

Phylogenetic Effects On Shoot Magnesium Concentrations

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IAPN - Magnesium Symposium
5th November 2014

Outline of Talk

1. An Introduction to Angiosperm Phylogenies
2. Molecular Physiology of Group II Elements
- Magnesium, Calcium, Strontium
3. Elemental Stoichiometries - Mg : Ca : Sr
4. Phylogenetic and Environmental Effects
on Shoot Ca & Mg Concentrations
5. Consequences for Diets and Ecology

Phylogenetics

Genetics at a Higher Level of Classification

Phylogenetics is the study of the relationships among groups of organisms (e.g. families, species, populations) based on DNA sequencing.

The result of phylogenetic studies are hypotheses about the evolutionary history of taxonomic groups.

Angiosperms – flowering plants.

A definition of phylogenetics and its utility

Phylogenetics Angiosperm Phylogeny

Volume 85
Number 4
1998

Annals
of the
Missouri
Botanic
Garden



Botanical Journal of the Linnean Society, 2003, 141, 399–436. With 1 figure

Botanical Journal of the Linnean Society, 2009, 161, 105–121. With 1 figure

An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering

AN ORDINAL
CLASSIFICATION FOR THE
FAMILIES OF FLOWERING
PLANTS

The Angiosperm Phylogeny Group

An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II

THE ANGIOSPERM PHYLOGENY GROUP*

Received June 2002; accepted for publication December 2002

ABSTRACT

Recent cladistic analyses are revealing the phylogeny of flowering plants in increasing resolution. The monophyly of many major groups above the family level. With many elements of the phylogeny established, a revised suprafamilial classification of flowering plants becomes possible. Here we present a classification of 462 flowering plant families in 40 putatively monophyletic, informal higher groups. The latter are the monocots, commelinids, rosids including euasterids I and II, and asterids including euasterids I and II. Under this system, we also listed a number of families without assignment to order. At the end of the system is a list of uncertain position for which no firm data exist regarding placement anywhere within the system.

A revised and updated classification for the families of the flowering plants is provided. Newly adopted orders include Austrobaileyales, Canellales, Gunnerales, Crossosomatales and Celastrales. Pertinent literature published since the first APG classification is included, such that many additional families are now placed in the phylogenetic scheme. Among these are Hydnoraceae (Piperales), Nartheciaceae (Dioscoreales), Corsiaceae (Liliales), Triuridaceae (Pandanales), Hanguanaceae (Commelinales), Bromeliaceae, Mayacaceae and Rapateaceae (all Poales), Barbeuiaceae and Gisekiaceae (both Caryophyllales), Geissolomataceae, Strasburgeriaceae and Vitaceae (unplaced to order, but included in the rosids), Zygophyllaceae (unplaced to order, but included in euasterids I), Bonnetiaceae, Ctenolophonaceae, Elatinaceae, Ixonanthaceae, Lophopyxidaceae, Podostemaceae (Malpighiales), Paracryphiaceae (unplaced in euasterid II), Sladeniaceae, Pentaphragmaceae (Ericales) and Cardiopteridaceae (Aquifoliales). Several major families are re-circumscribed. Salicaceae are expanded to include a large part of Flacourtiaceae, including the type genus of that family; another portion of former Flacourtiaceae is assigned to an expanded circumscription of Achariaceae. Euphorbiaceae are restricted to the uniovulate subfamilies; Phyllanthoideae are recognized as Phyllanthaceae and Oldfieldioideae as Picrodendraceae. Scrophulariaceae are re-circumscribed to include Buddlejaceae and Myoporaceae and exclude several former members; these are assigned to Calceolariaceae, Orobanchaceae and Plantaginaceae. We expand the use of bracketing families that could be included optionally in broader circumscriptions with other related families; these include Agapanthaceae and Amaryllidaceae in Alliaceae *s.l.*, Agavaceae, Hyacinthaceae and Rusaceae (among many other Asparagales) in Asparagaceae *s.l.*, Dichapetalaceae in Chrysobalanaceae, Turneraceae in Passifloraceae, Erythroxylaceae in Rhizophoraceae, and Diervillaceae, Dipsacaceae, Linnaeaceae, Morinaceae and Valerianaceae in Caprifoliaceae *s.l.* © 2003 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2003, 141, 399–436.

ADDITIONAL KEYWORDS: angiosperms – gene sequences – phylogenetics.

compiled by Birgitta Bremer, Kåre Bremer, E. Soltis, Pamela S. Soltis and Peter F. Xiang and Sue Zmarzty (in alphabetical order only, with contributions from Otmstead, Paula J. Rudall, Kenneth J. Xiang and Sue Zmarzty (in alphabetical order only, with contributions from the Royal Swedish Academy of Sciences, PO Box 116, S-113 85 Stockholm, Sweden; Peter F. Xiang, Department of Plant Biology, University of Florida, Gainesville, FL 32611-8525, USA; D. E. Soltis, Department of Biology, University of Florida, Gainesville, FL 32611-8525, USA; P. S. Soltis, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611-7800, USA; and P. F. Stevens, Missouri Botanic Garden, PO Box 299, St. Louis, MO 63110, USA).

2009

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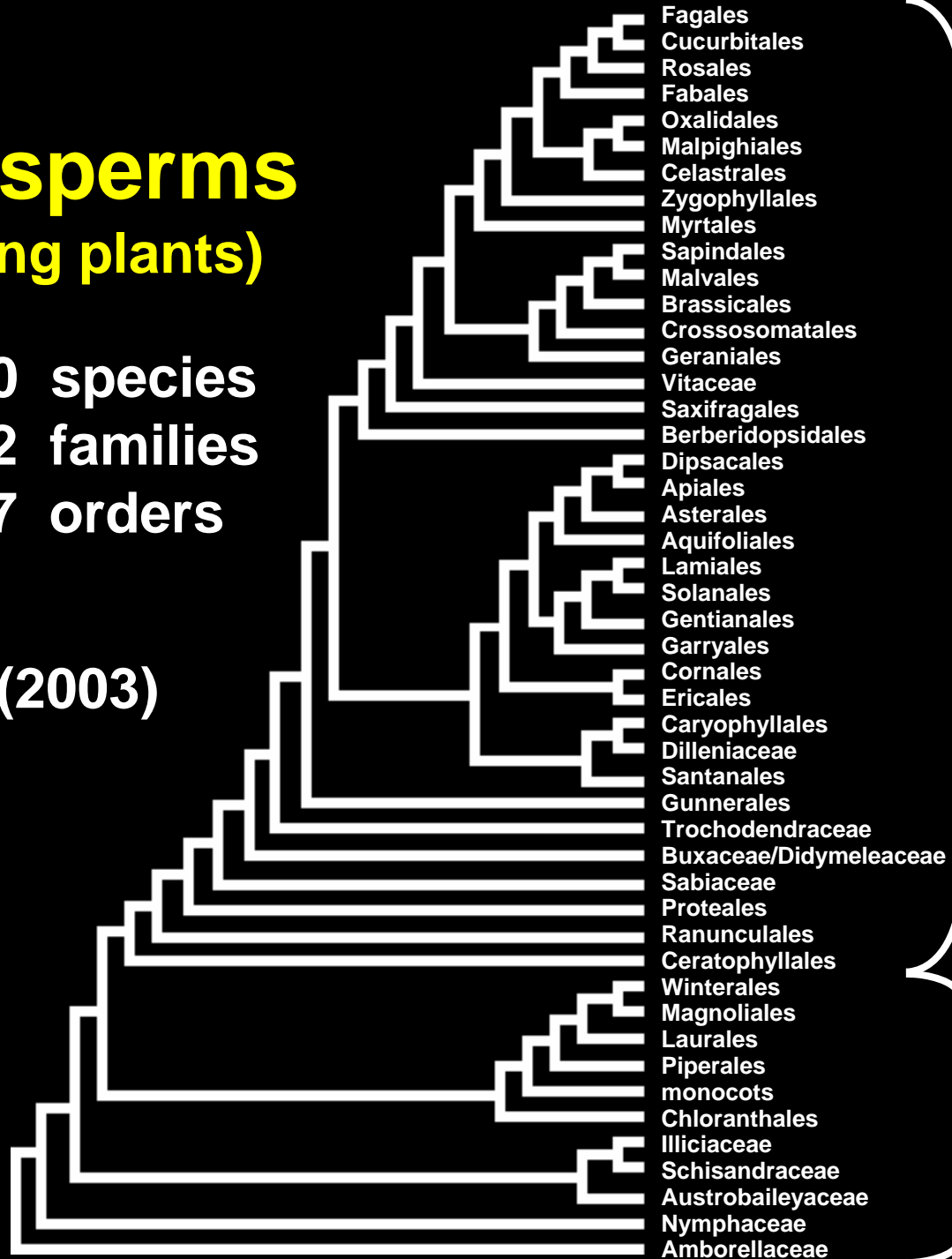
sification – phylogenetic classification – DNA phylogenetics –

The Angiosperm Phylogeny Group (1998, 2003, 2009)

Angiosperms (flowering plants)

250,000 species
462 families
47 orders

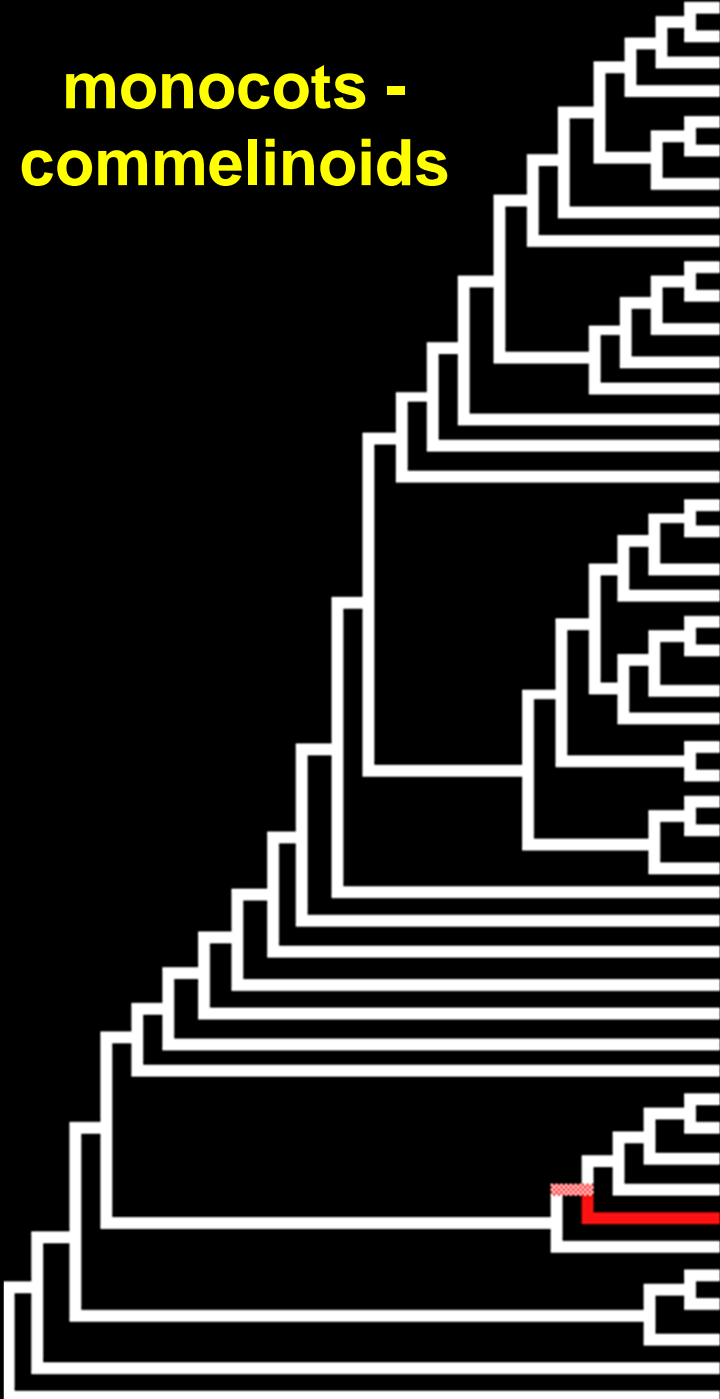
APG II (2003)



