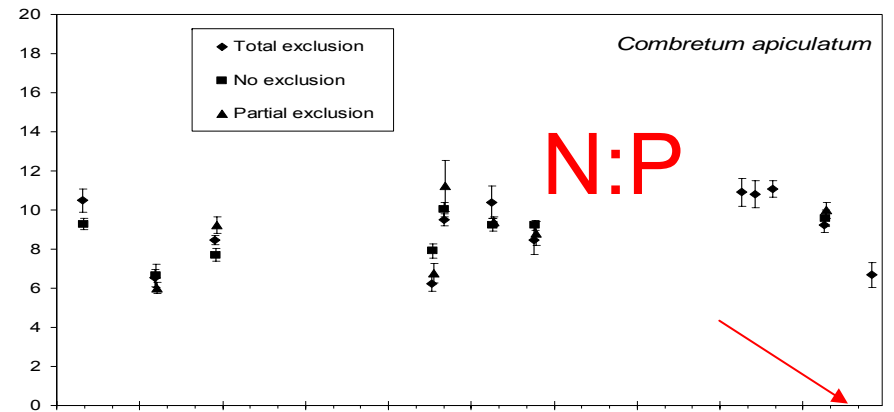
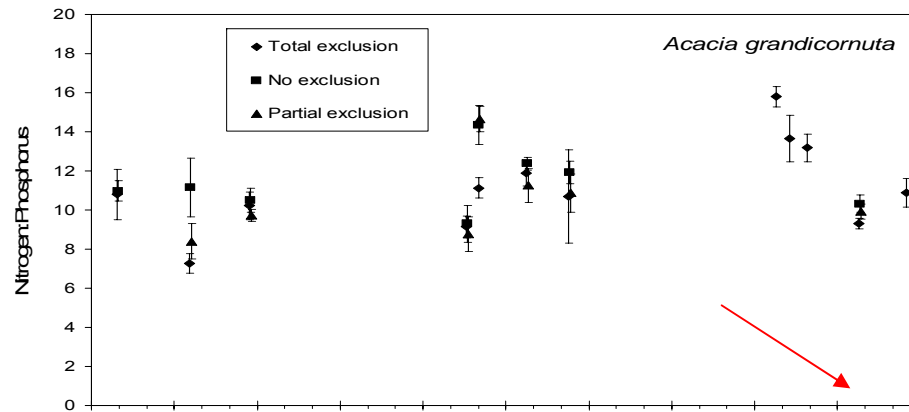
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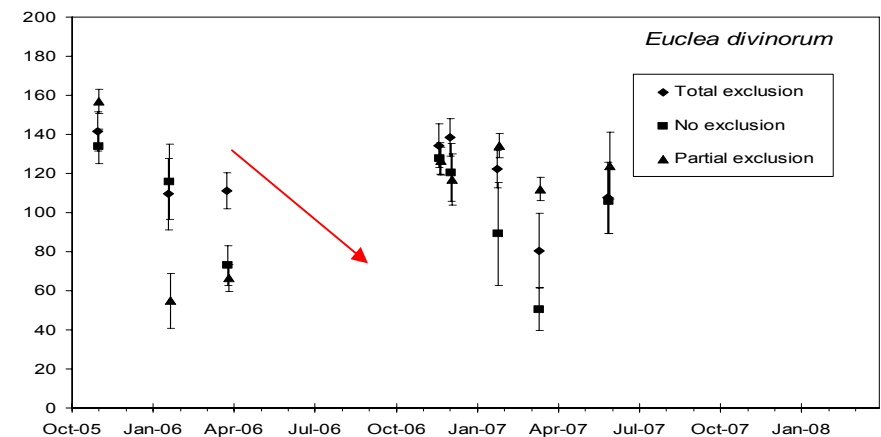
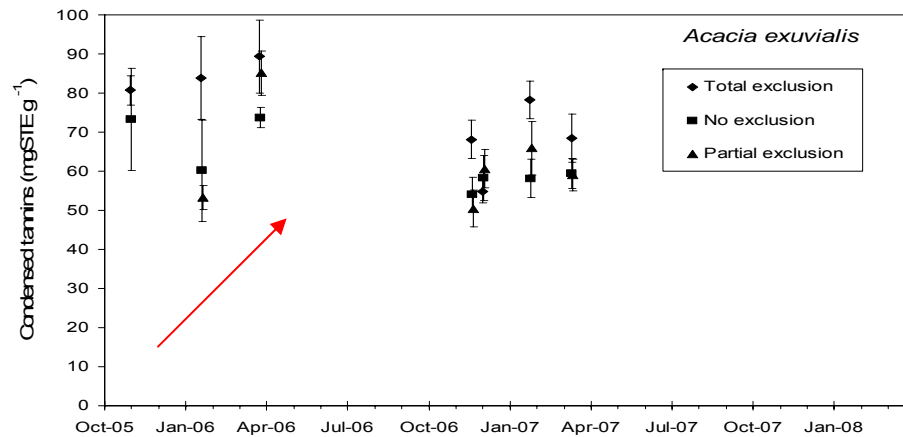
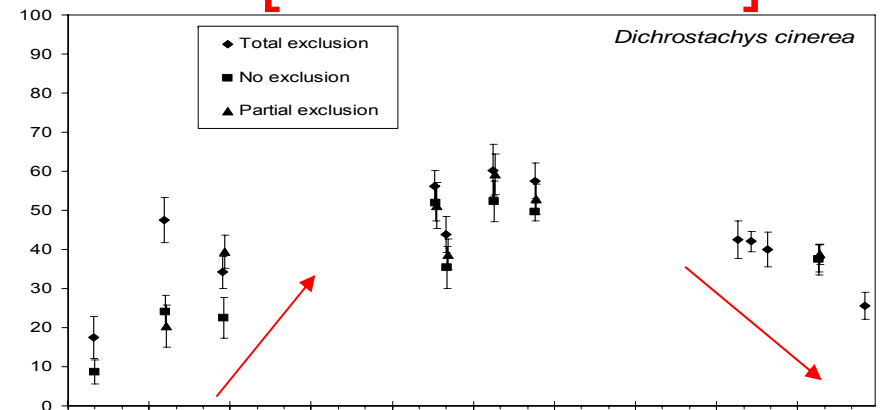
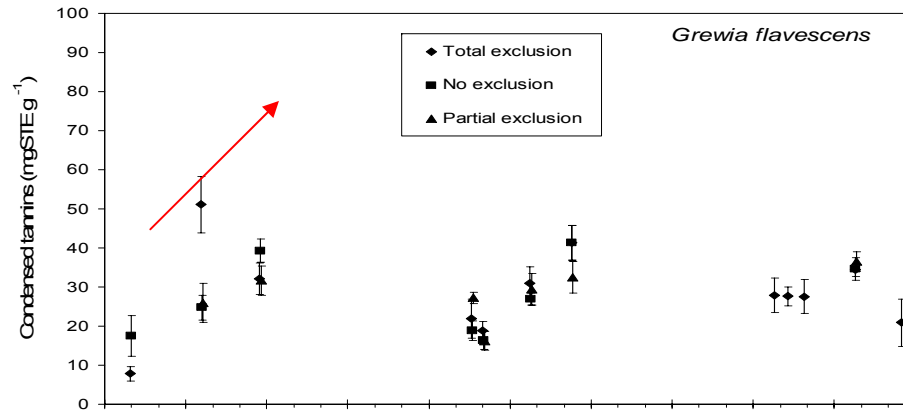
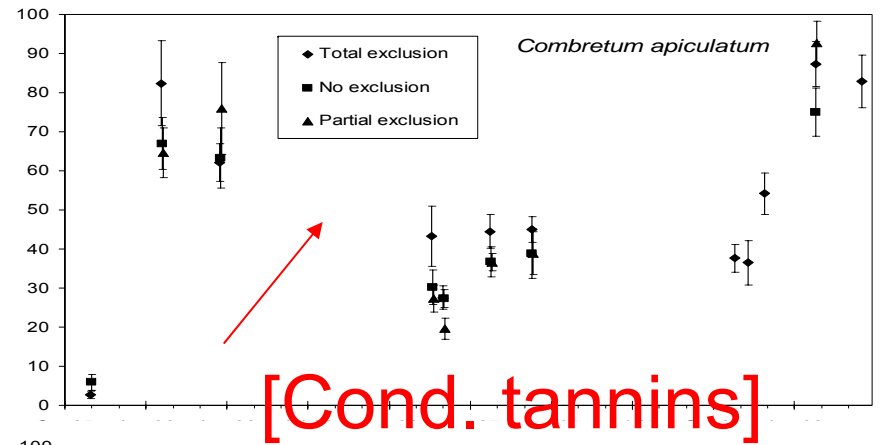
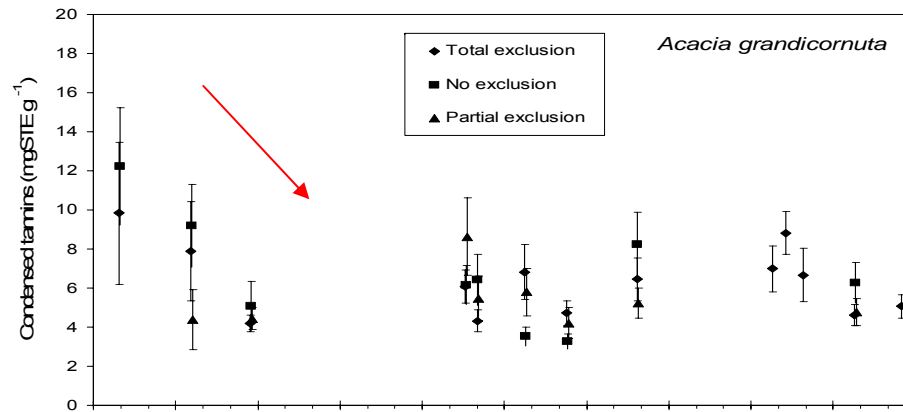
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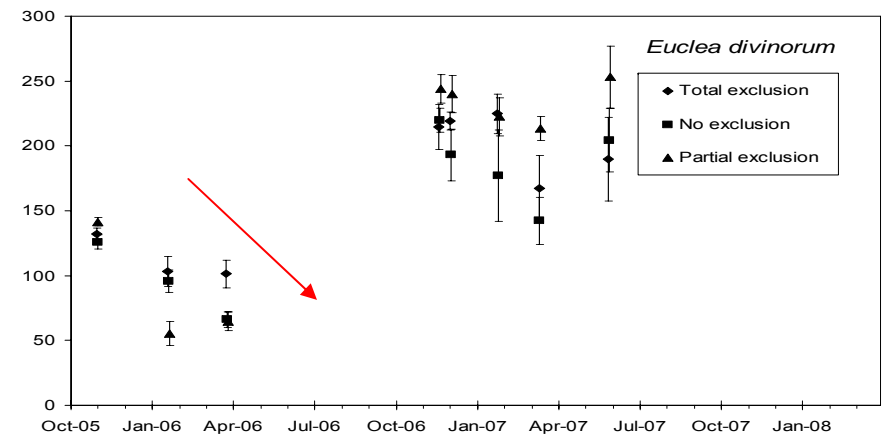
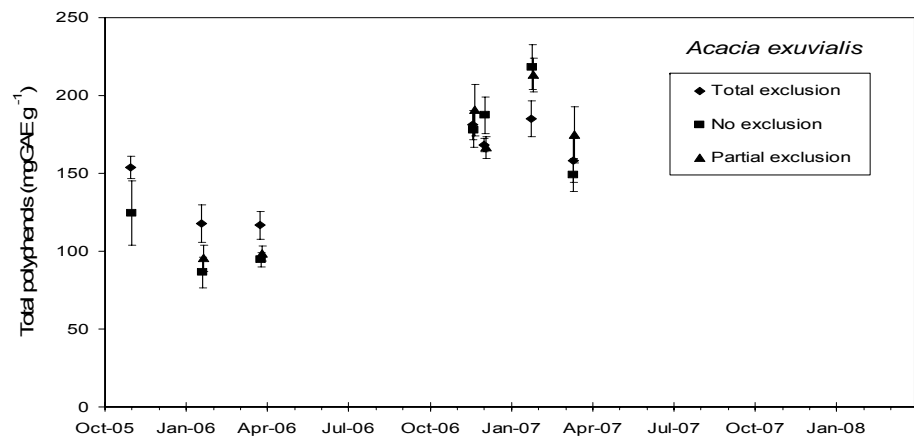
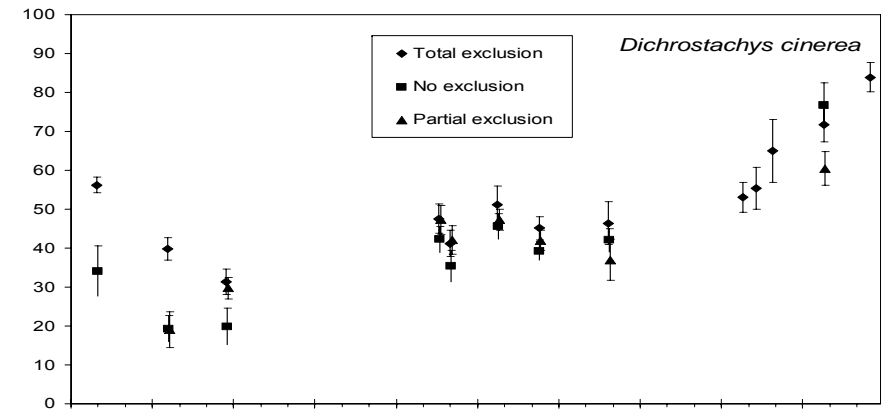
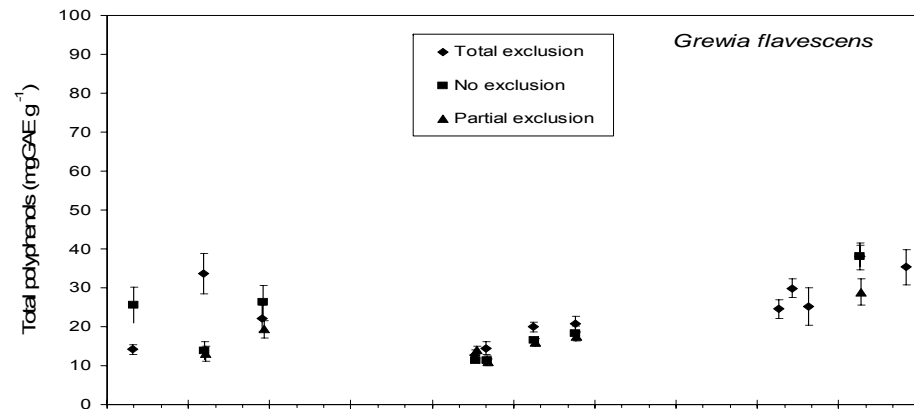
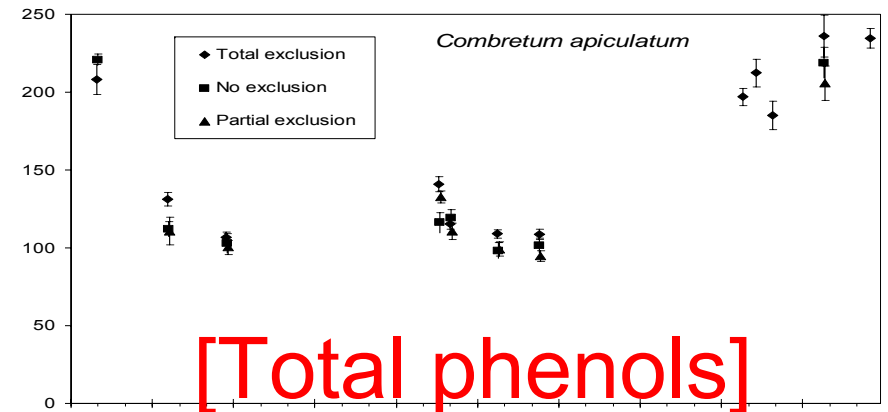
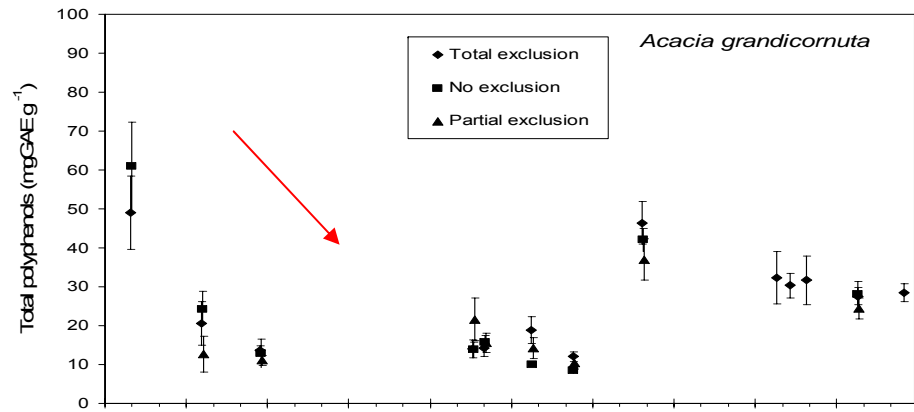