eudicots

basal angiosperms
and magnoliids

**monocots -
commelinoids**



Grass



Bromeliad



Bamboo

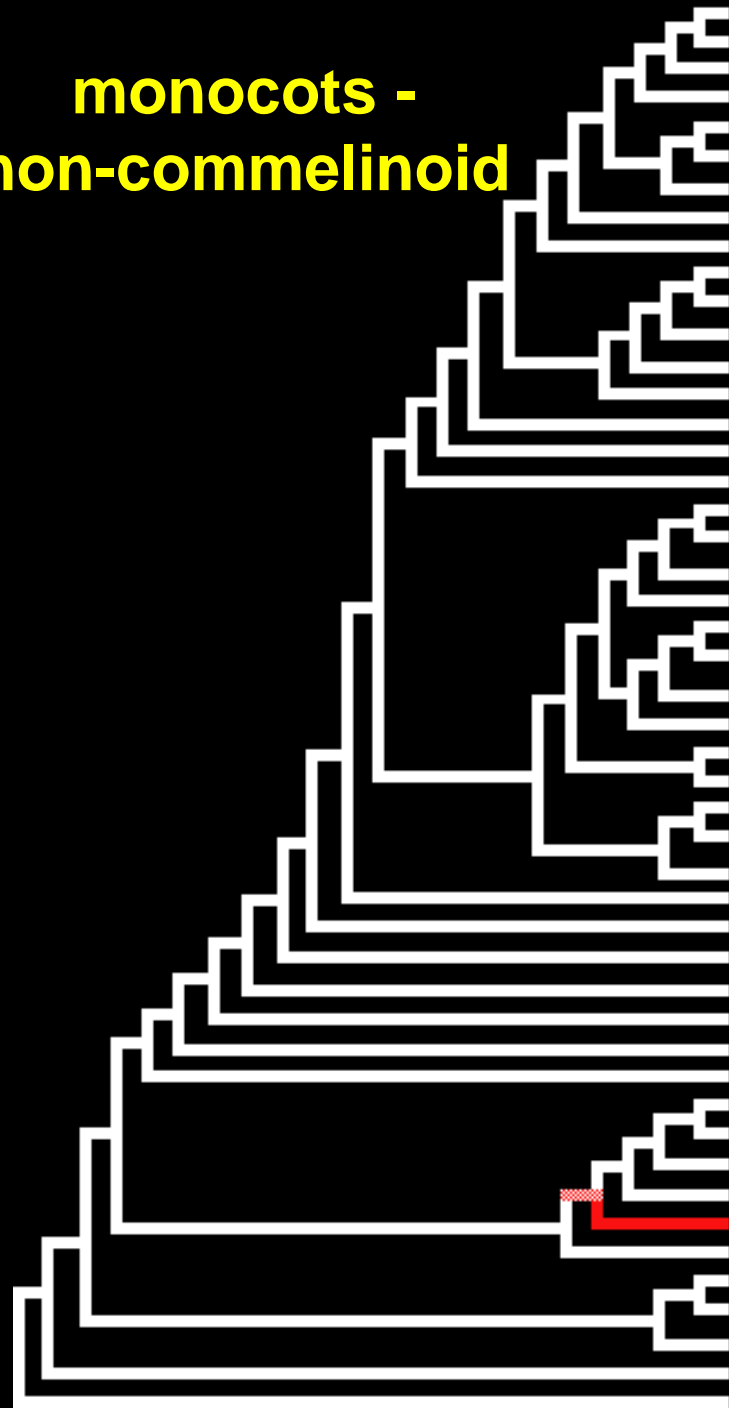


Costus

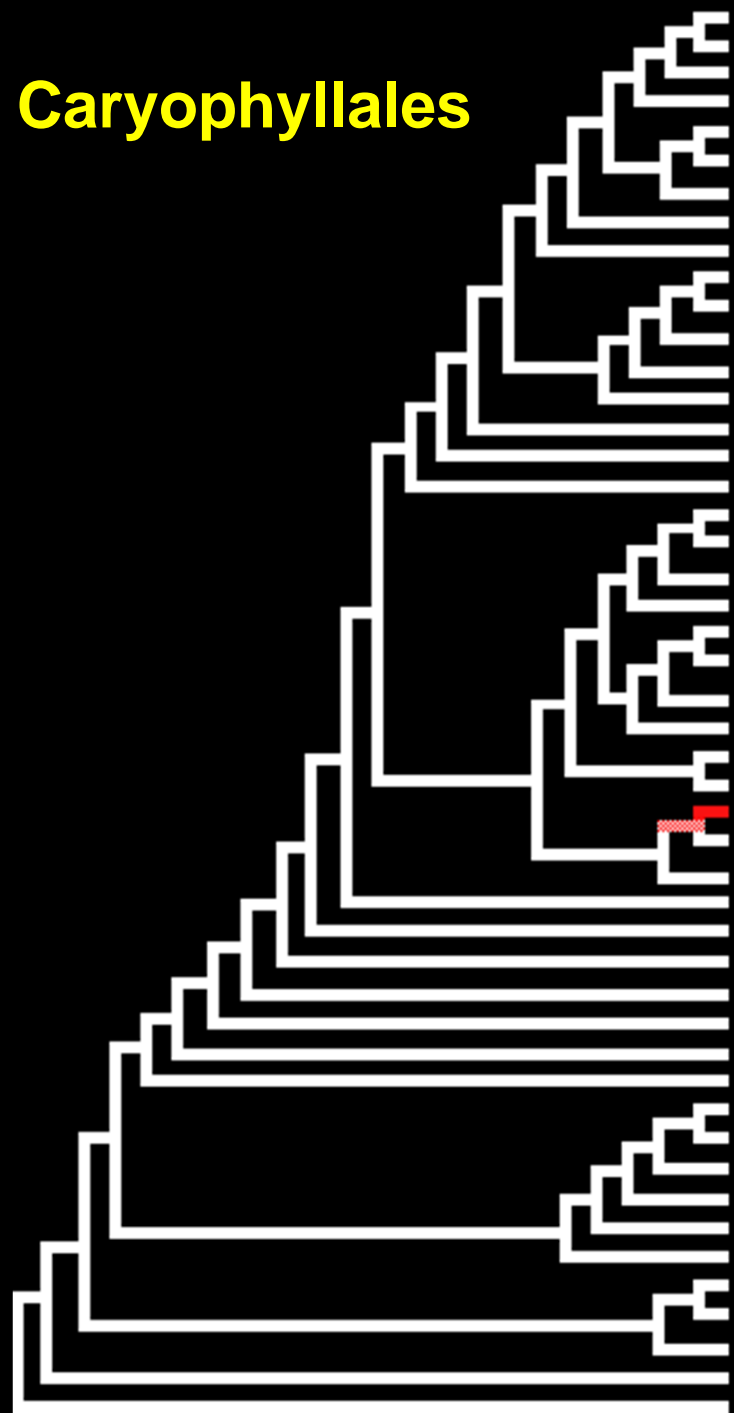


Banana

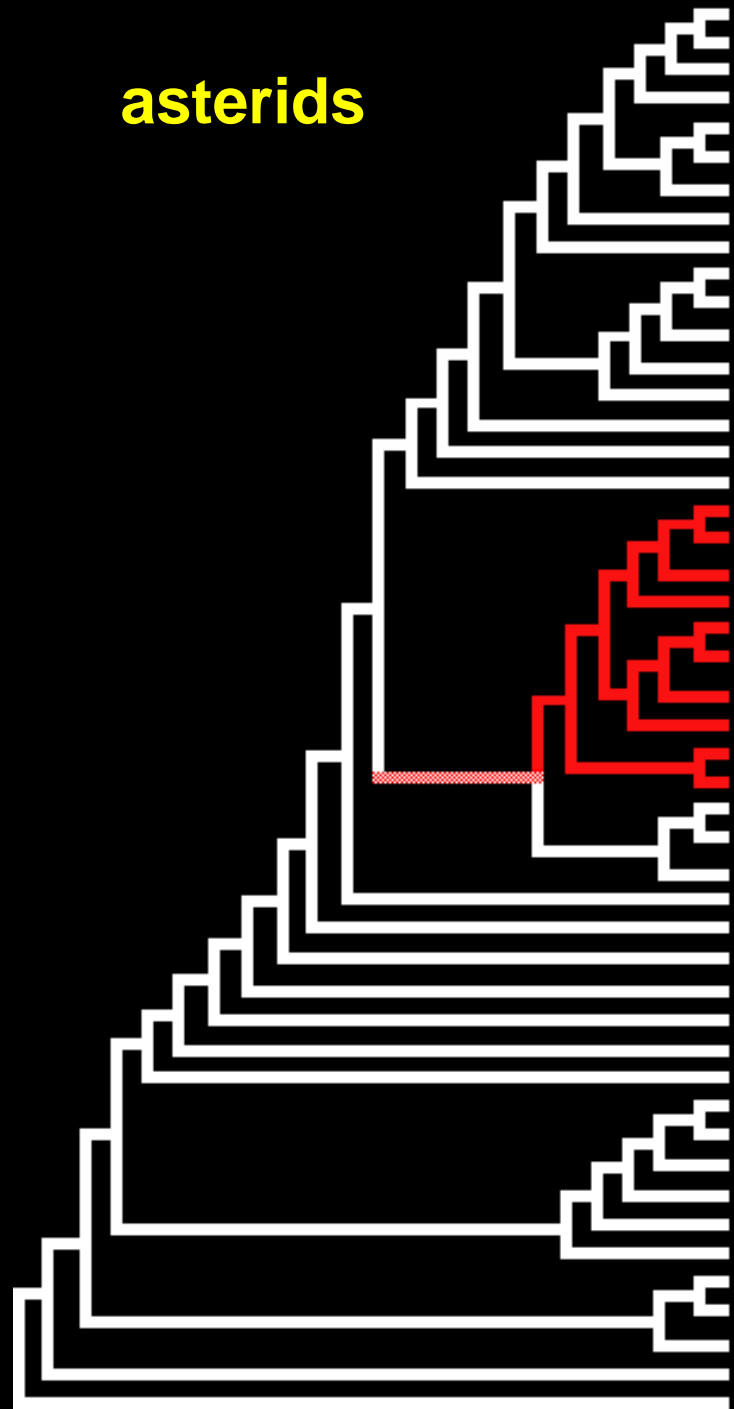
**monocots -
non-commelinoid**



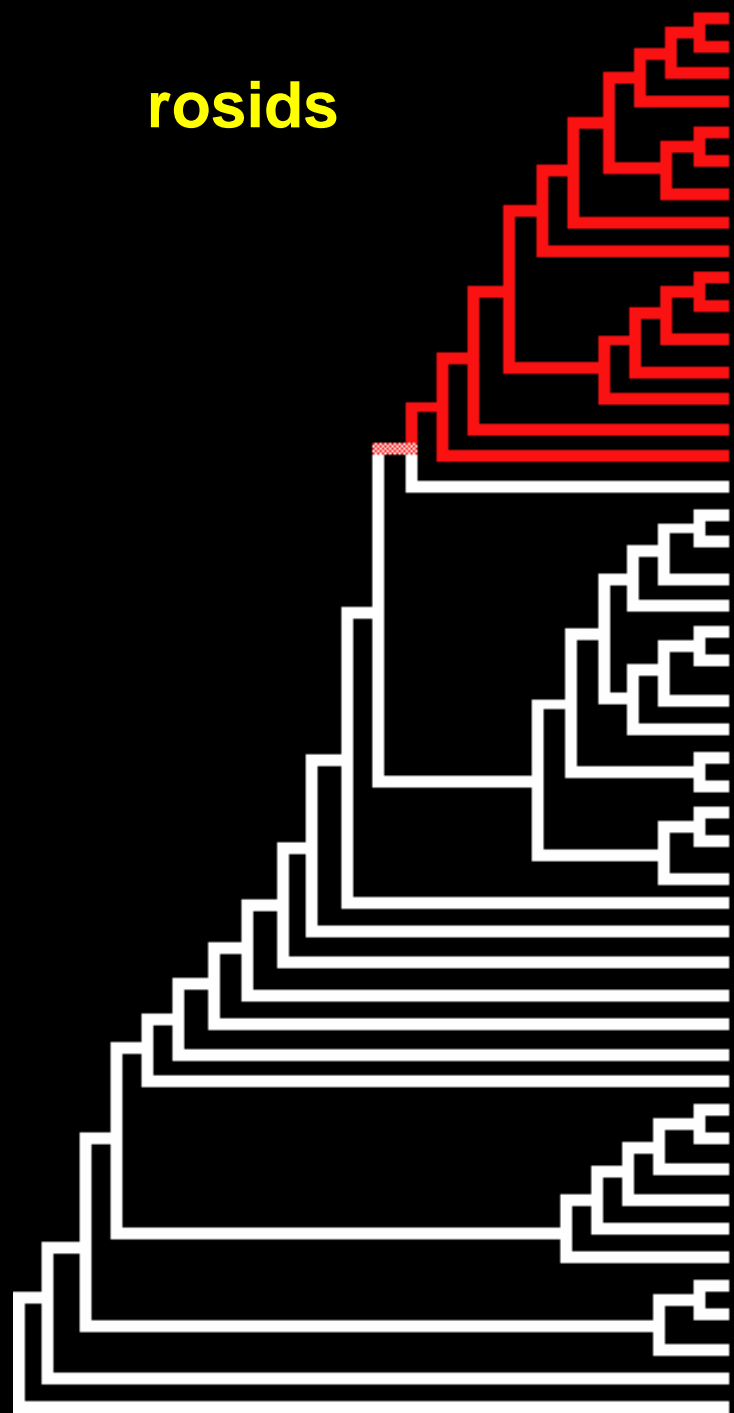
Caryophyllales



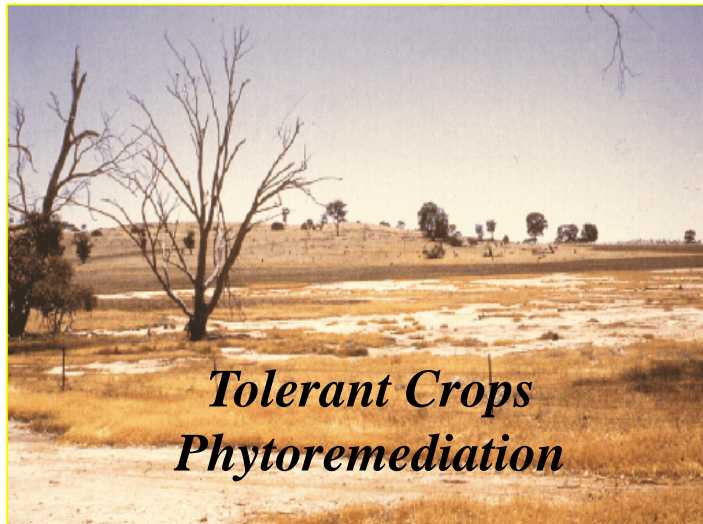
asterids



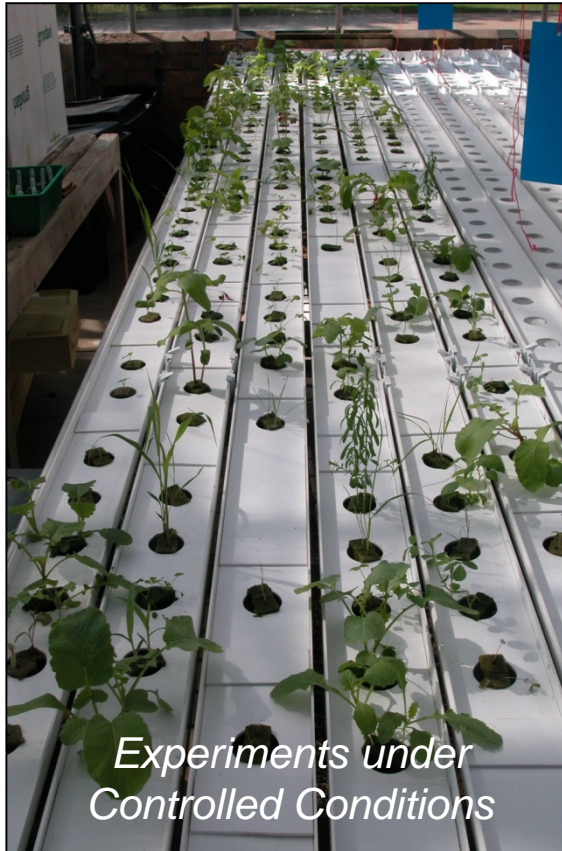
rosids



Plant Species Differ In Their Shoot Elemental Composition (Ionome)



Evolution of the Angiosperm Ionome Data Sources



Insights to the Angiosperm Ionome – Sources of Data

Phylogenetic Effects on Shoot Concentrations of Group II Elements

Magnesium & Calcium
Essential Mineral Elements

1																	2				
<u>H</u>																	<u>He</u>				
3	4															5	6	7	8	9	10
<u>Li</u>	<u>Be</u>															<u>B</u>	<u>C</u>	<u>N</u>	<u>O</u>	<u>F</u>	<u>Ne</u>
11	12															13	14	15	16	17	18
<u>Na</u>	<u>Mg</u>															<u>Al</u>	<u>Si</u>	<u>P</u>	<u>S</u>	<u>Cl</u>	<u>Ar</u>
19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36				
<u>K</u>	<u>Ca</u>	<u>Sc</u>	<u>Ti</u>	<u>V</u>	<u>Cr</u>	<u>Mn</u>	<u>Fe</u>	<u>Co</u>	<u>Ni</u>	<u>Cu</u>	<u>Zn</u>	<u>Ga</u>	<u>Ge</u>	<u>As</u>	<u>Se</u>	<u>Br</u>	<u>Kr</u>				
37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54				
<u>Rb</u>	<u>Sr</u>	<u>Y</u>	<u>Zr</u>	<u>Nb</u>	<u>Mo</u>	<u>Tc</u>	<u>Ru</u>	<u>Rh</u>	<u>Pd</u>	<u>Ag</u>	<u>Cd</u>	<u>In</u>	<u>Sn</u>	<u>Sb</u>	<u>Te</u>	<u>I</u>	<u>Xe</u>				