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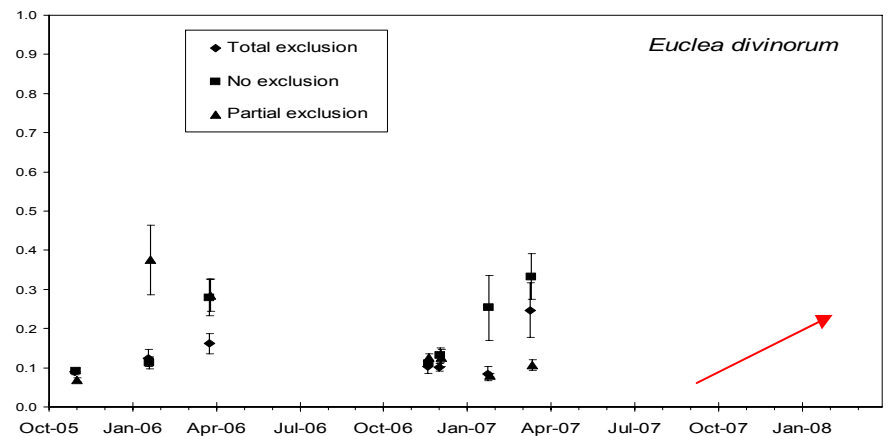
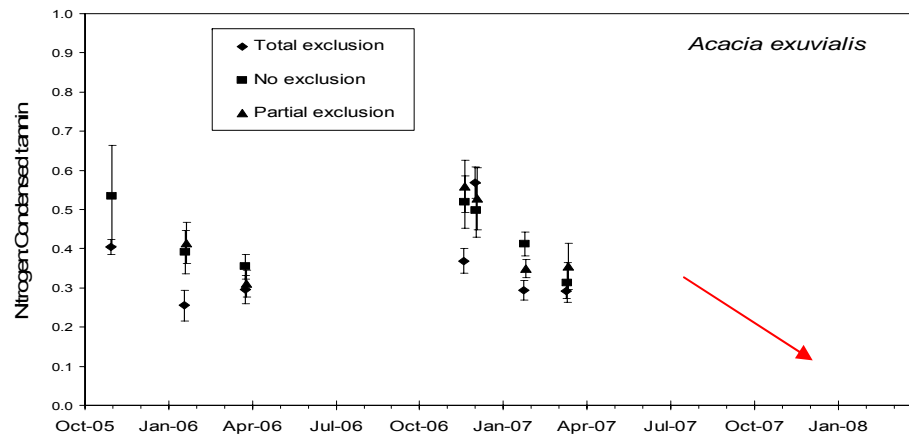
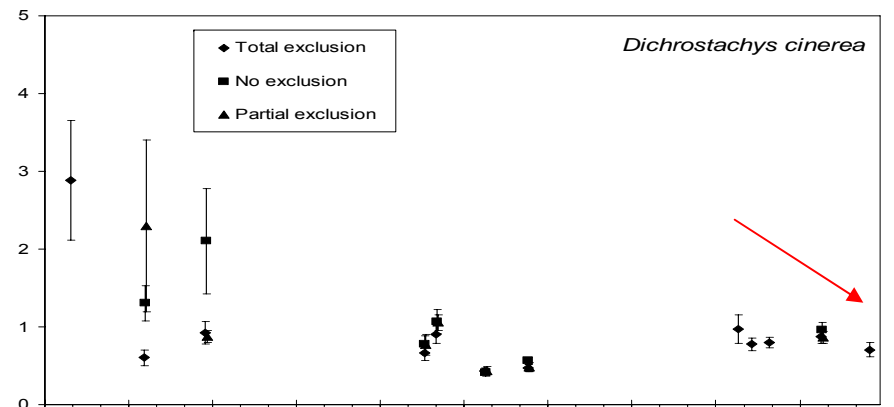
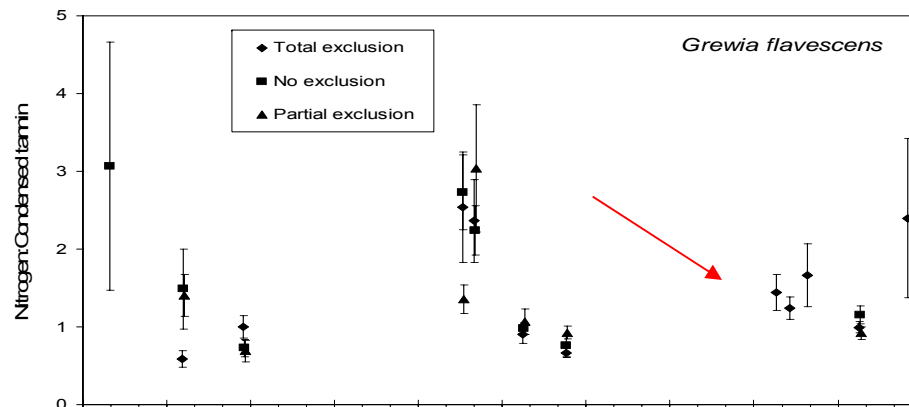
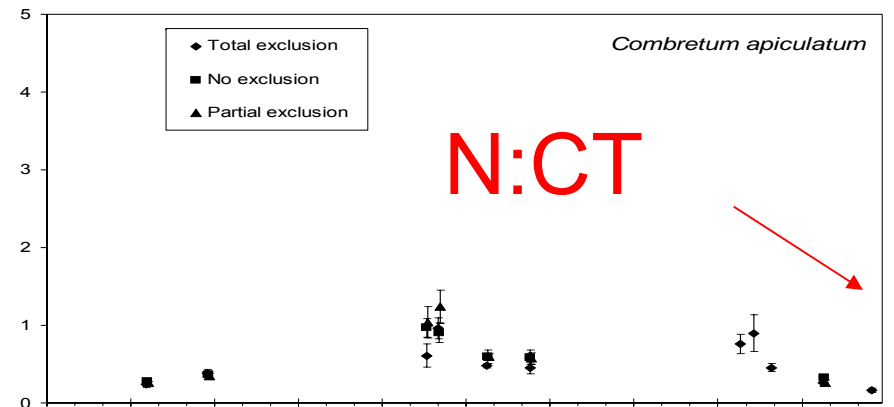
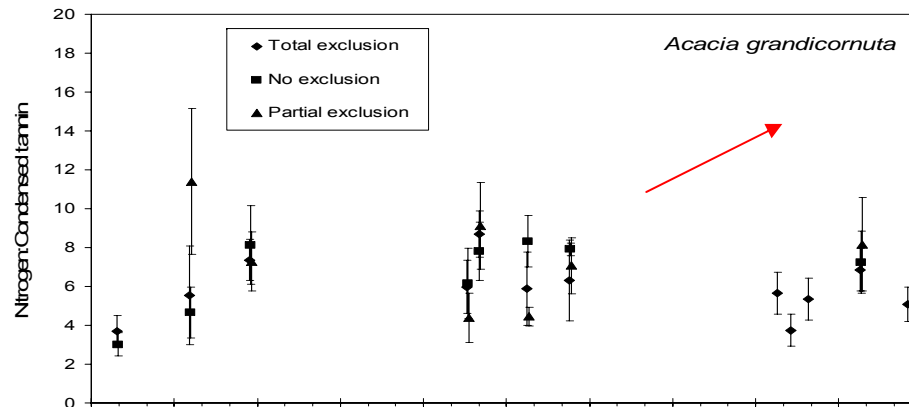
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If we can generalise seasonal chemistry (for this group of 6 species)...

- From start to end of the wet season:
 - [CT] **increased** in *crest* species
 - [CT] & [TP] **decreased** in *sodic* species
 - [N], [P] and N:P **decreased** in *all* species
(except *Euclea divinorum*)
 - N:CT **decreased** in *crest* species
 - N:CT **increased** in *sodic* species

- Sodic species have not “read the book”!

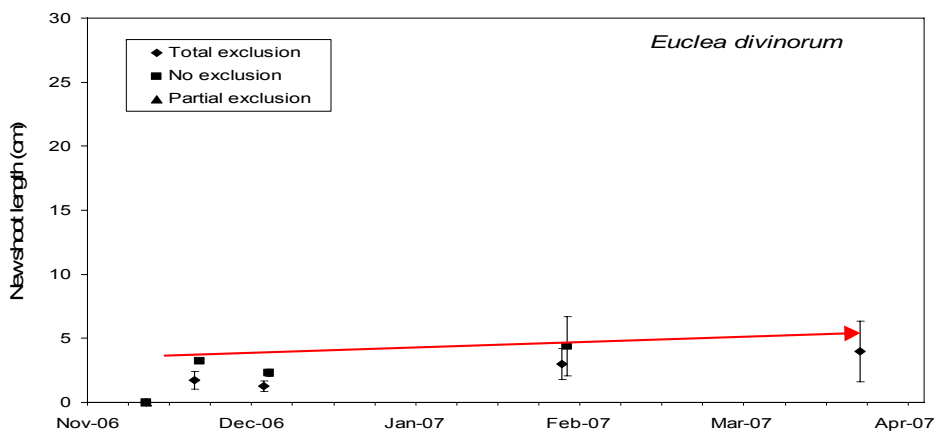
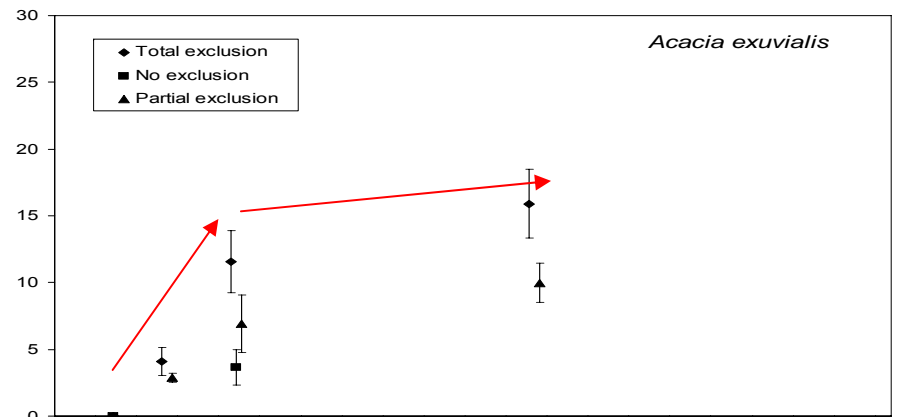
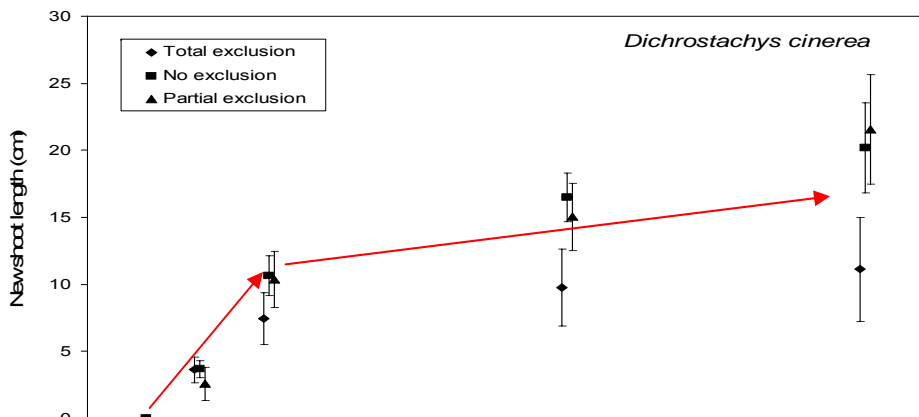
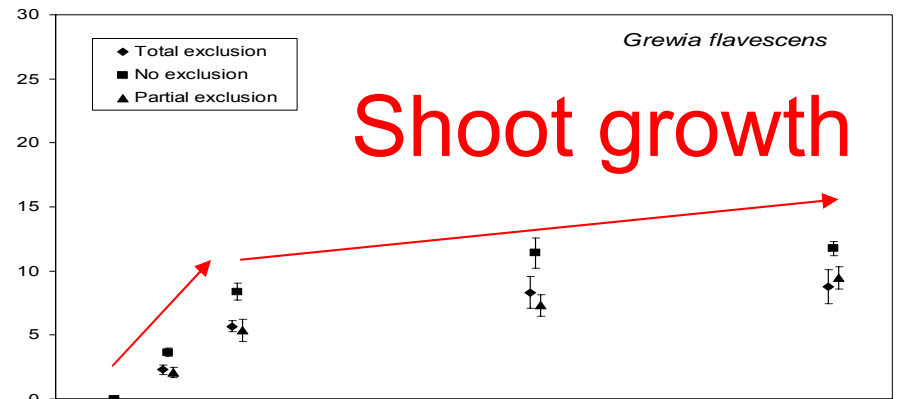
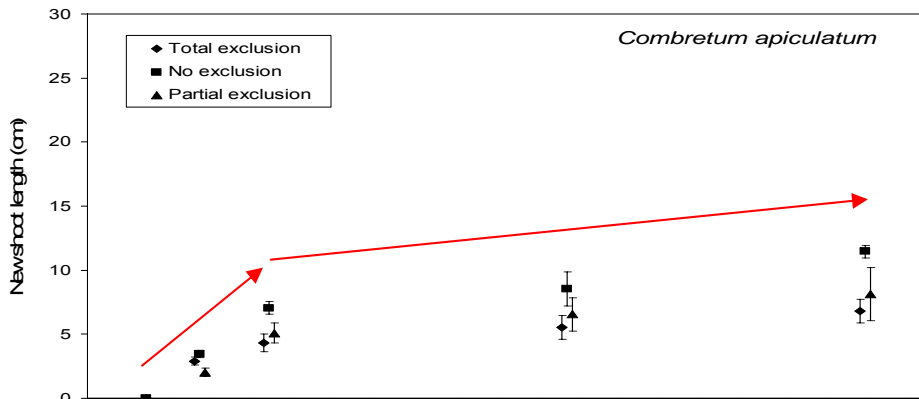
Does relative growth rate have something to do with crest vs sodic differences?

Annual stem growth of the study species observed from March 2007 to March 2008 at Nkuhlu

Species	Annual circumference growth (mm)	Annual radial growth (mm)	Annual relative growth rate (%)
<i>A. grandicornuta</i>	2.38	0.38	0.54
<i>C. apiculatum</i>	4.52	0.72	1.47
<i>G. flavescens</i>	7.85	1.26	6.71
<i>D. cinerea</i>	10.79	1.73	6.43
<i>A. exuvialis</i>	6.64	1.06	4.14
<i>E. divinorum</i>	2.11	0.34	1.10

“Soap-box” moment!

Species	[CT]	[TP]	[N]	[P]	N:CT	N:P
	(%)	(%)	(%)	(%)		
F,S <i>Acacia grandicornuta</i>	<1	1-5	2-4	0.2-0.4	3-11	6-16
<i>Combretum apiculatum</i>	3-10	10-25	2-3	0.2-0.4	<1.5	6-12
<i>Grewia flavescens</i>	1-5	1-5	2-4	0.2-0.4	0.5-3.5	6-16
F,S <i>Dichrostachys cinerea</i>	1-5	1-10	2-4	0.2-0.4	0.5-3.5	6-16
F,S <i>Acacia exuvialis</i>	5-10	10-25	2-4	0.2-0.4	<0.5	6-12
E <i>Euclea divinorum</i>	5-15	10-25	1-2	0.2-0.4	<0.5	4-7



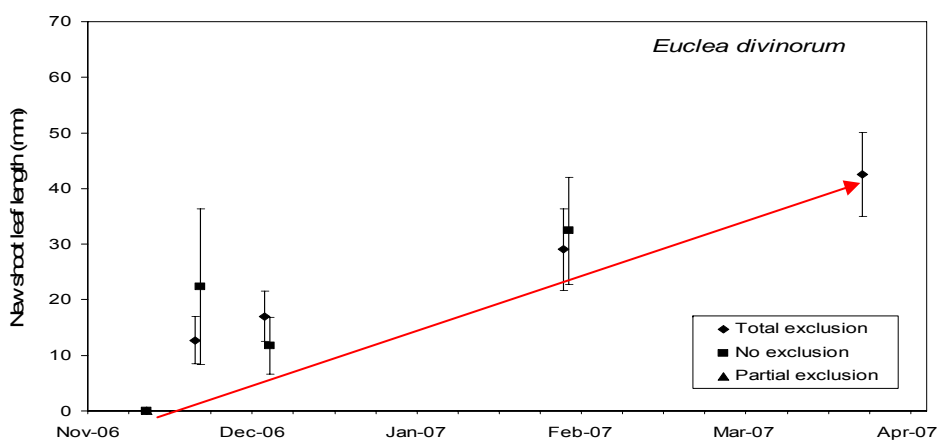
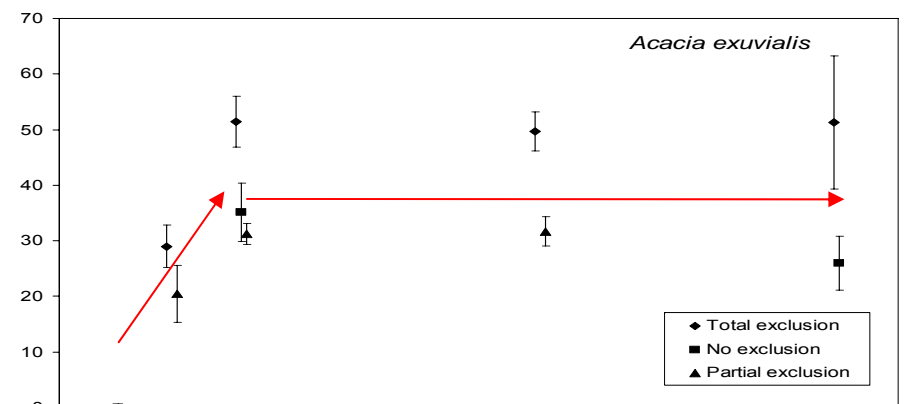
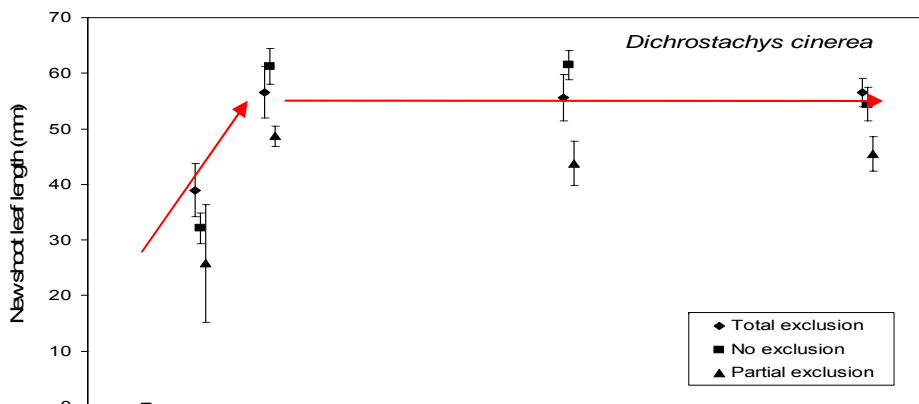
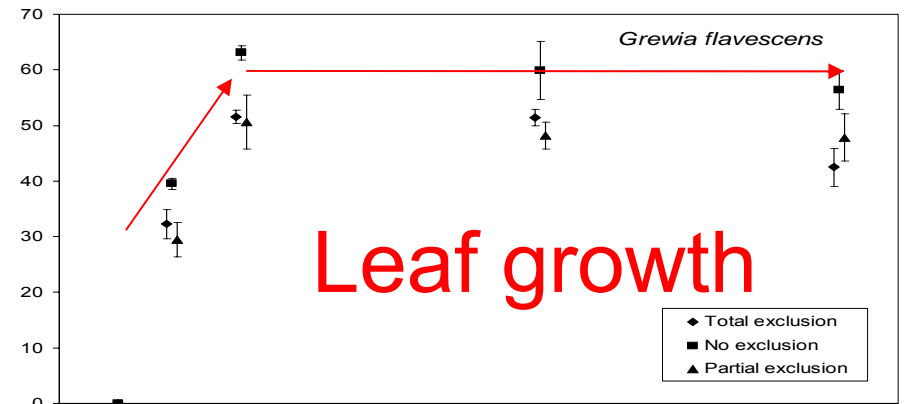
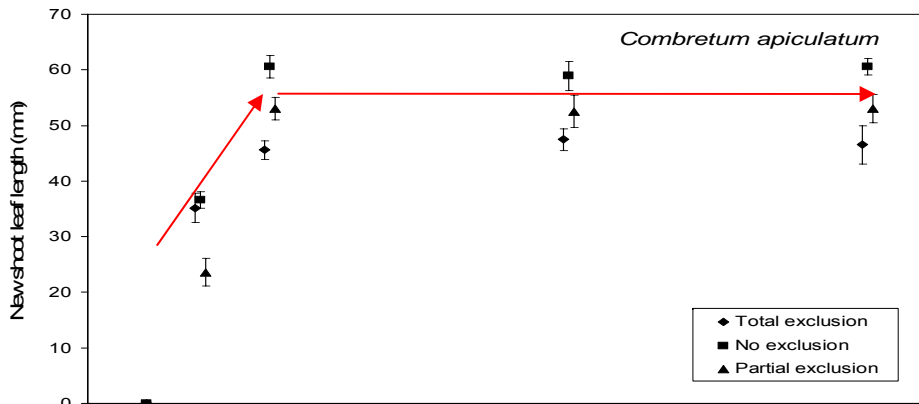
Nov-06 Dec-06 Jan-07 Feb-07 Mar-07 Apr-07