55	56	57	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86				
<u>Cs</u>	<u>Ba</u>	<u>La</u>	<u>Hf</u>	<u>Ta</u>	<u>W</u>	<u>Re</u>	<u>Os</u>	<u>Ir</u>	<u>Pt</u>	<u>Au</u>	<u>Hg</u>	<u>Tl</u>	<u>Pb</u>	<u>Bi</u>	<u>Po</u>	<u>At</u>	<u>Rn</u>				
87	88	89	104	105	106	107	108	109	110	111	112	113	114								
<u>Fr</u>	<u>Ra</u>	<u>Ac</u>	<u>Rh</u>	<u>Db</u>	<u>Sg</u>	<u>Bh</u>	<u>Sh</u>	<u>Mt</u>	<u>Uun</u>	<u>Uuu</u>	<u>Uub</u>	<u>Uut</u>	<u>Uuq</u>								
lanthanons			58	59	60	61	62	63	64	65	66	67	68	69	70	71					
			<u>Ce</u>	<u>Pr</u>	<u>Nd</u>	<u>Pm</u>	<u>Sm</u>	<u>Eu</u>	<u>Gd</u>	<u>Tb</u>	<u>Dy</u>	<u>Ho</u>	<u>Er</u>	<u>Tm</u>	<u>Yb</u>	<u>Lu</u>					
actinons			90	91	92	93	94	95	96	97	98	99	100	101	102	103					
			<u>Th</u>	<u>Pa</u>	<u>U</u>	<u>Np</u>	<u>Pu</u>	<u>Am</u>	<u>Cm</u>	<u>Bk</u>	<u>Cf</u>	<u>Es</u>	<u>Fm</u>	<u>Md</u>	<u>No</u>	<u>Lr</u>					

Broadley et al. (2003) *J. Exp. Bot.* 54: 1431-1446

Broadley et al. (2004) *J. Exp. Bot.* 55: 321-336

Magnesium in Plant Physiology

Proteins – chlorophyll (5-50%)

Enzyme activities (photosynthesis, energy metabolism, protein synthesis)

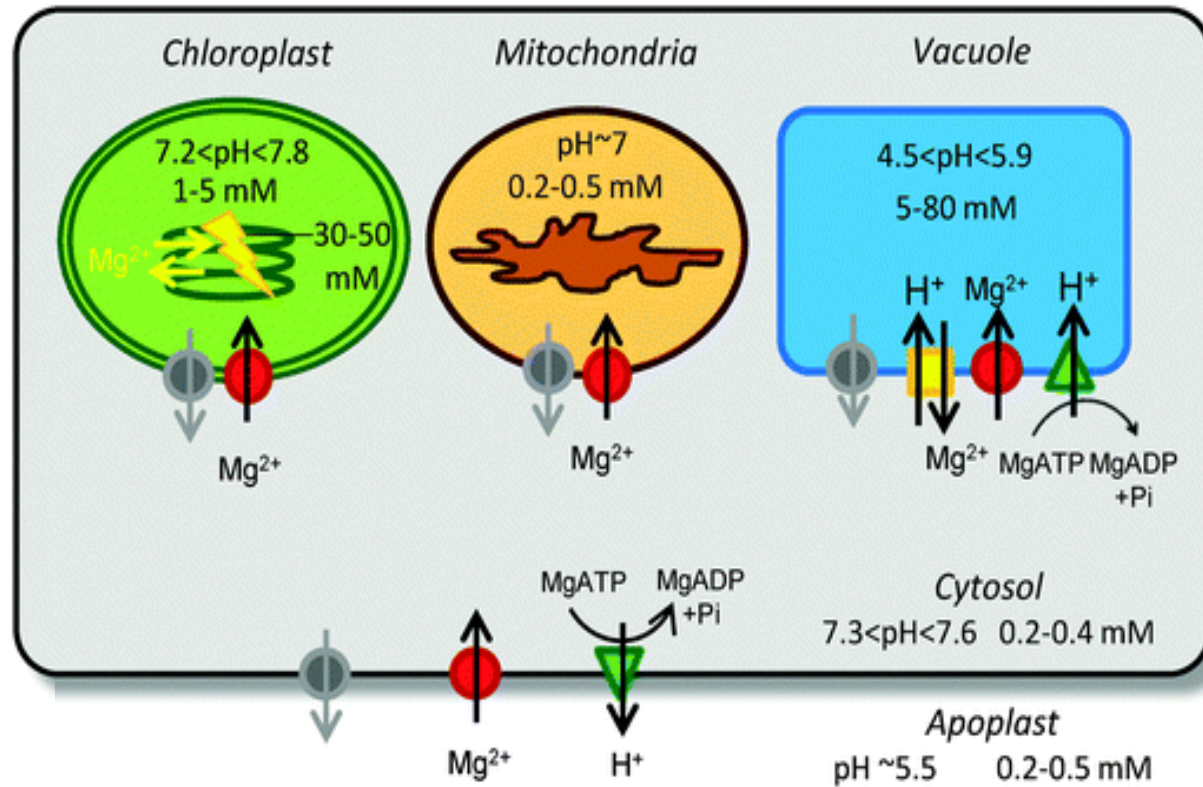
Bound to cell wall components (5-10%)

TABLE 6.11 Concentration and binding form of Mg in one-year-old needles of Norway spruce growing on two soil types

Soil type	Total Mg concentration (mg g ⁻¹ dw)	Proportion of total Mg		
		Water-soluble	Pectate, phosphate	Chlorophyll
Rendzina	1.47	91.2	2.6	6.2
Podsol	0.31	64.8	10.0	25.2

Based on Fink (1992a).