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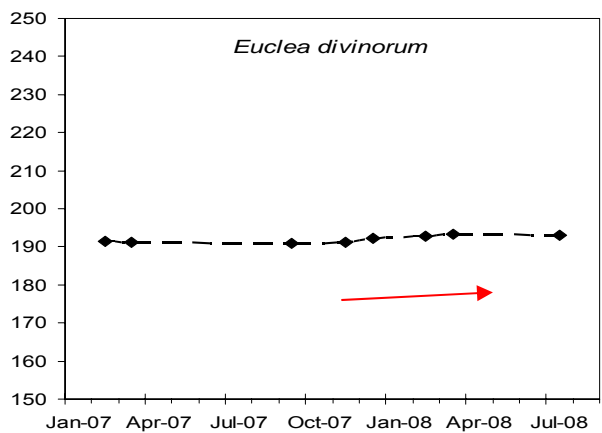
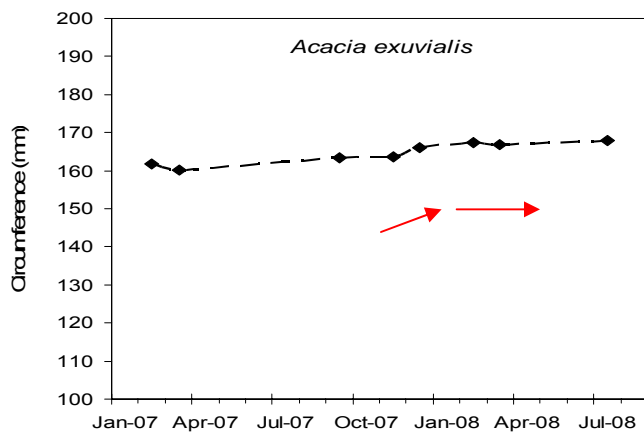
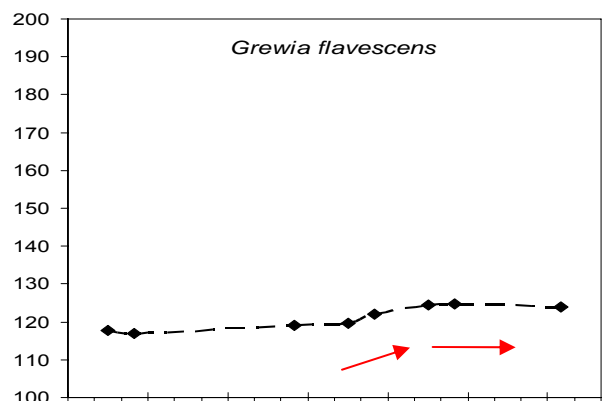
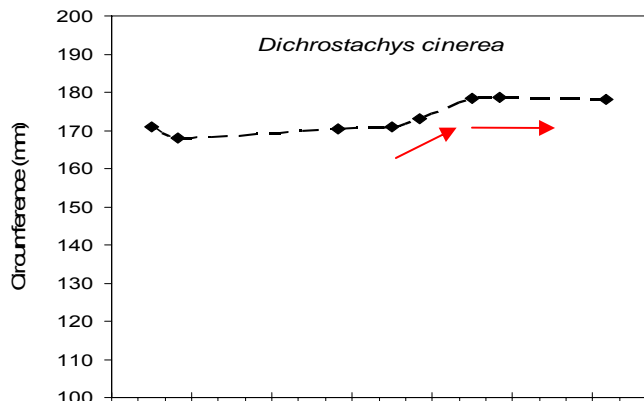
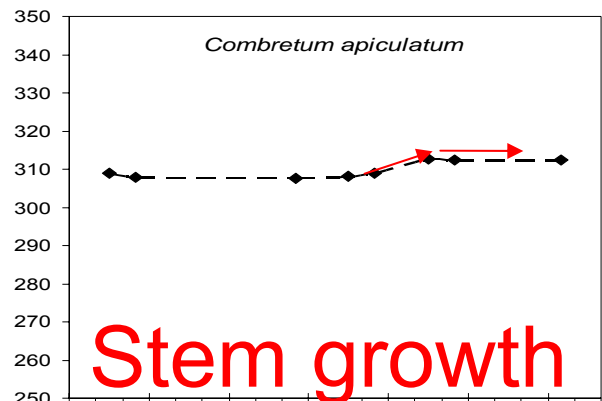
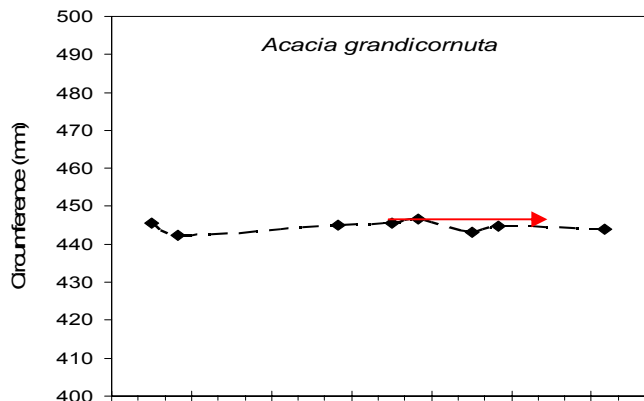
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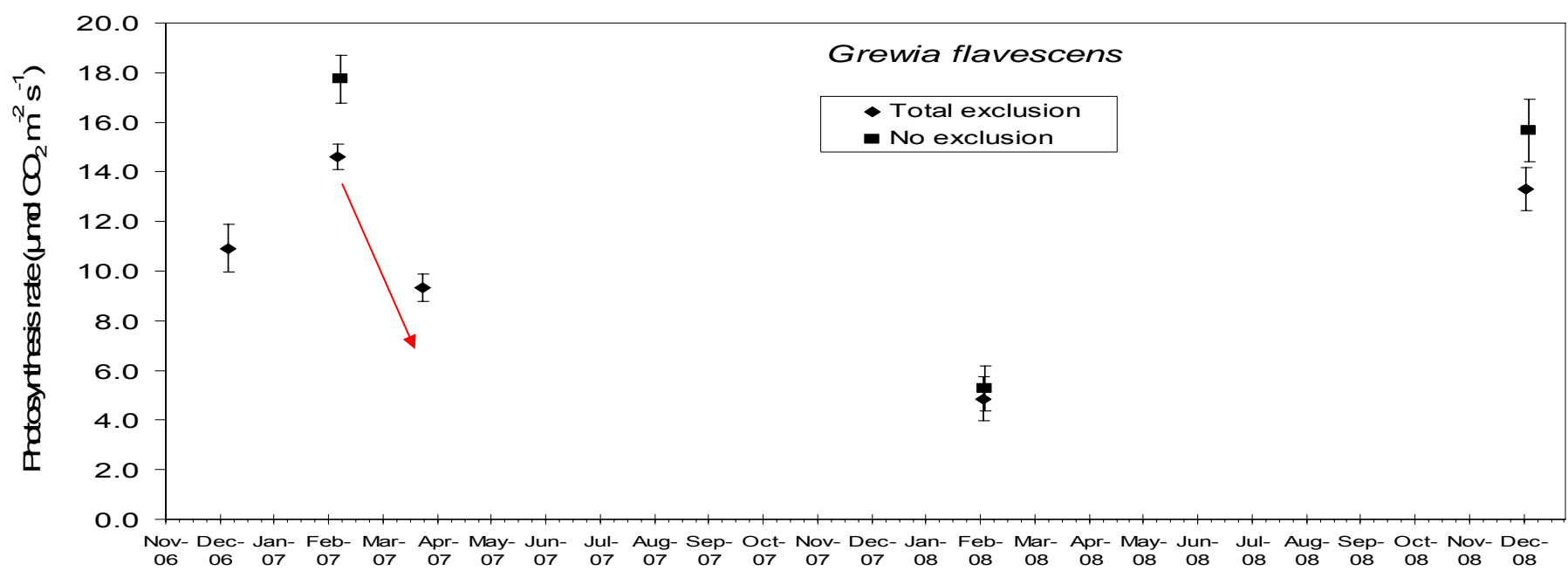
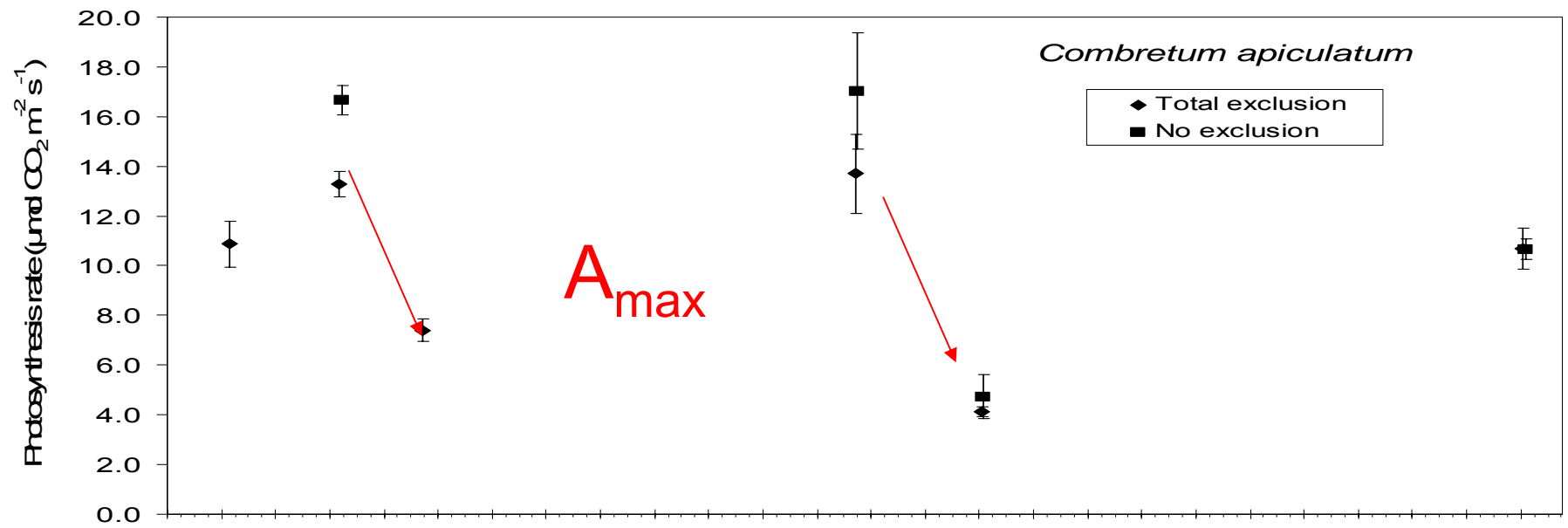
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Side-track...

Rainfall (mm) at Skukuza within 3, 7, 14 and 21 days preceding photosynthesis observations at Nkuhlu (December 2008 not included - data were not available)

Sampling date	Rainfall (mm) in previous number of days			
	3 days	7 days	14 days	21 days
2006/12/07	0.0	0.0	0.0	55.9
2007/02/06	6.9	37.8	37.8	40.8
2007/03/27	0.5	0.5	1.0	1.0
2007/11/26	43.1	47.3	47.6	69.8
2008/02/04	0.0	0.0	1.6	7.0

 = days with high A_{\max}

More generalisations! (for this group of species)...

- From start to end of the wet season:
 - Shoot/leaf growth rate **decreased** in *all* species (except *Euclea divinorum*)
 - Stem radial growth rate **decreased** in *crest* species (sodic spp. didn't grow radially)
 - Photosynthesis rate was **variable** and slowed down whenever soil had dried out for 3-4 weeks (but seemed to be **lowest late in the wet season**)
- *Euclea* grows differently
- Photosynthesis not maintained at high levels

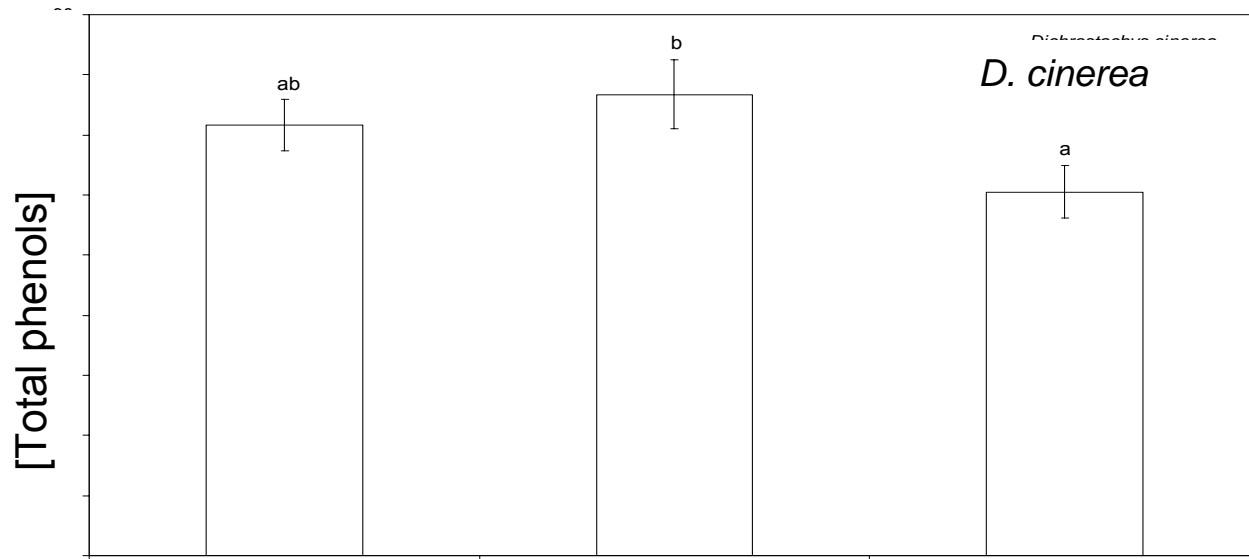
Some predictions...

- Concentrations of condensed tannins (CT) and total phenols (TP) are lowest early in the wet season (and increase)
- **Browsed plants have (vs unbrowsed):**
 - lower [CT] or [TP] early in the wet season
 - **higher [CT] / [TP] late in the wet season**

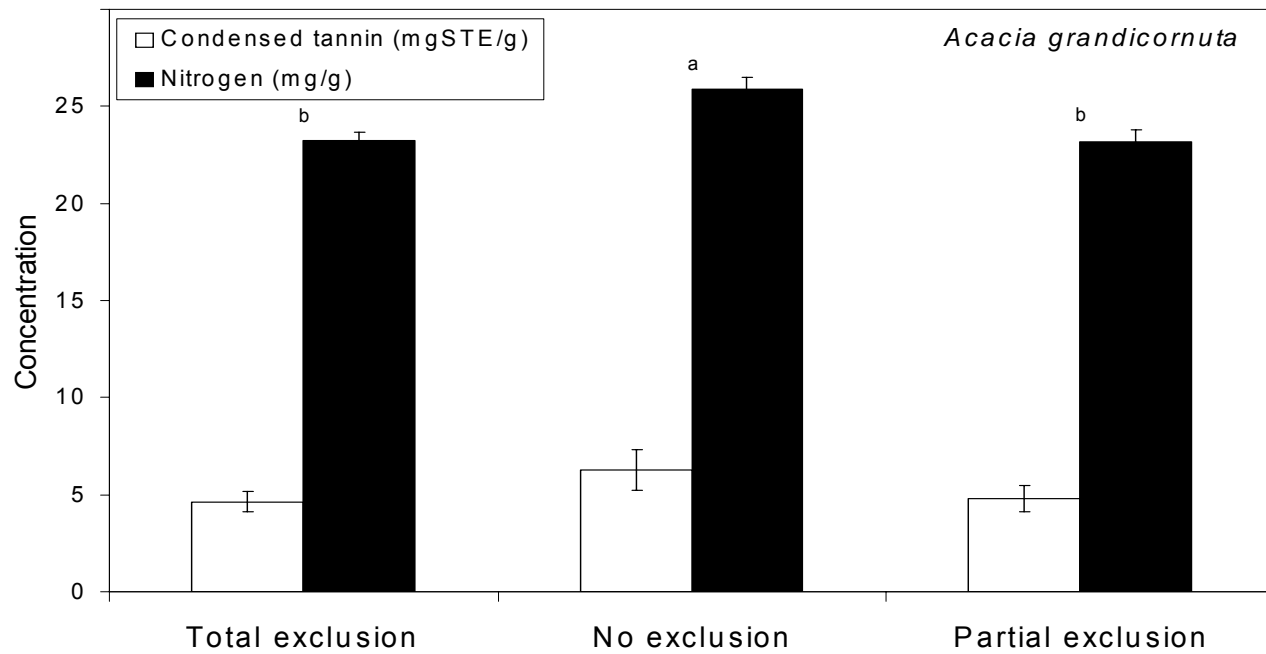
(We chose to examine the mid-late wet season for the highly scientific reason that it just seemed to be a more predictable time of the wet season compared to the start.)

Jan '08

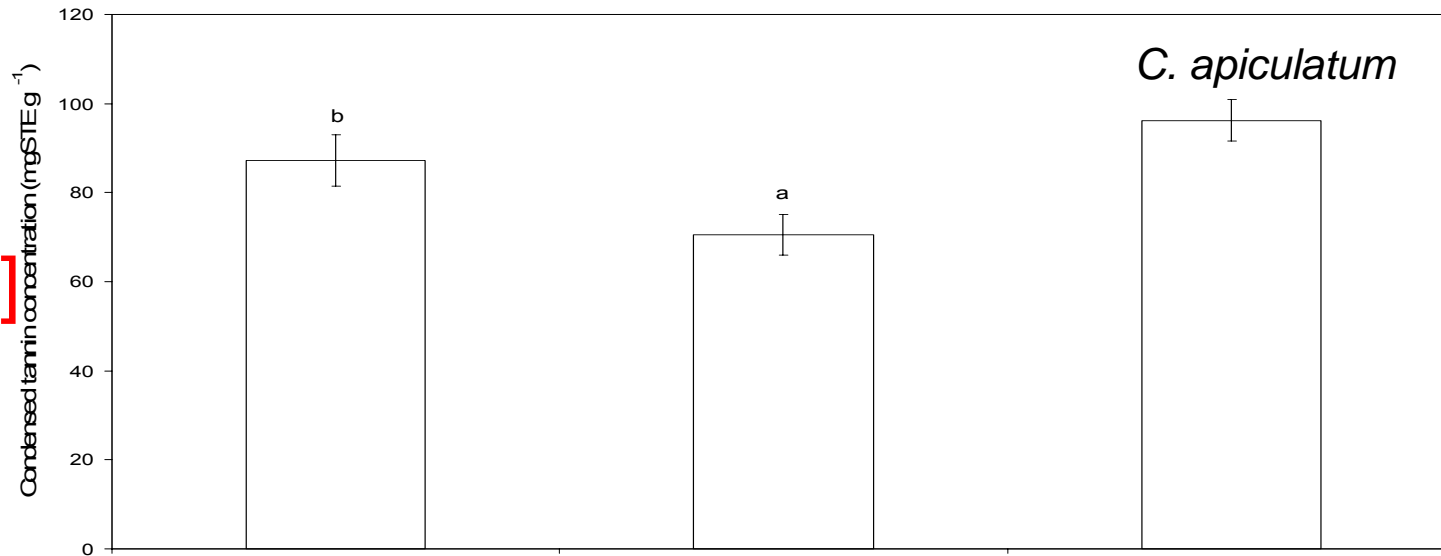
[TP]



[N]

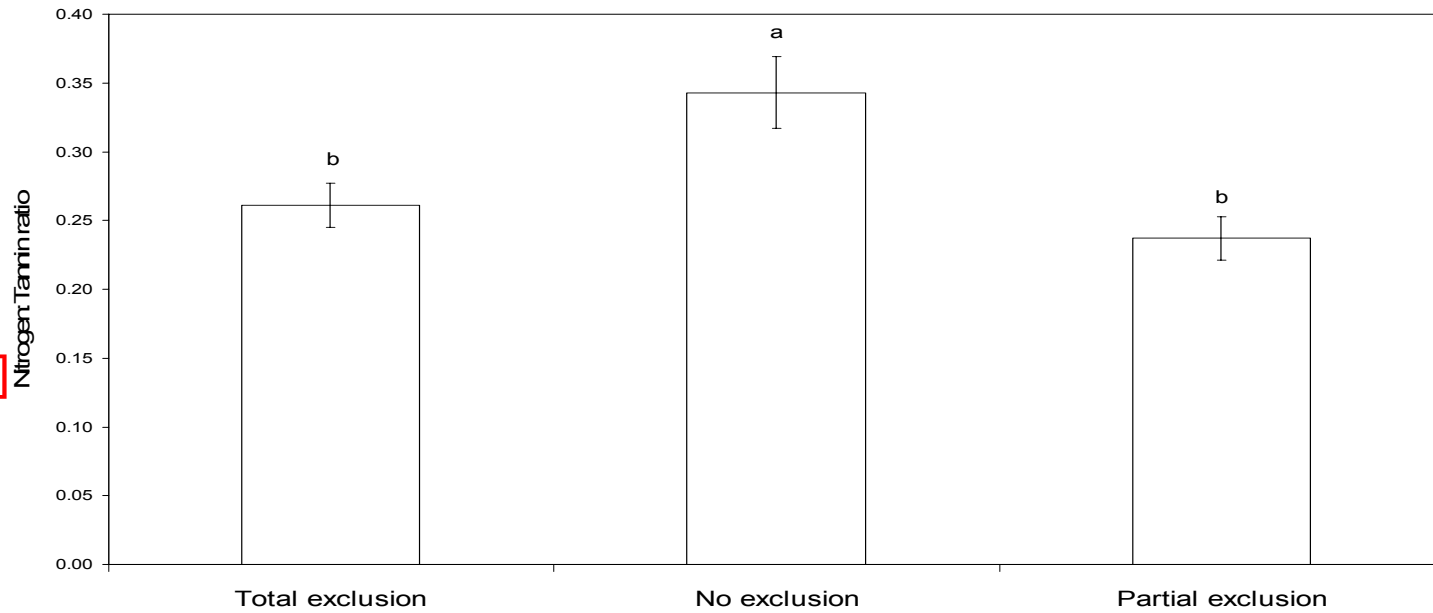


[CT]