Magnesium Transport Within A Plant

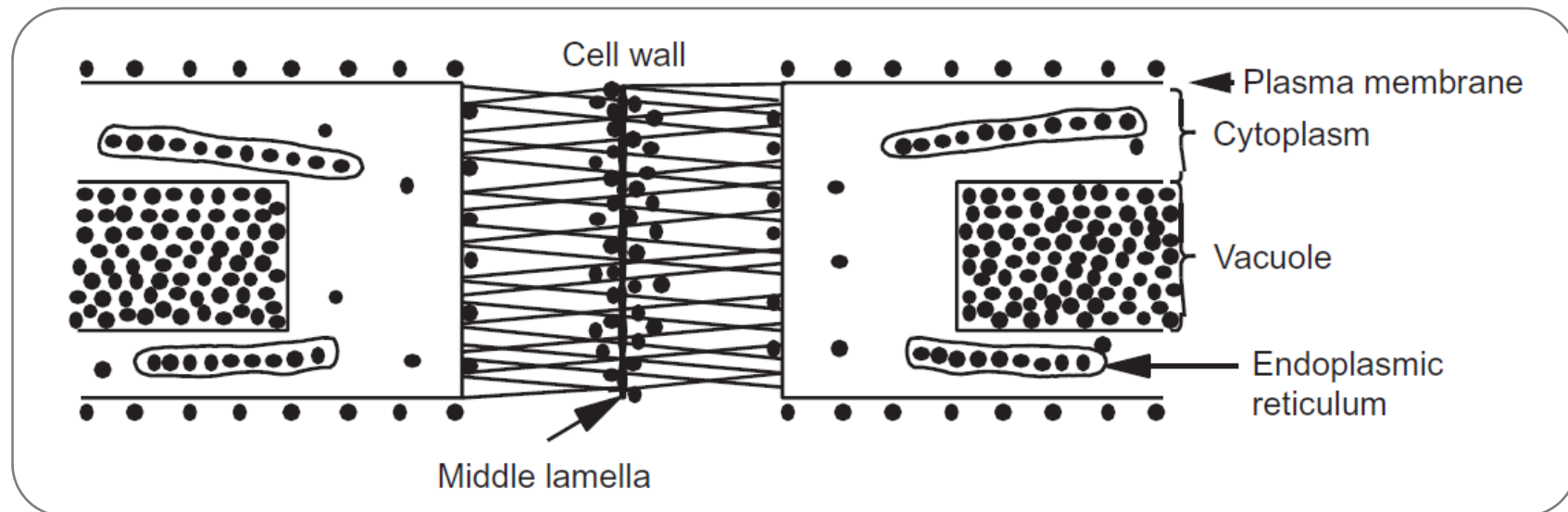


MRS/MGT ● MHX (Mg/H⁺ exchanger) ■

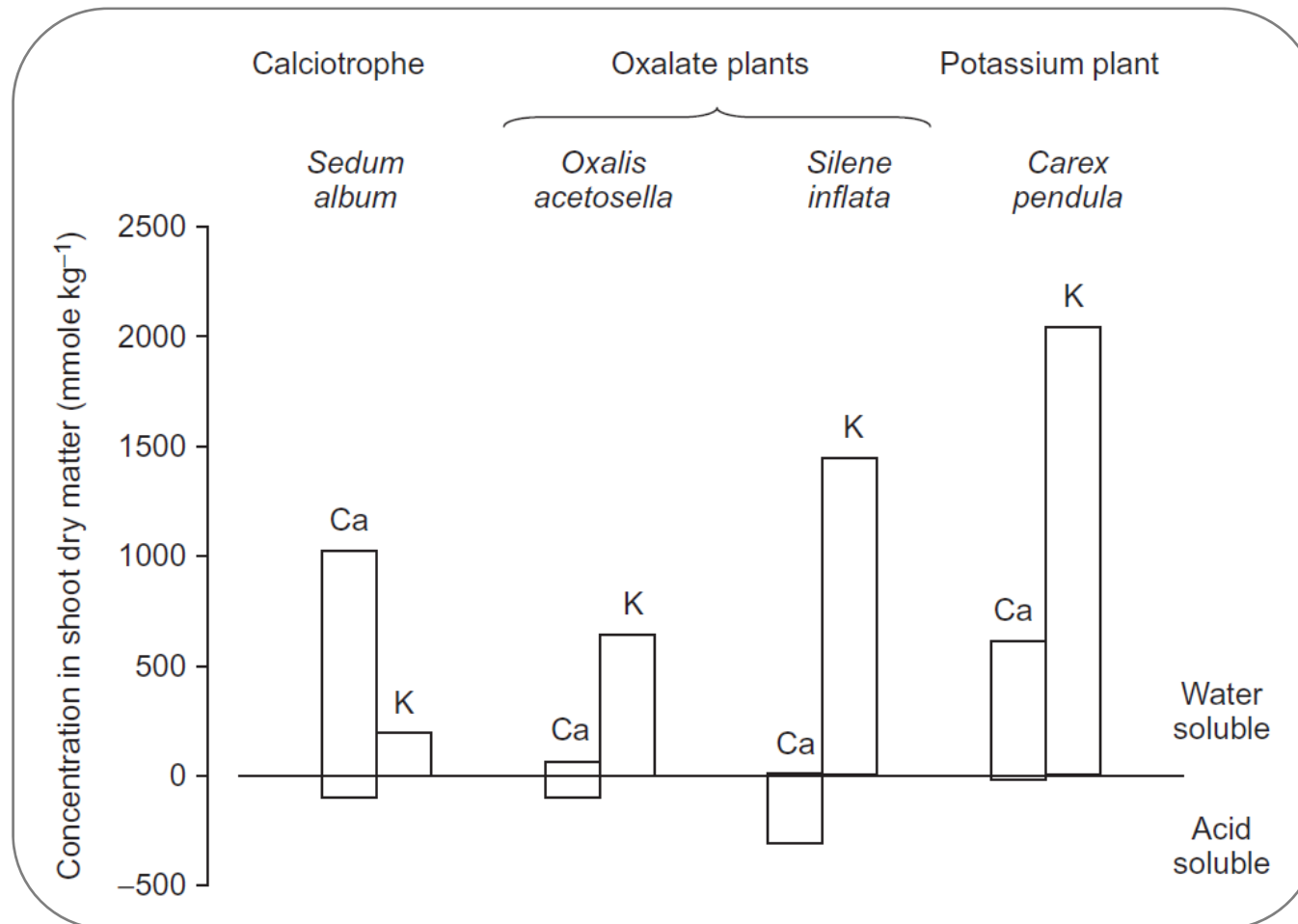
Hermans et al. (2013) *Metallomics* 5: 1170-1183

Calcium in Plant Physiology

Stability of cell walls and membranes
Signal transduction through cytosolic Ca^{2+} concentration
Cation/anion balance and osmoregulation

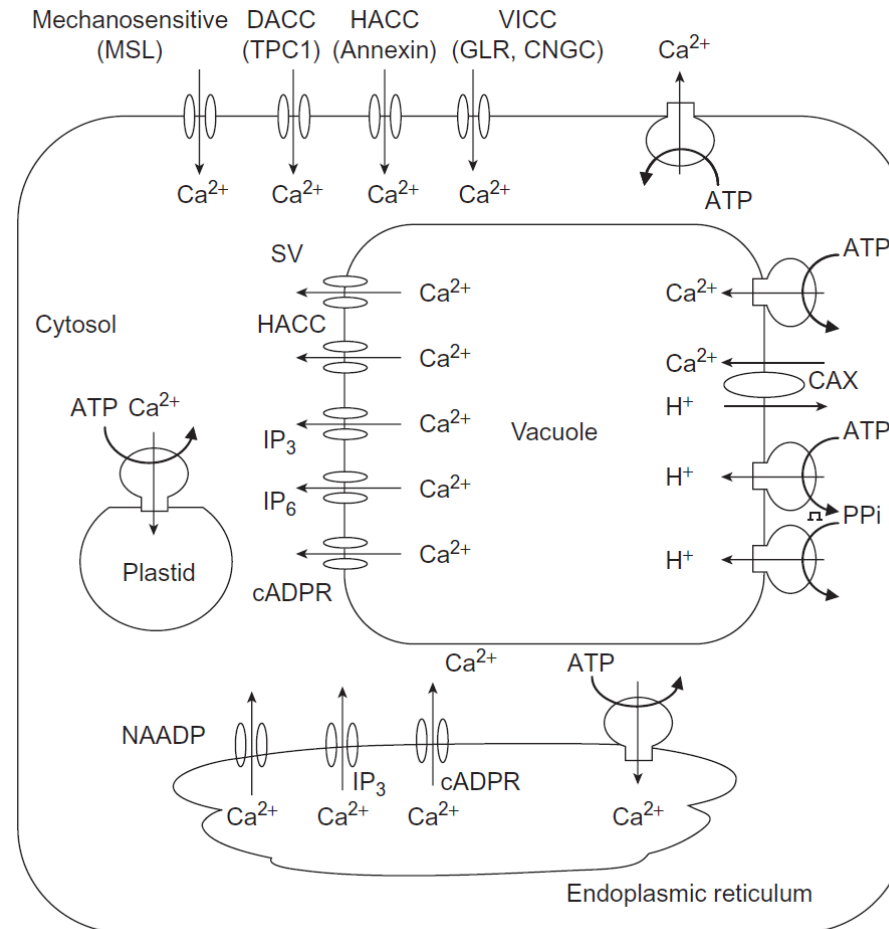


Calcium in Plants



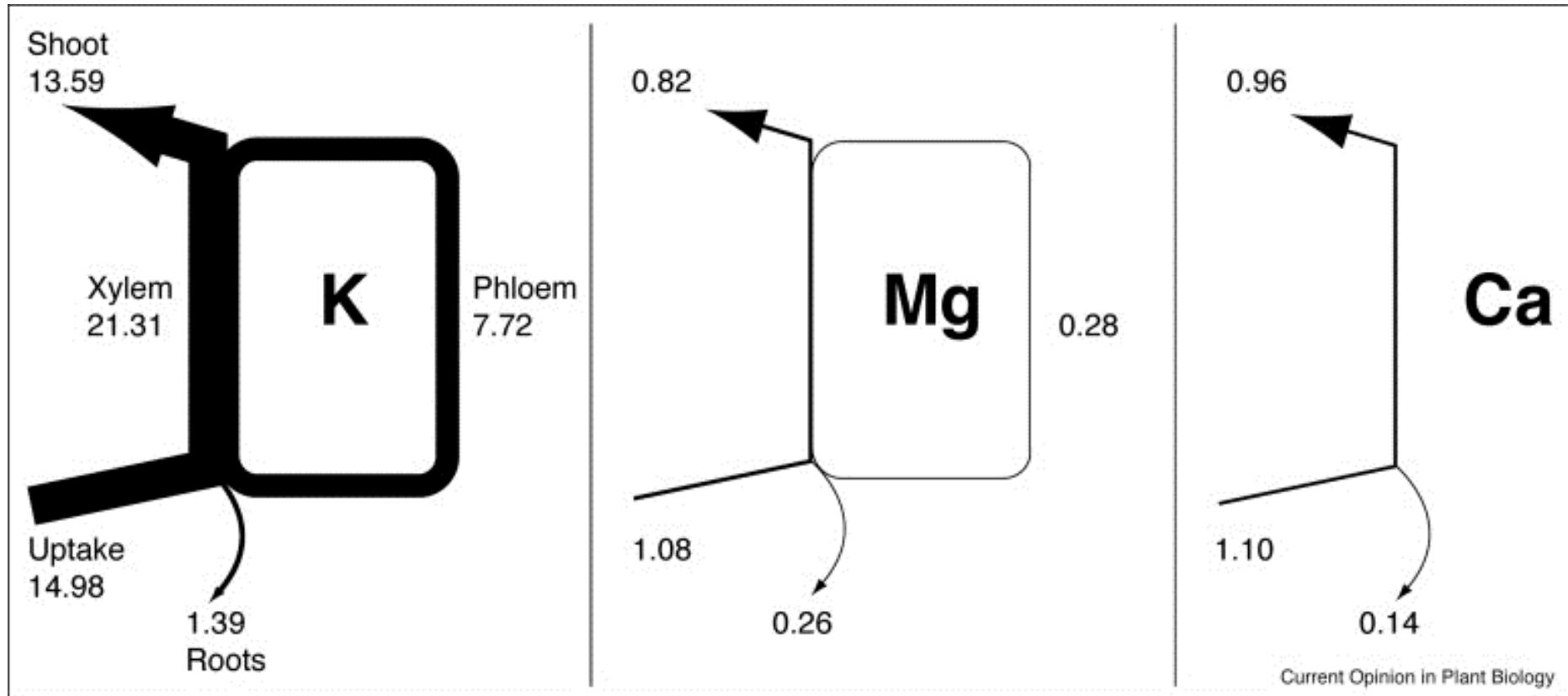
White (2005) In: *Plant Nutritional Genomics*, pp. 66-86

Calcium Transport in Plant Cells



White & Broadley (2003) *Annals of Botany* 92: 487-511

Cation Transport Within A Plant

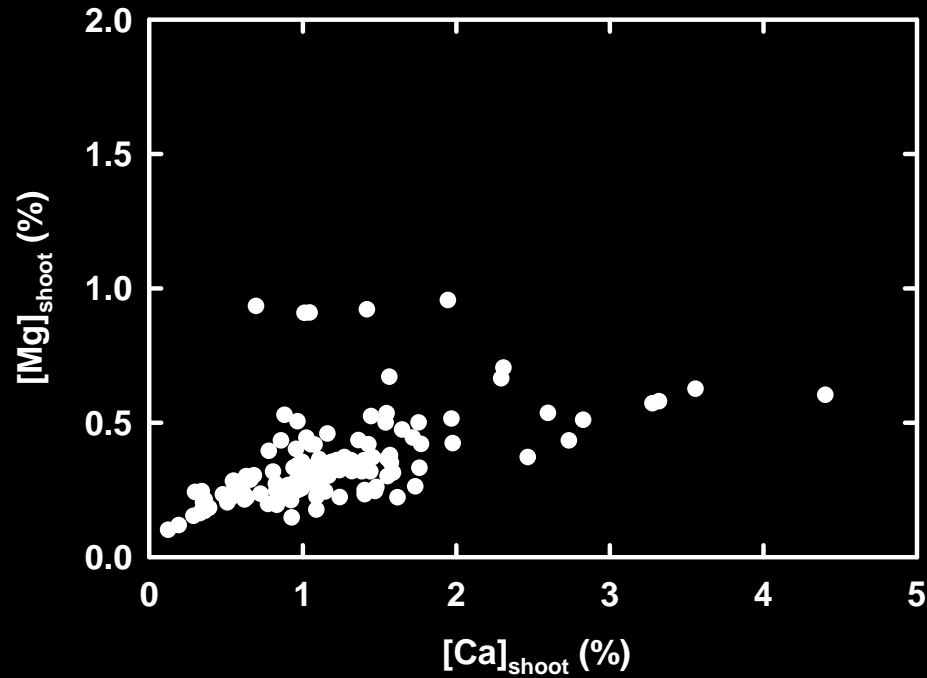


Karley & White (2009) *Curr Opin Plant Biol* 12: 291-298

Magnesium : Calcium Ratios in Shoot Tissues

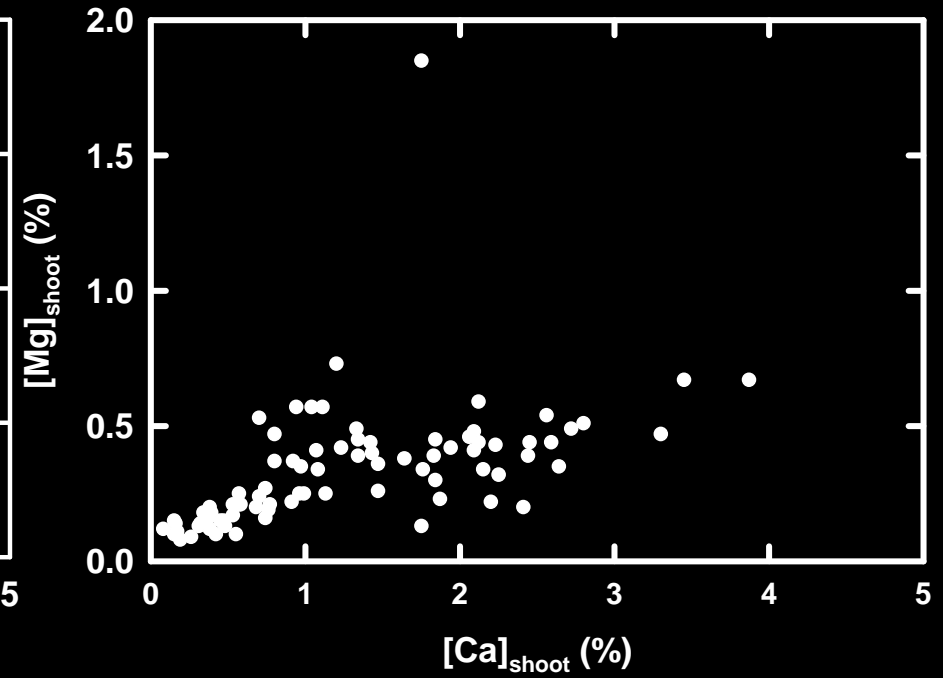
Hydroponics

Broadley et al. (2004)



Sampled from the field

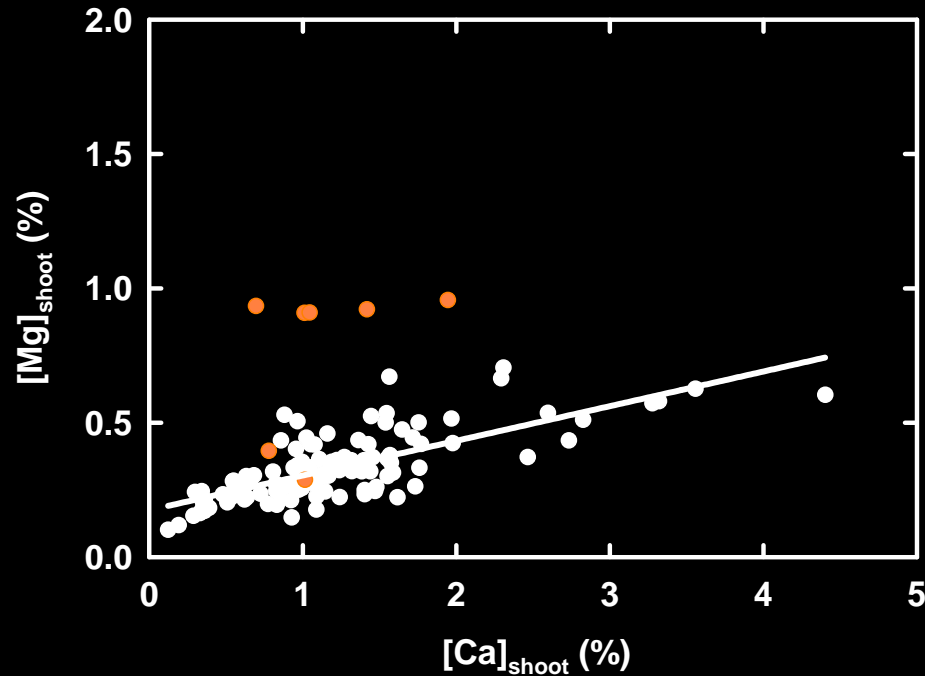
Thompson et al. (1997)



Magnesium : Calcium Ratios in Shoot Tissues

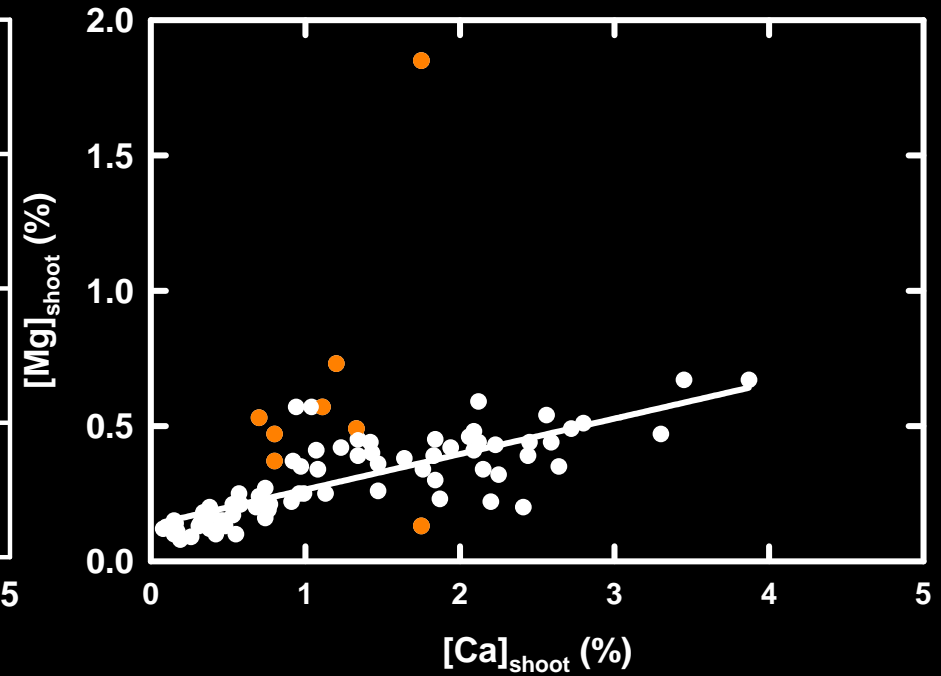
Hydroponics

Broadley et al. (2004)



Sampled from the field

Thompson et al. (1997)

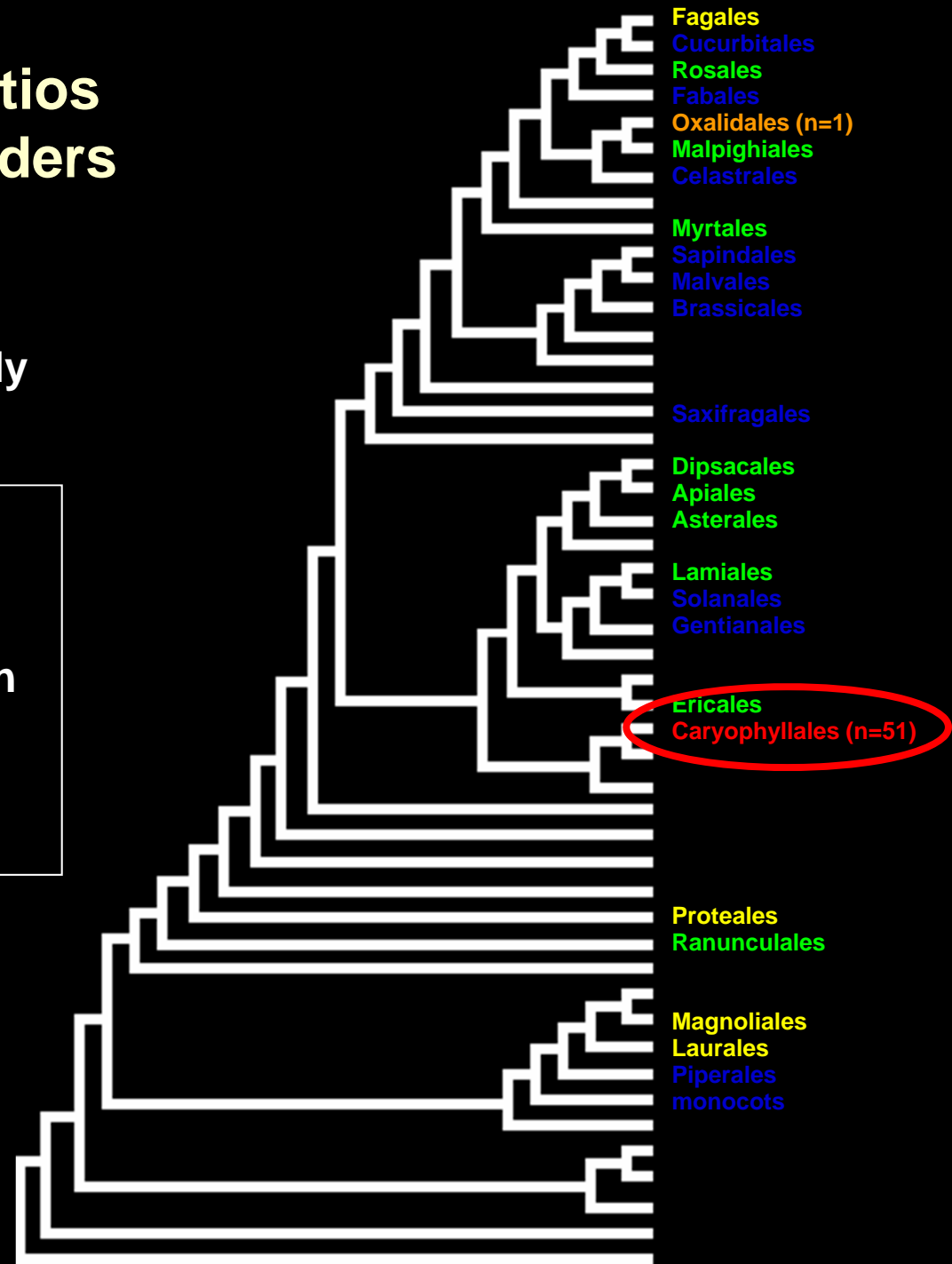
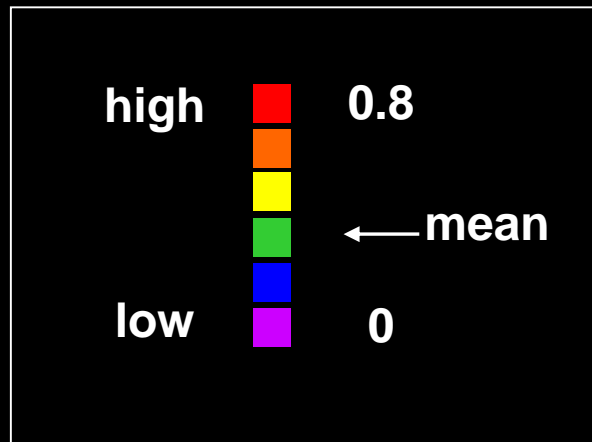


● All other taxa

● Caryophyllales (e.g. sugar beet, carnation)

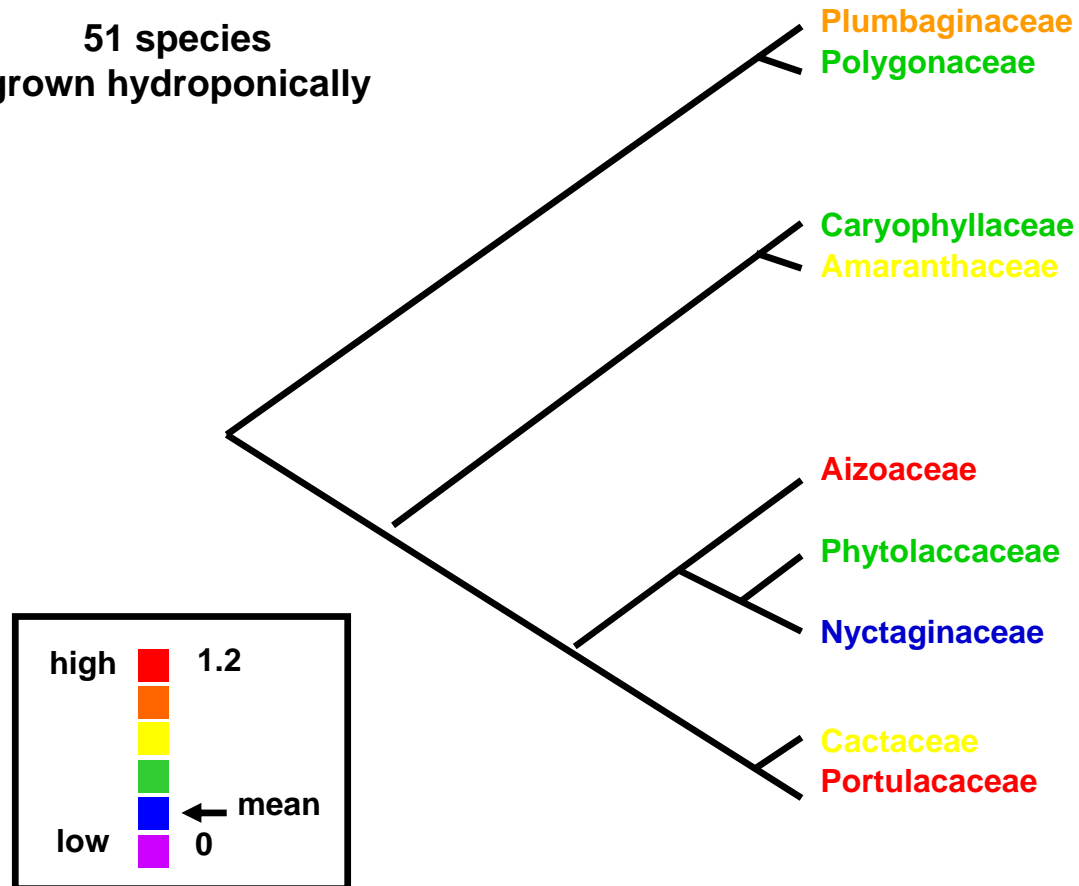
Shoot Mg / Ca Ratios of Angiosperm Orders