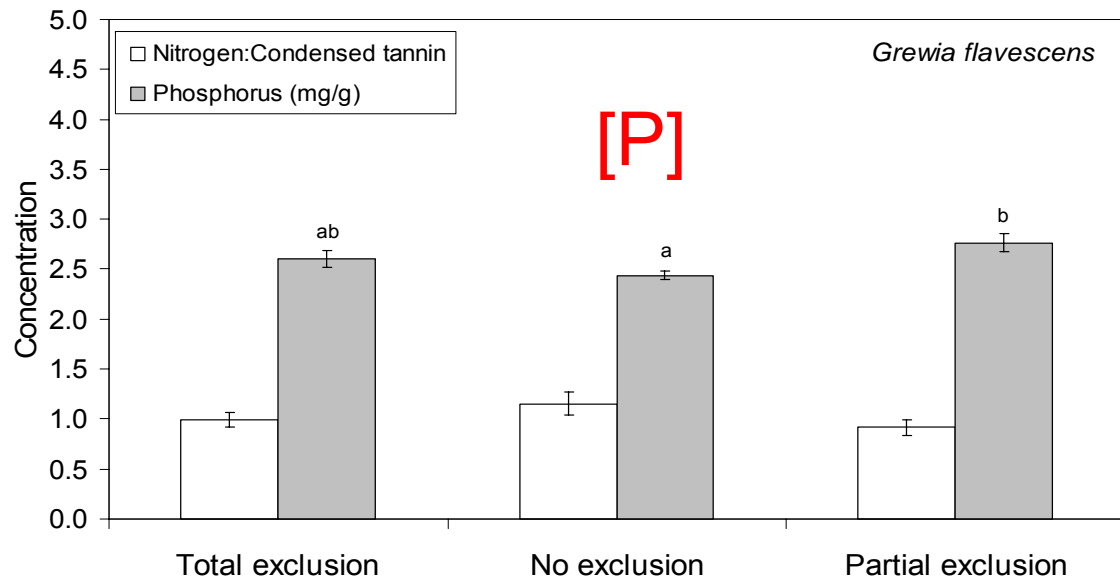
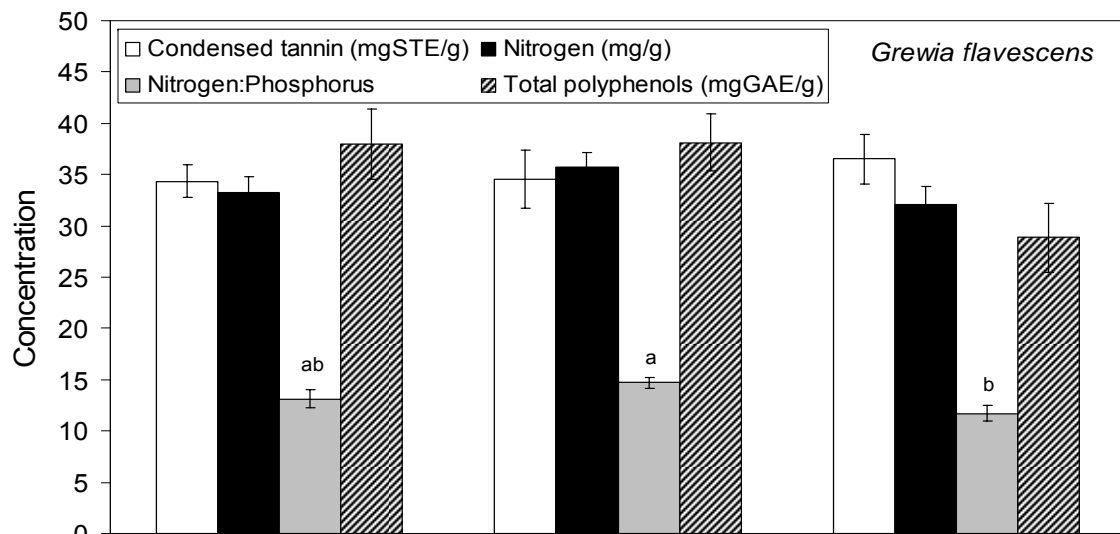


Jan '08

[N:CT]

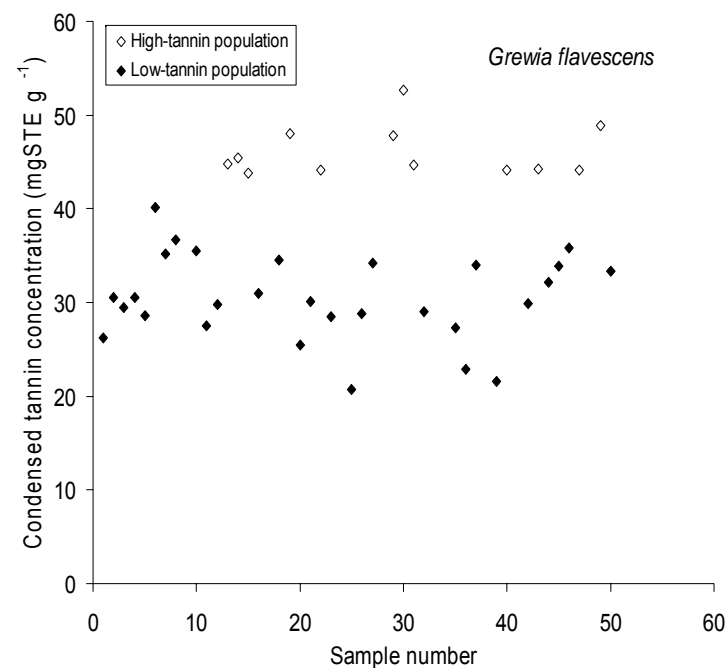


[N:P]



[P]

Jan '08



High [CT] = var. *olukondae*?

Low [CT] = var. *flavescens*?
(exclusion increased [CT])

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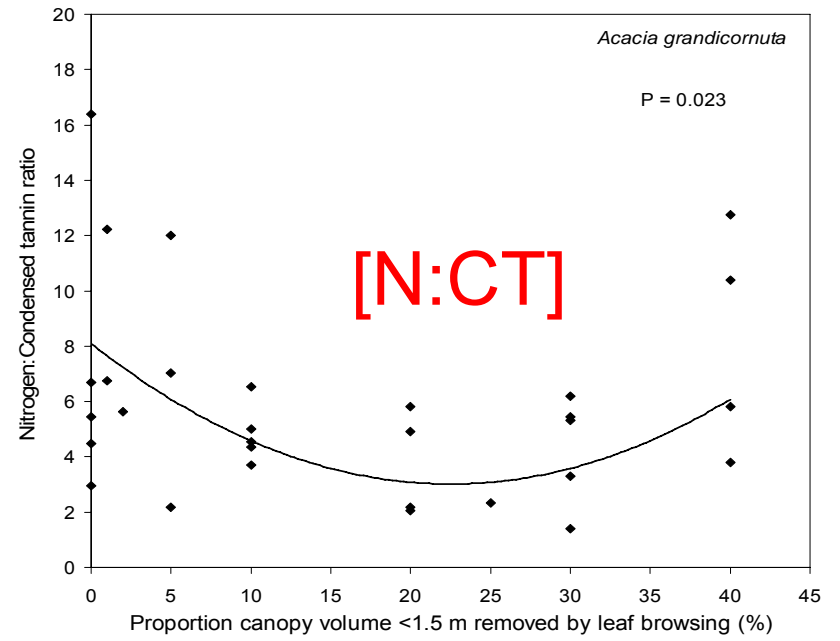
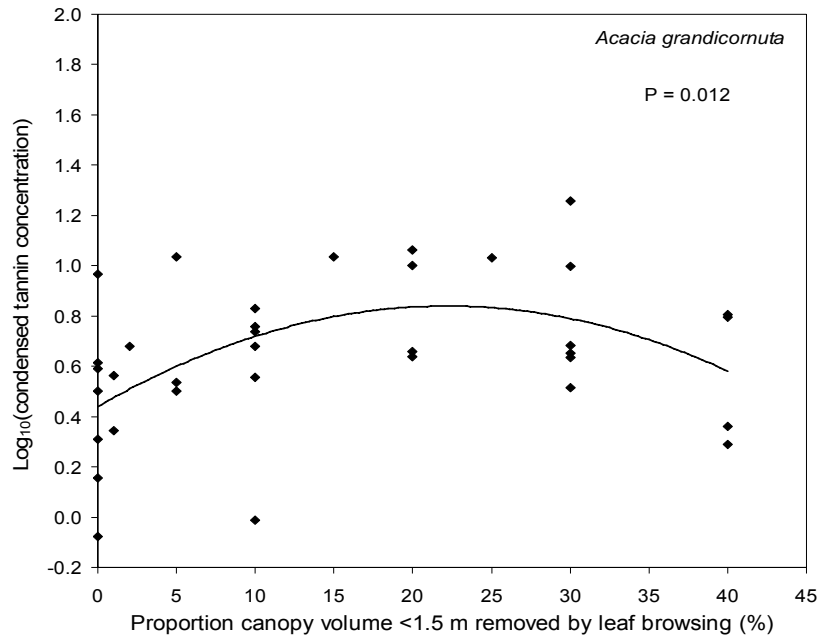
Browsing impacts

Jan '08

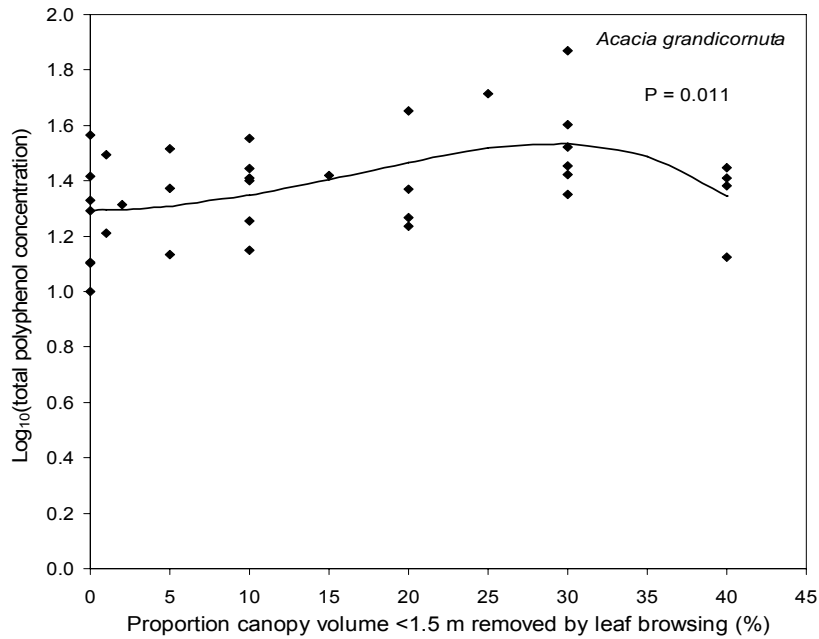
Average proportion (%) of productive canopy volume estimated to be missing due to leaf browsing below 1.5 m and above 1.5 m, and accumulated shoot browsing below 1.5 m and above 1.5 m, recorded for individuals of the study species sampled at 36 sites per species outside the total exclusion plot in January 2008

Species	Leaf browsing			Shoot browsing		
	<1.5 m	>1.5 m	Sum	<1.5 m	>1.5 m	Sum
<i>A. grandicornuta</i>	15.4	0.6	16.0	6.1	1.8	7.9
<i>C. apiculatum</i>	1.9	0.2	2.1	9.1	2.3	11.4
<i>G. flavescens</i>	2.6	3.0	5.6	3.9	4.6	8.5
<i>D. cinerea</i>	0.0	0.1	0.1	1.3	2.8	4.1

[CT]



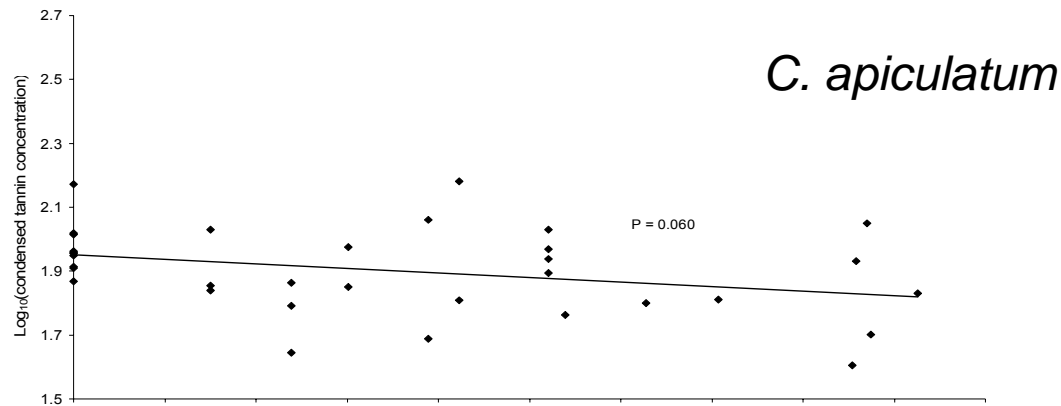
[TP]



A. grandicornuta

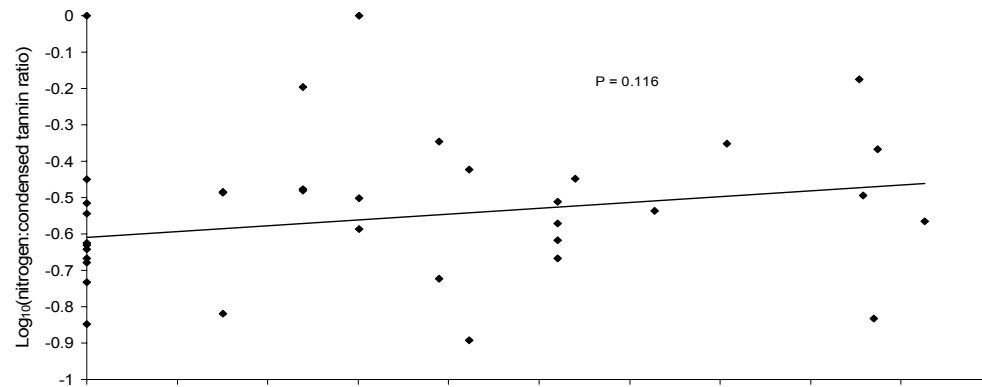
Jan '08

[CT]

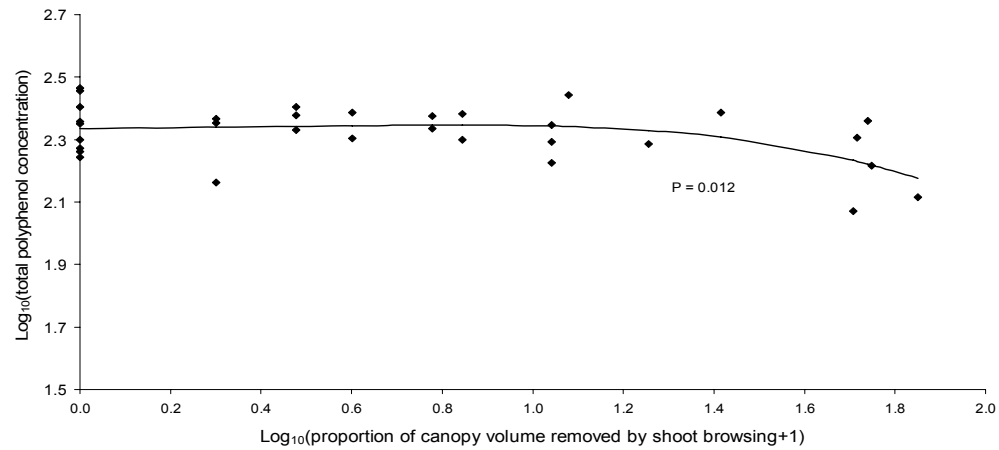


Jan '08

[N:CT]

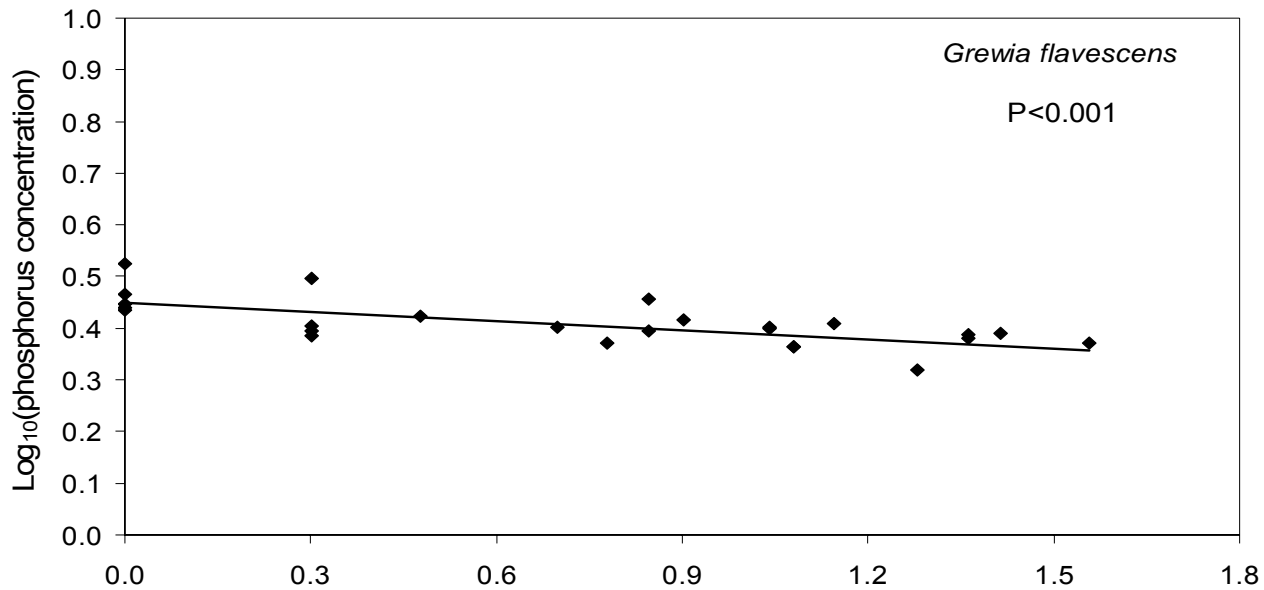


[TP]