> 200 species
grown hydroponically



Shoot Mg / Ca Ratios in the Caryophyllales

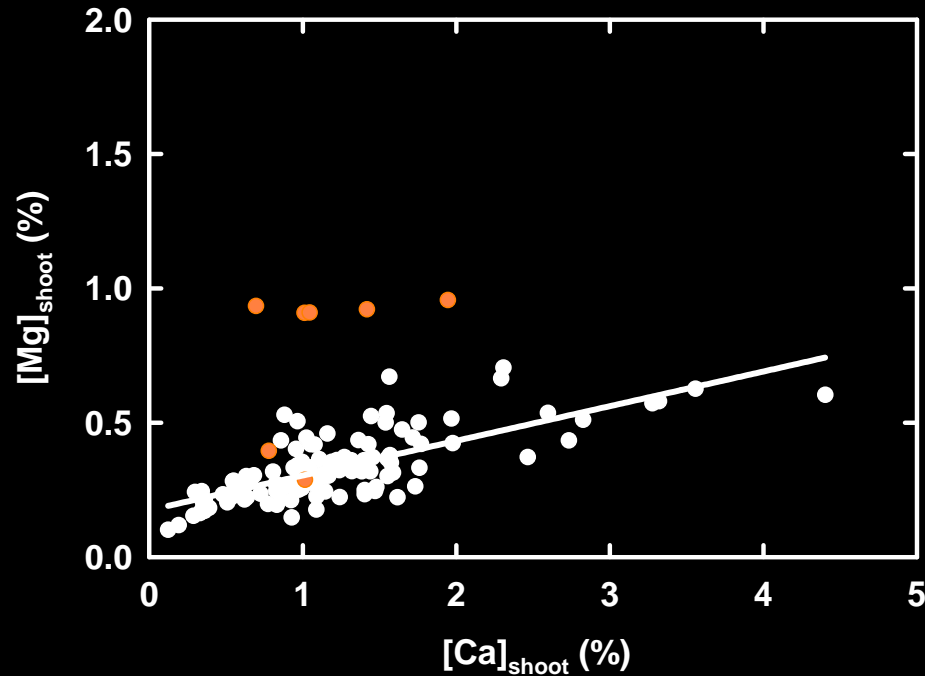
51 species
grown hydroponically



Magnesium : Calcium Ratios in Shoot Tissues

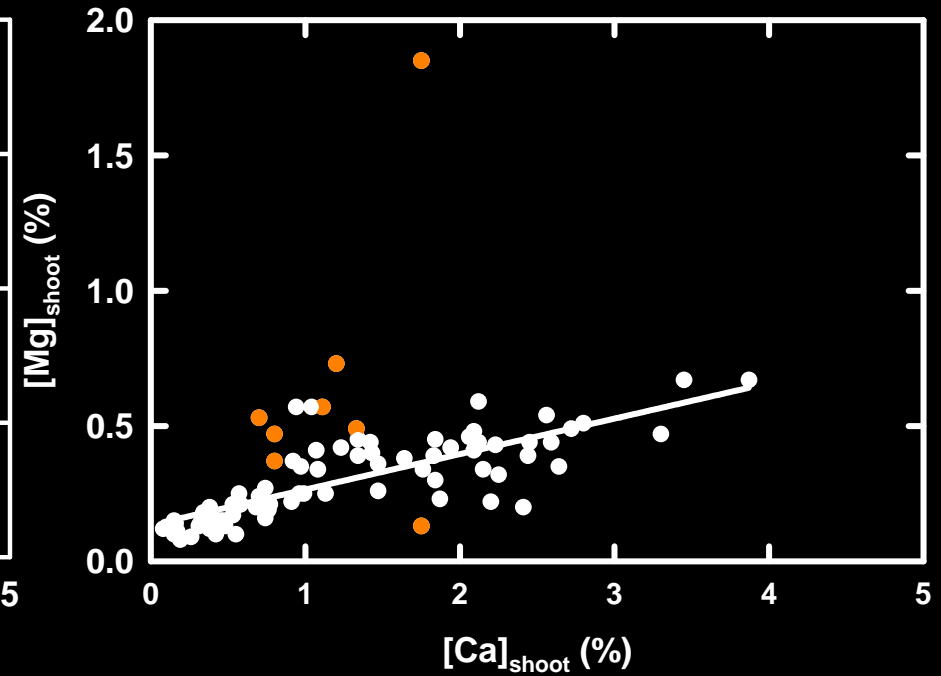
Hydroponics

Broadley et al. (2004)



Sampled from the field

Thompson et al. (1997)



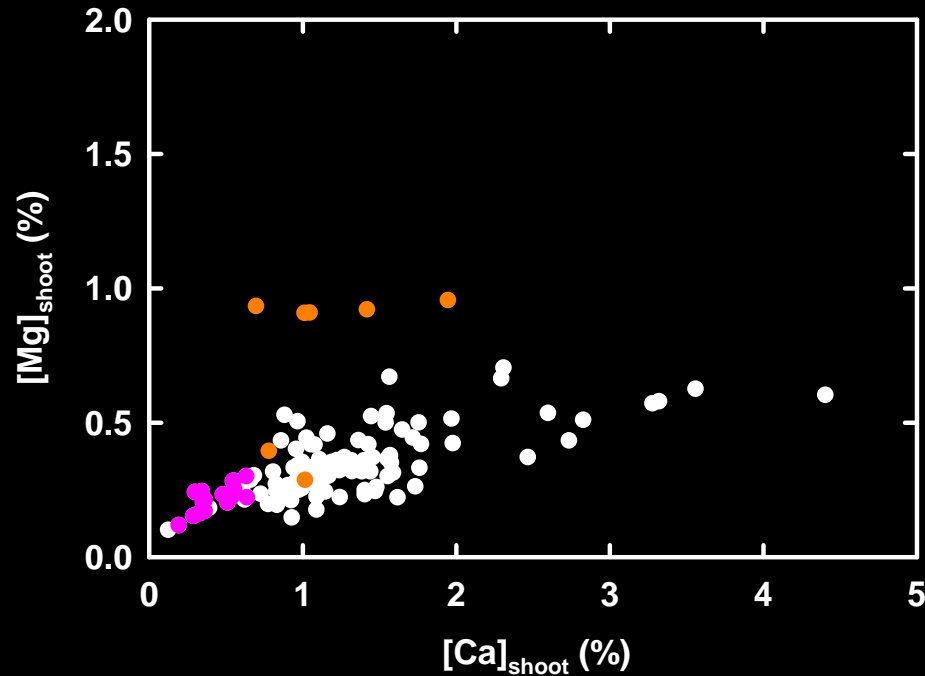
● All other taxa

● Caryophyllales (e.g. sugar beet, carnation)

Magnesium : Calcium Ratios in Shoot Tissues

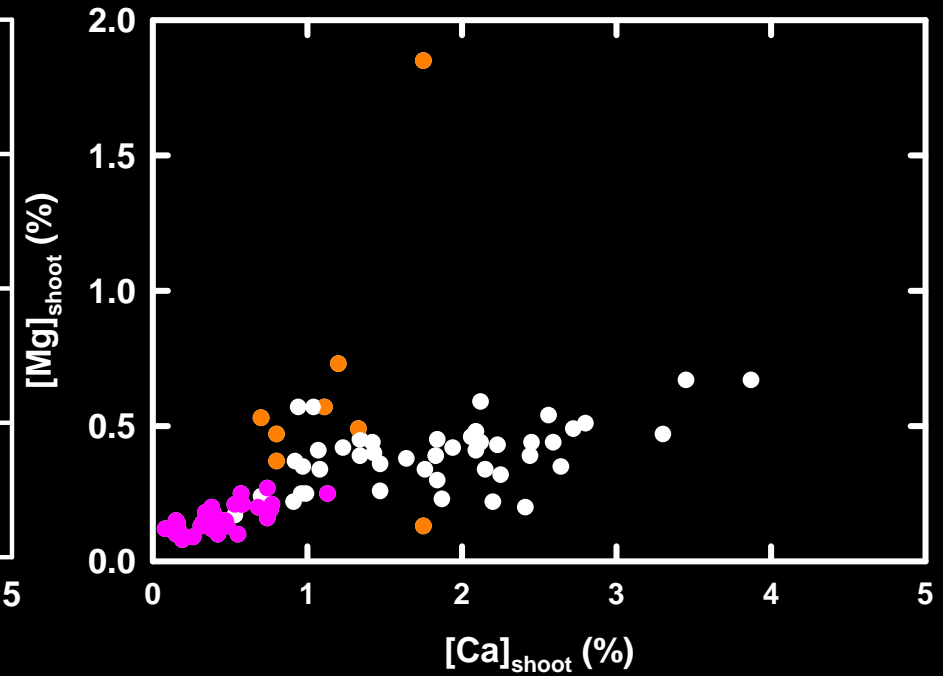
Hydroponics

Broadley et al. (2004)



Sampled from the field

Thompson et al. (1997)

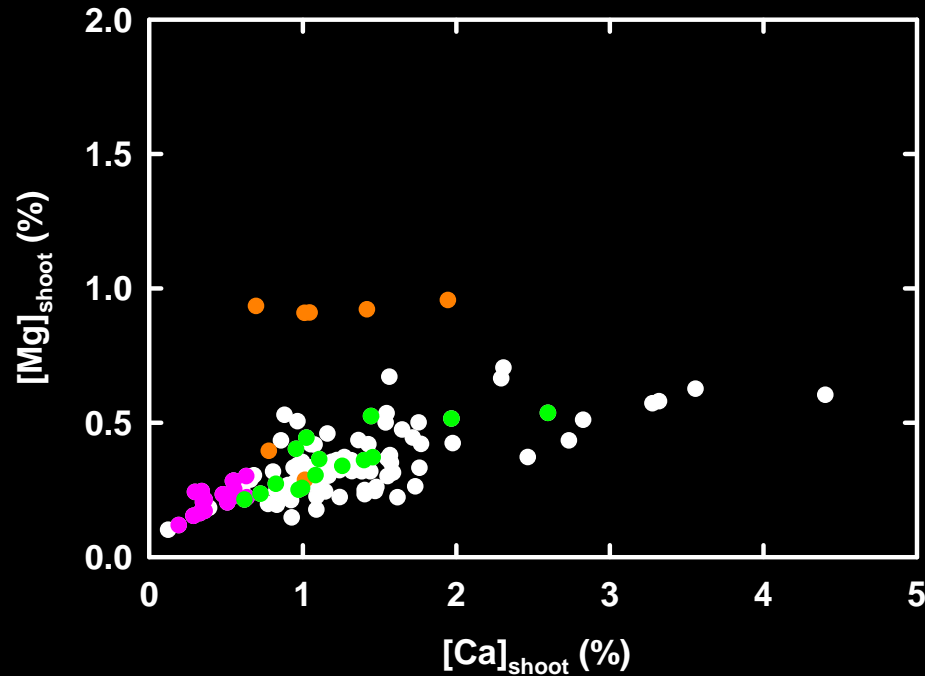


- All other taxa
- Caryophyllales (e.g. sugar beet, carnation)
- Poales (e.g. the grass / cereal family, Poaceae)

Magnesium : Calcium Ratios in Shoot Tissues

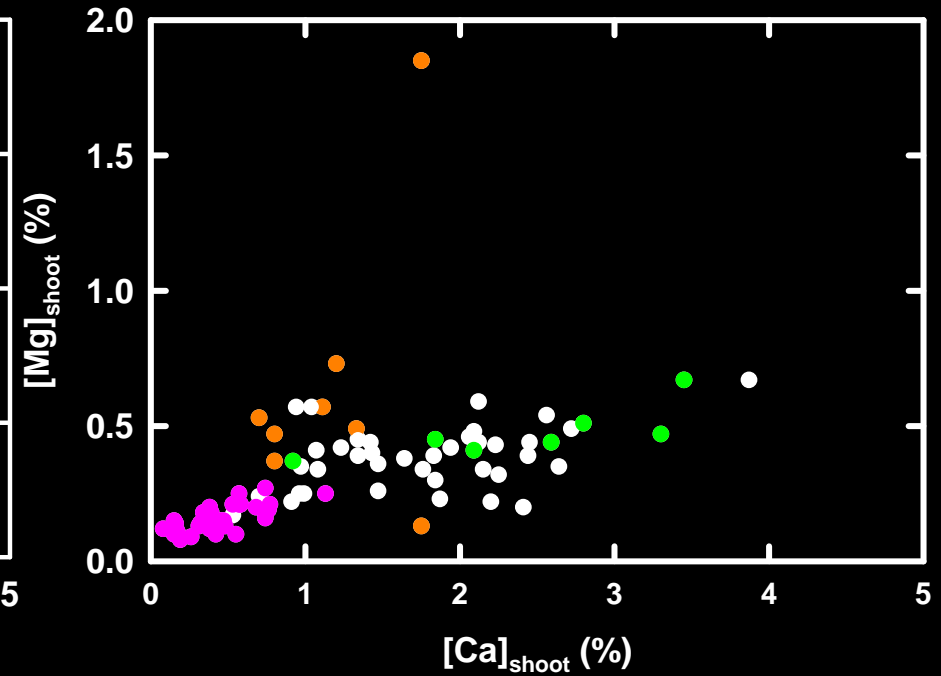
Hydroponics

Broadley et al. (2004)



Sampled from the field

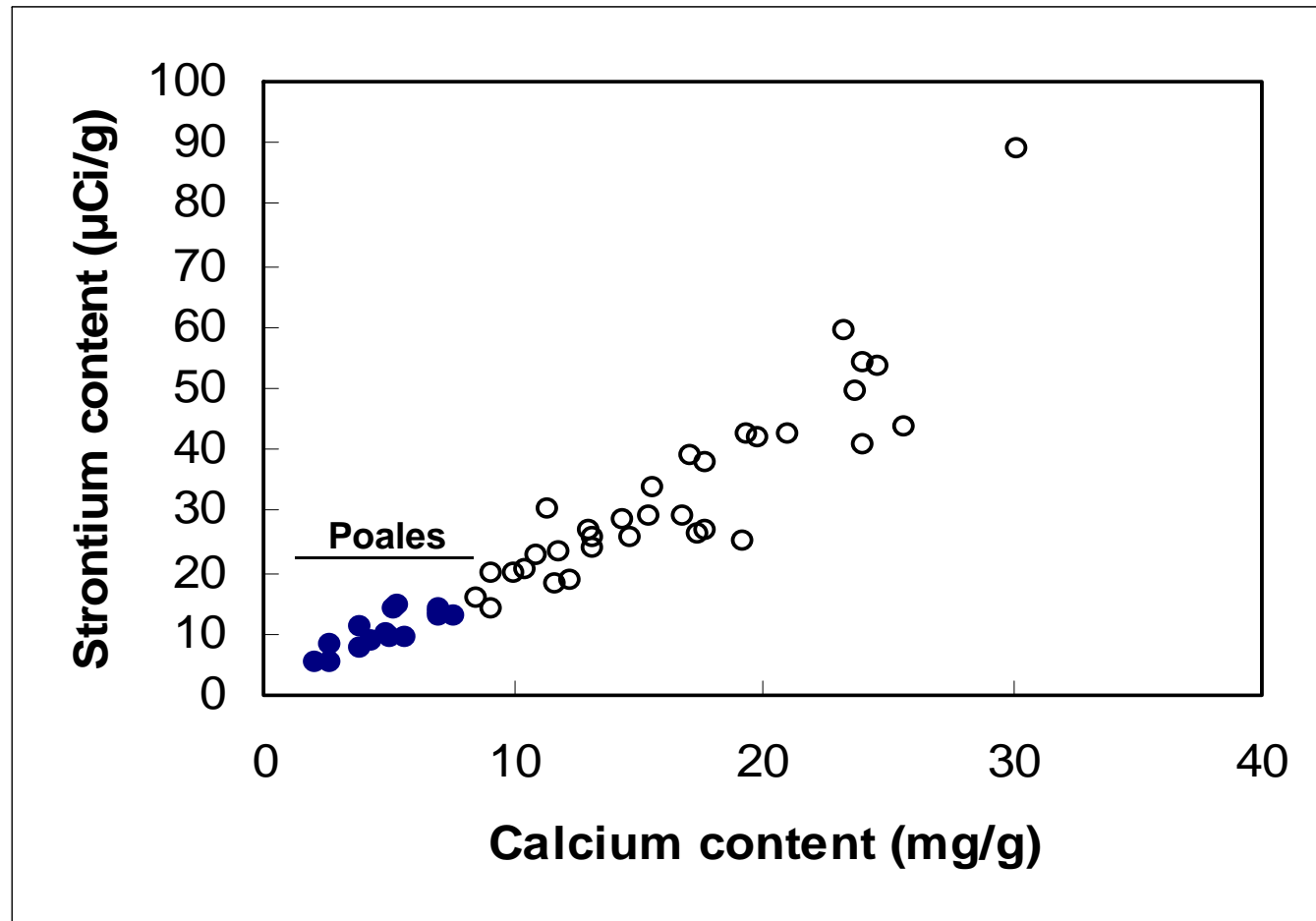
Thompson et al. (1997)



- All other taxa
- Caryophyllales (e.g. sugar beet, carnation)
- Poales (e.g. the grass / cereal family, Poaceae)
- Asterales (e.g. the daisy / sunflower family Asteraceae)

Strontium : Calcium Ratios

In Shoots of 44 Plant Species



Andersen AJ (1967) *Risö Report 170*

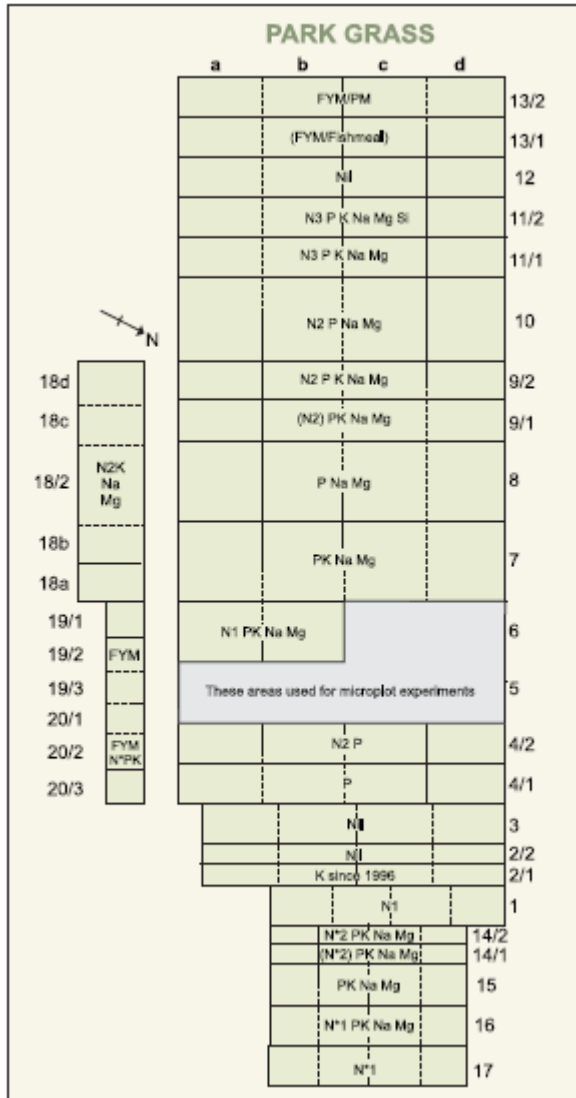
Phylogenetic Variation In Shoot Mineral Concentrations

	Proportion of Genetic Variation		
	Ca	Mg	Sr
order and above (%)	64	65	76
within order (%)	36	35	24

Ancient evolutionary origin of variation
in Ca, Mg & Sr concentrations

Broadley et al. (2004) *J. Exp. Bot.* 55: 321-336

Phylogenetic and Environmental Effects on the Plant Ionome



Park Grass, Rothamsted
1856-2014

Botanical Composition of Park Grass Plots (Crawley *et al.*, 1991-2000)

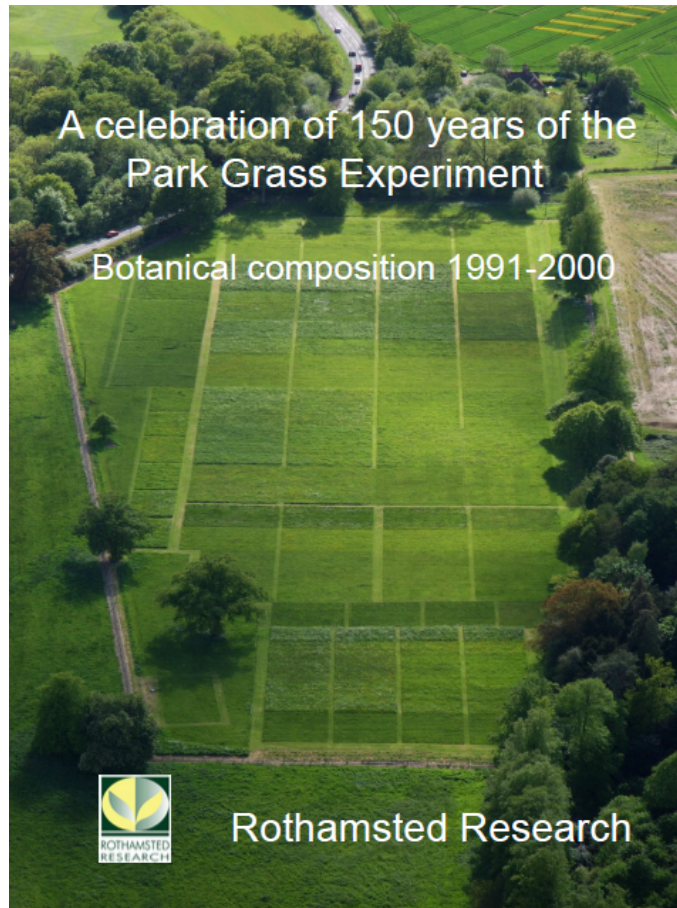


Table 3. Species comprising at least 10% of herbage, and total number of species; mean 1991-2000.

Percentage of dry matter (Species names are listed below)

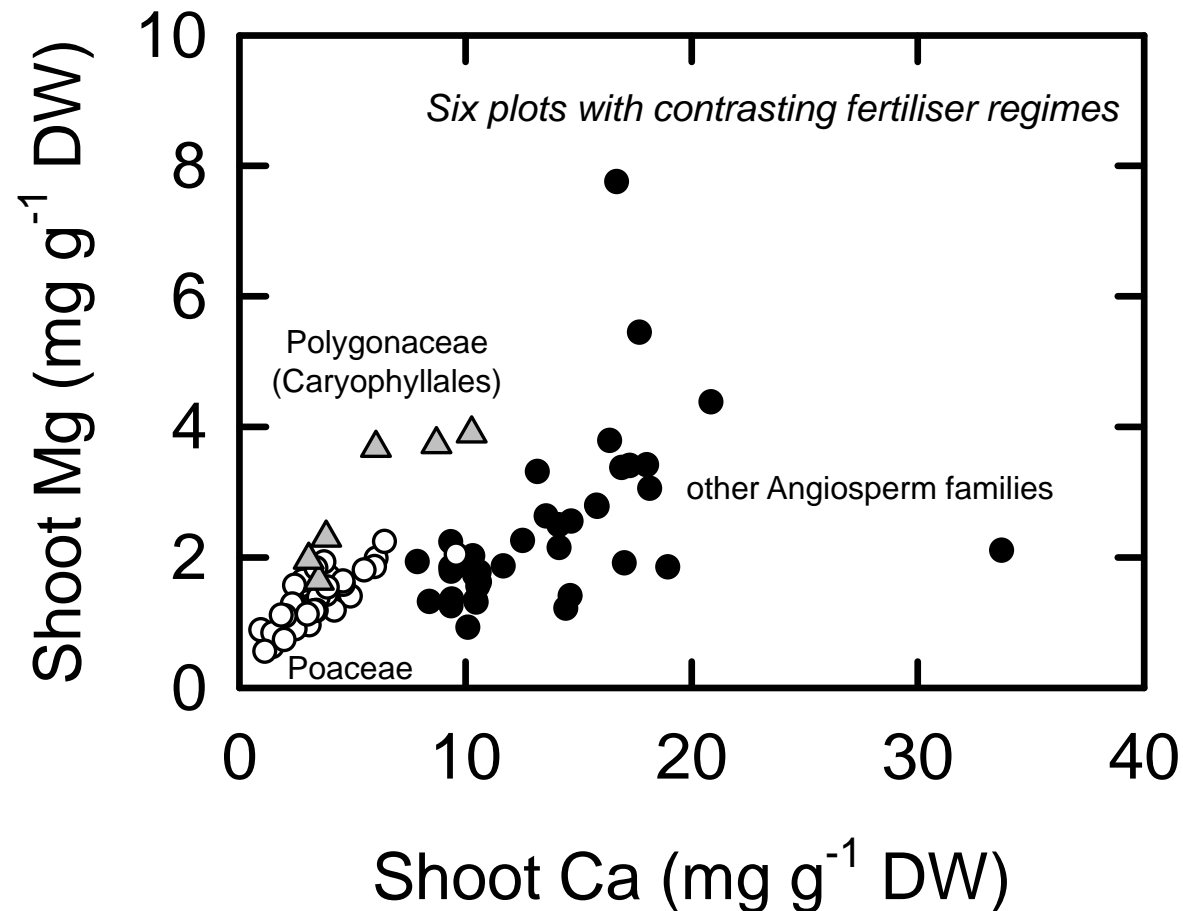
Treatment	Plot	1990-02	AD	AP	AD	AT	2D	FD	HP	ML	LaP	TP	AD	GV	HD	LV	PL	PaA	PaB	SM	Total no. of species
M	3a	7.2	13	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	18
	b	6.4	19	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	38
	c	5.3	38	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	37
	d	5.2	45	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	35
F	41a	5.0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	24
	b	6.1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	34
	c	5.3	39	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	29
	d	5.3	28	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	32
FMSMtg	18a	5.7	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	28
	b	6.6	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	27
	c	5.0	23	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	25
	d	4.9	43	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	27
F1	17a	7.1	13	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	32
	b	6.4	15	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	34
	c	5.8	25	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	34
	d	6.6	35	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	34
F2PMtg	140a	5.0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	24
	b	6.4	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	24
	c	5.1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	21
	d	5.6	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	22
M1	1a	7.1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	33
	b	6.6	28	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	31
	c	5.3	39	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	33
	d	6.1	65	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	15
M2Mtg	18a	7.1	15	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	32
	b	6.3	38	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	29
	c	5.4	35	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	21
	d	3.8	88	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	9
M3P	40a	5.0	19	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	22
	b	6.2	15	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	14
	c	5.3	33	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	18
	d	3.7	38	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	15
M3PMtg	50a	5.0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	22
	b	6.3	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	17
	c	5.0	33	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	18
	d	3.7	15	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	4
M3PMtg	110a	5.2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	14
	b	6.3	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	15
	c	4.9	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	13
	d	3.6	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	3
FMSM1	130a	5.8	38	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	29
	b	6.1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	35
	c	5.3	23	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	32
	d	6.1	35	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	34

After Crawley *et al.*, 2005, *American Naturalist*, 165, 179-192.
Data are from surveys immediately before hay harvest, rounded to the nearest 5% of dry matter, mean 1991-2000. (Selected plots only)
+, species present at least 10%; ●, species not identified on that plot.
Species that do not occur at 10%, or more, on any one plot are not shown.