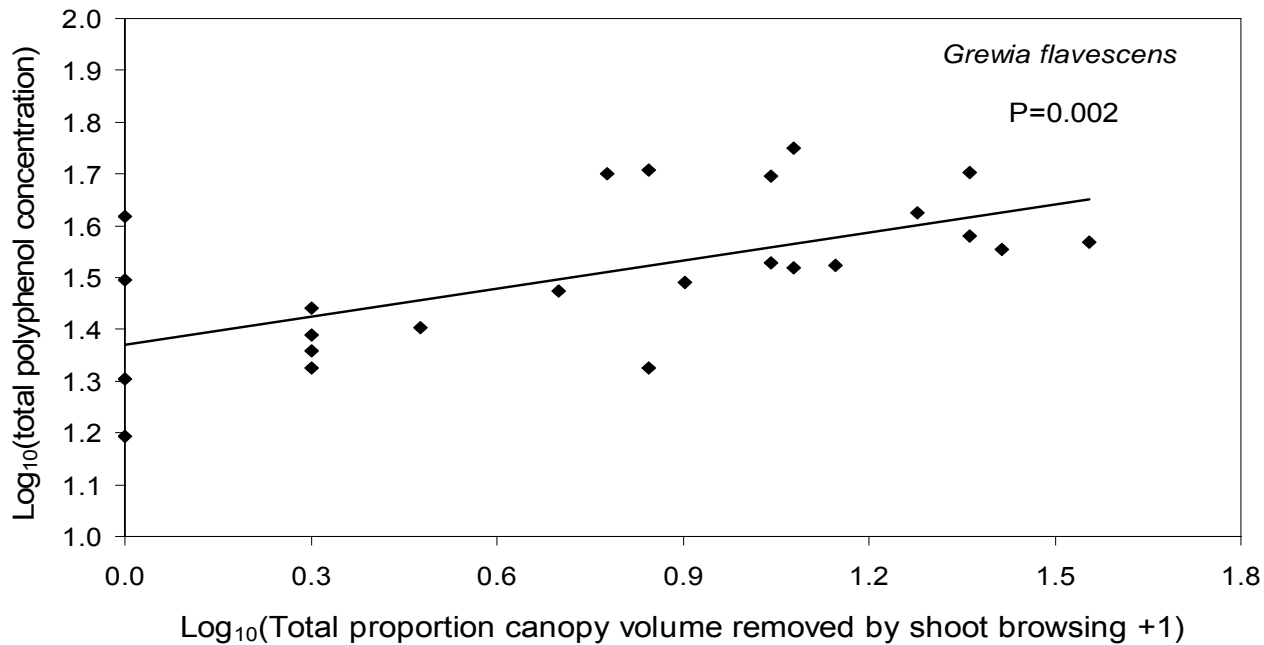


Jan '08

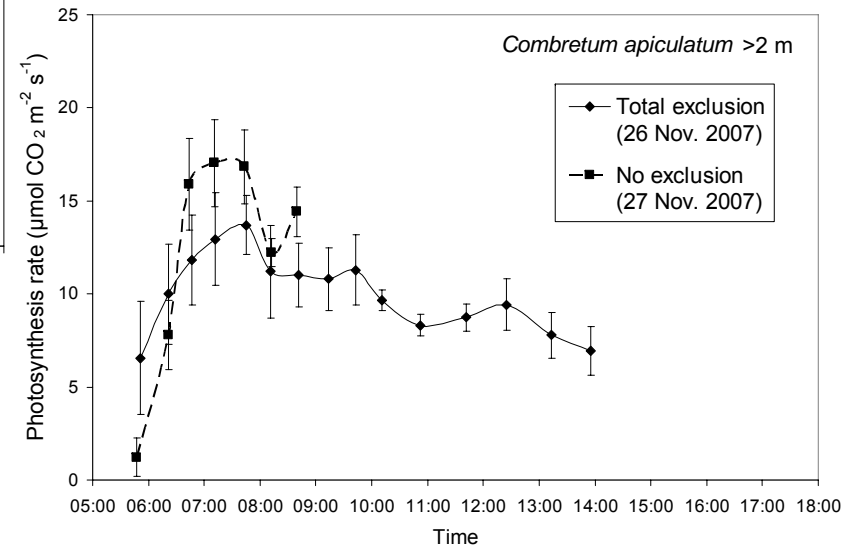
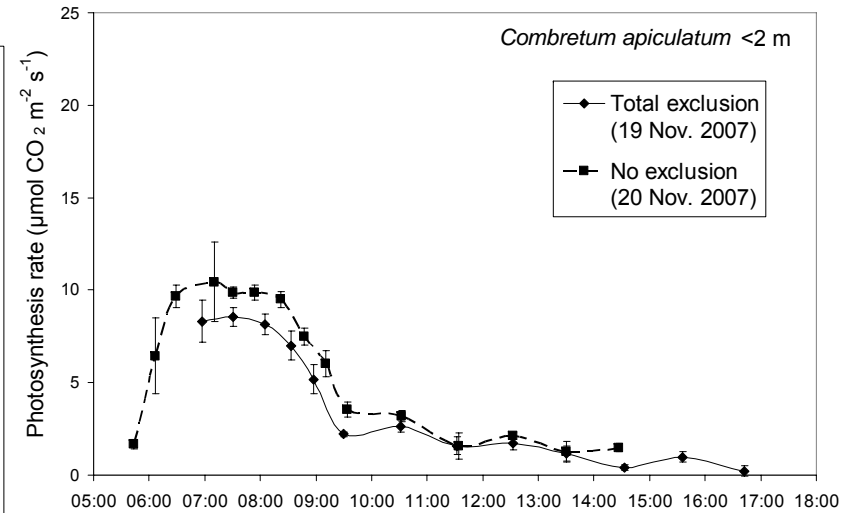
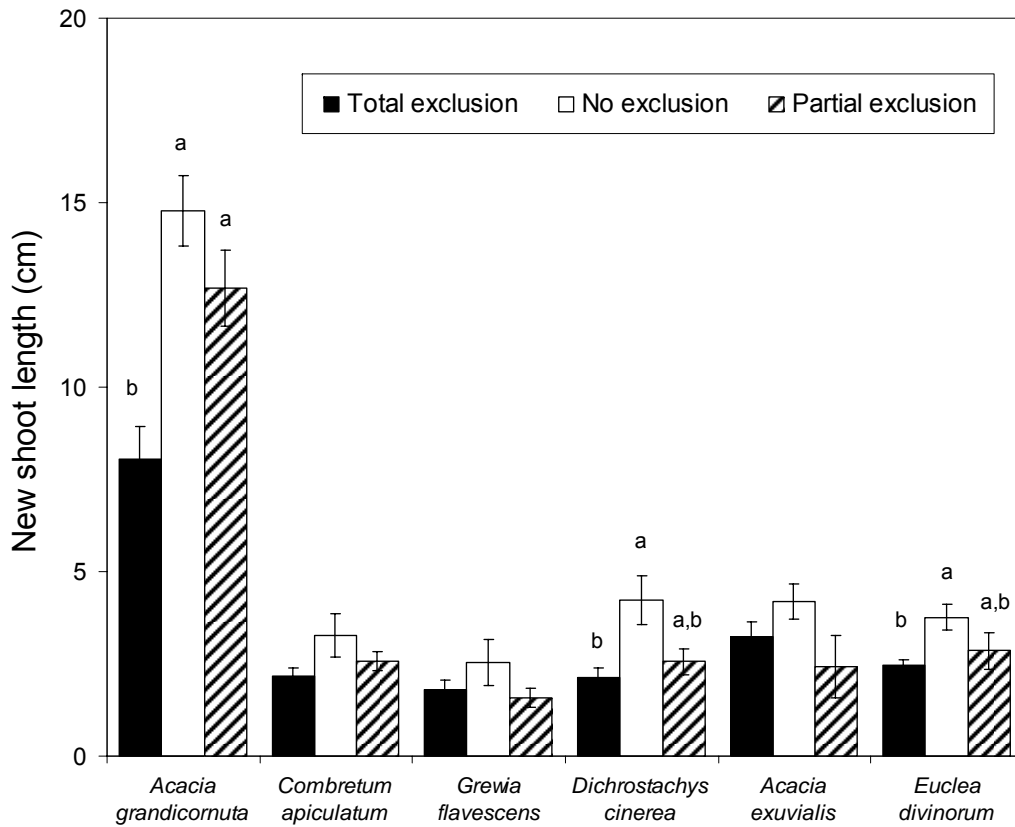
[P]



[TP]



Shoot length and photosynthesis, Nov. 2007



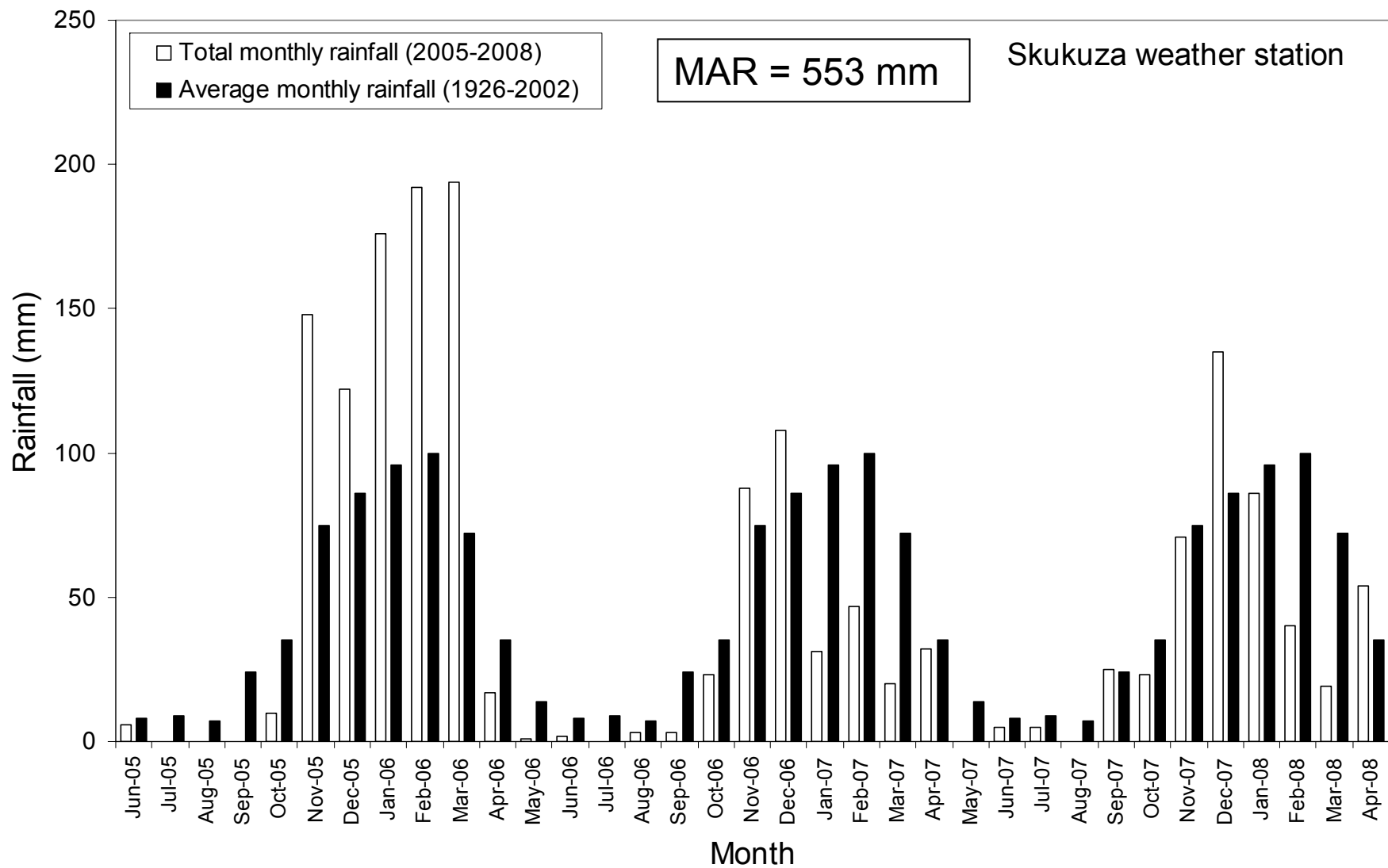
Some conclusions (*for now*) (in this group of species)...

- Exclusion of elephants or elephants+others:
 - **increased [CT]** or decreased [N] in January 2008 (except *Dichrostachys cinerea*)
 - *three spp.* became potentially **less** “palatable” (?)
 - *D. cinerea* became potentially **more** “palatable” (✓)
- Indirect and direct effects on phenolics vary with tree species
- Responses depend on intensity of browsing
- Plant-level responses different to landscape

More speculation (*for now*) (in this group of species)...

- Browsing by elephants (+others?):
 - stimulates shoot growth and photosynthesis in some species (but not all)
 - reduce tannins, or increase N
 - become potentially more “palatable”
 - more prone to repeated browsing
 - recruitment into adult sizes suppressed

- Ummm... it depends...



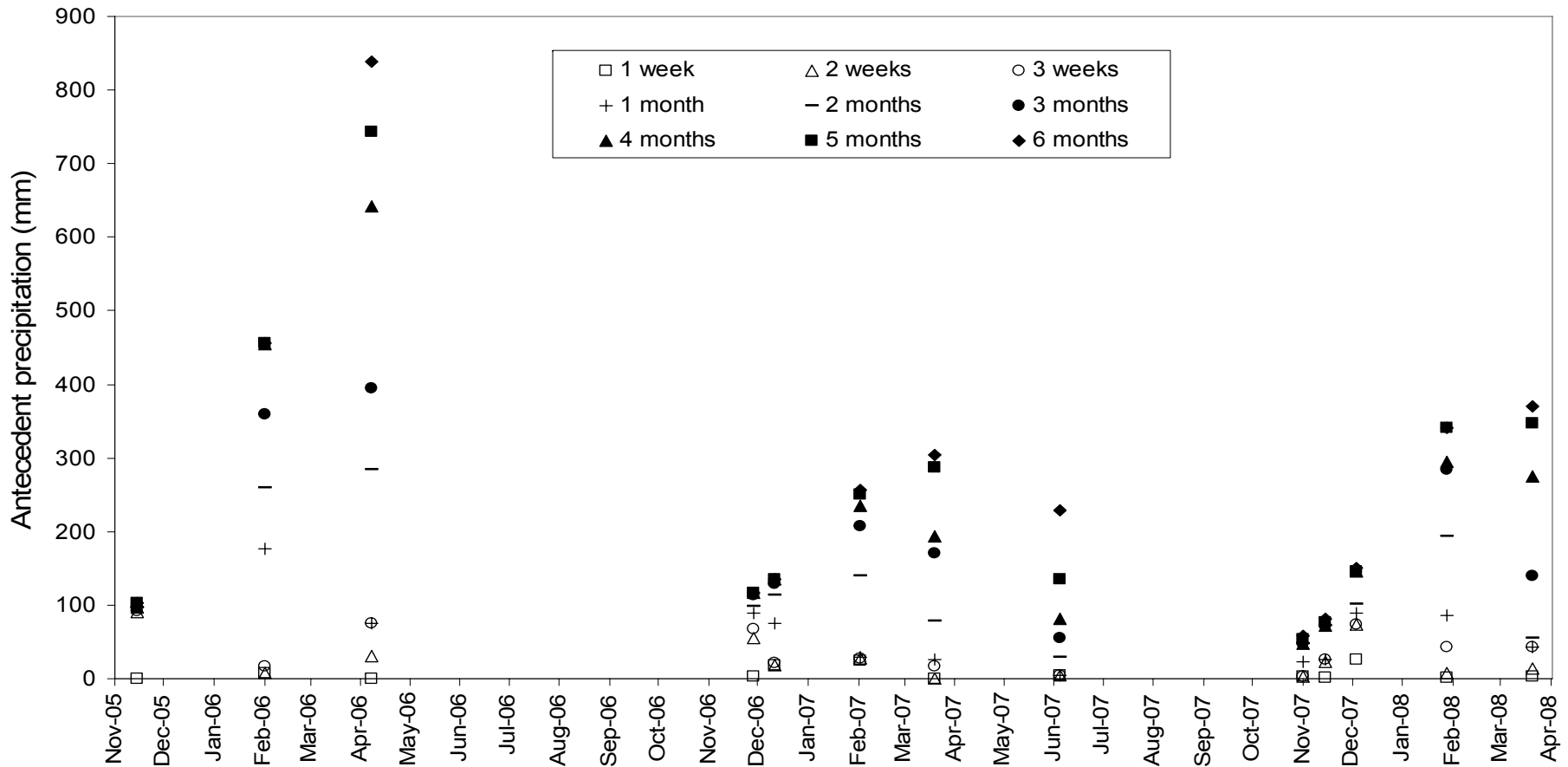
860 mm

354 mm

453 mm

Does [P] decrease and [TP] increase during “drier” years following “wetter” years?

Are exclusion effects greater in “wetter” years?



Will we ever see both woods and trees, or will we continue barking up the wrong tree?

- Avoid snapshots – they are misleading
- Spatial and temporal scales relevant to herbivores (landscape/population-individual/branch; weeks-years)
- Match with equally high res obs of herbivores
- Replicated multifactor experiments on a suite of selected species, with water/nutrients and browsing intensity/frequency at 4-5 levels

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