Grasses: <i>Agrostis capillaris</i> <i>Alpinurus pratensis</i> <i>Anthoxanthum odoratum</i> <i>Arrhenatherum elatius</i> <i>Deschampsia glomerata</i> <i>Festuca rubra</i> <i>Holcus lanatus</i> <i>Lolium perenne</i>	Common Bents: <i>Molinia caerulea</i> Sweet Vernal Grass: <i>Festuca ovina</i> Cocksfoot: <i>Festuca ovina</i> Red Fescue: <i>Festuca rubra</i> Oxeye Daisy: <i>Leucanthemum vulgare</i> Yorkshire Fog: <i>Calluna vulgaris</i> Pennine Ryegrass: <i>Lolium perenne</i>	Forbs: <i>Anthriscus sylvestris</i> <i>Cerastium triviale</i> <i>Horridulum sphondylium</i> <i>Leontodon hispidus</i> <i>Plantago lanceolata</i> <i>Ranunculus acris</i> <i>Rumex acetosa</i> <i>Sanguisorba minor</i>	Cow Parsley: <i>Oenanthe lachnoides</i> Common Nettle: <i>Urtica dioica</i> Hogweed: <i>Heracleum sphondylium</i> Rough Hawkbit: <i>Leontodon hispidus</i> Ribwort Plantain: <i>Plantago lanceolata</i> Meadow Buttercup: <i>Ranunculus acris</i> Common Sorrel: <i>Rumex acetosa</i> Salted Burdock: <i>Arctium lappa</i>
Legumes: <i>Lathyrus pratensis</i> <i>Trifolium pratense</i>	Meadow Vetching: <i>Vicia cracca</i> Red Clover: <i>Trifolium pratense</i>		

Crawley *et al.* (2005) *American Naturalist* 165, 179-192

Calcium : Magnesium Ratios In Plants Receiving Contrasting Fertilisers



White et al. (2012) *New Phytologist* 196: 101-109

Phylogenetic and Environmental Effects on the Plant Ionome

Ecological Survey

% Variance	Species	Site
Calcium	81.4	18.6
Magnesium	62.6	37.4

Rothamsted Park Grass Experiment (six plots)

% Variance	Species	Treatment	Residual
Calcium	70.8	8.2	21.0
Magnesium	32.8	19.9	47.3

Thompson et al. (1997) *New Phytologist* 136, 679-689

White et al. (2012) *New Phytologist* 196, 101-109

Plant Calcium - Dietary Consequences

calcium deficiency disorders arise
when populations change from
bean-rich to cereal-rich diets

Normal anatomy



Rickets



Normal spine



Osteoporotic spine

Lateral (side) view
of the skull and spine

Thacher (2006) *Ann. Trop. Paediatrics* 26, 1-16
White & Broadley (2009) *New Phytol.* 182, 49-84

Ecological Implications - Serpentine Flora

name is derived from the mineral serpentine
 $((\text{Mg,Fe})_3\text{Si}_2\text{O}_5(\text{OH})_4)$

high Mg and Fe; low Ca
high Ni, Cr and Co; low organic matter; little water; low N, P and K



Edmonstons Chickweed - *Cerastium nigrescens* (Caryophyllaceae).
World distribution restricted to the serpentine debris on Unst

Proctor J (1999) Toxins, nutrient shortages and droughts: the serpentine challenge.
Trends in Ecology and Evolution, 14, 334-335

Growth & Survival in Solutions With Large Mg/Ca Quotients



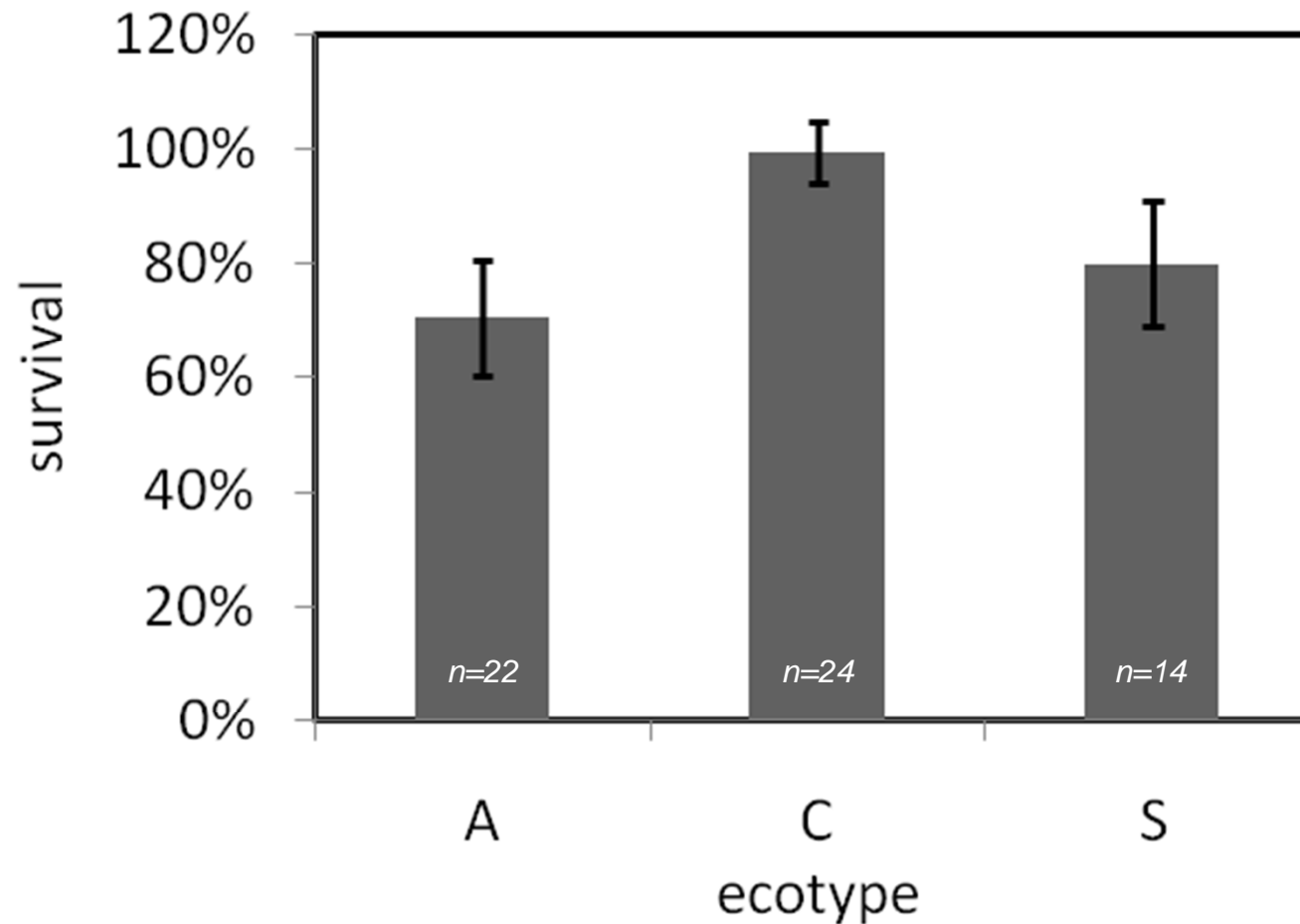
65 plant species:
26 Caryophyllales
16 serpentine flora
23 other angiosperms

2 treatments:
0.75 & 10 mM Mg

measured:
survival & shoot biomass
 $[Mg]_{\text{shoot}}$, $[Ca]_{\text{shoot}}$

White, Shaw, Thompson & Wright, unpublished data

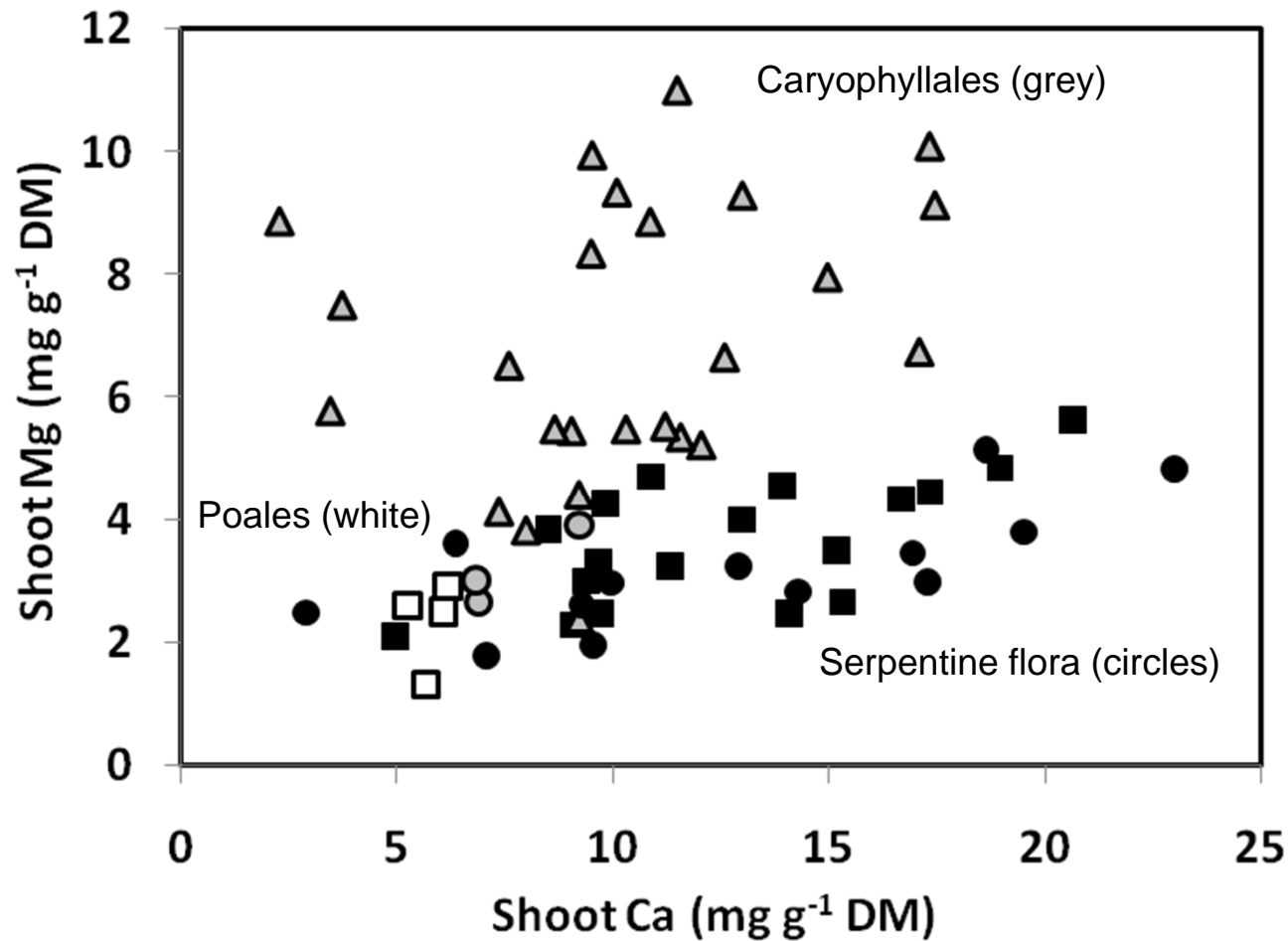
Growth & Survival in Solutions With Large Mg : Ca Ratios



White, Shaw, Thompson & Wright, unpublished data

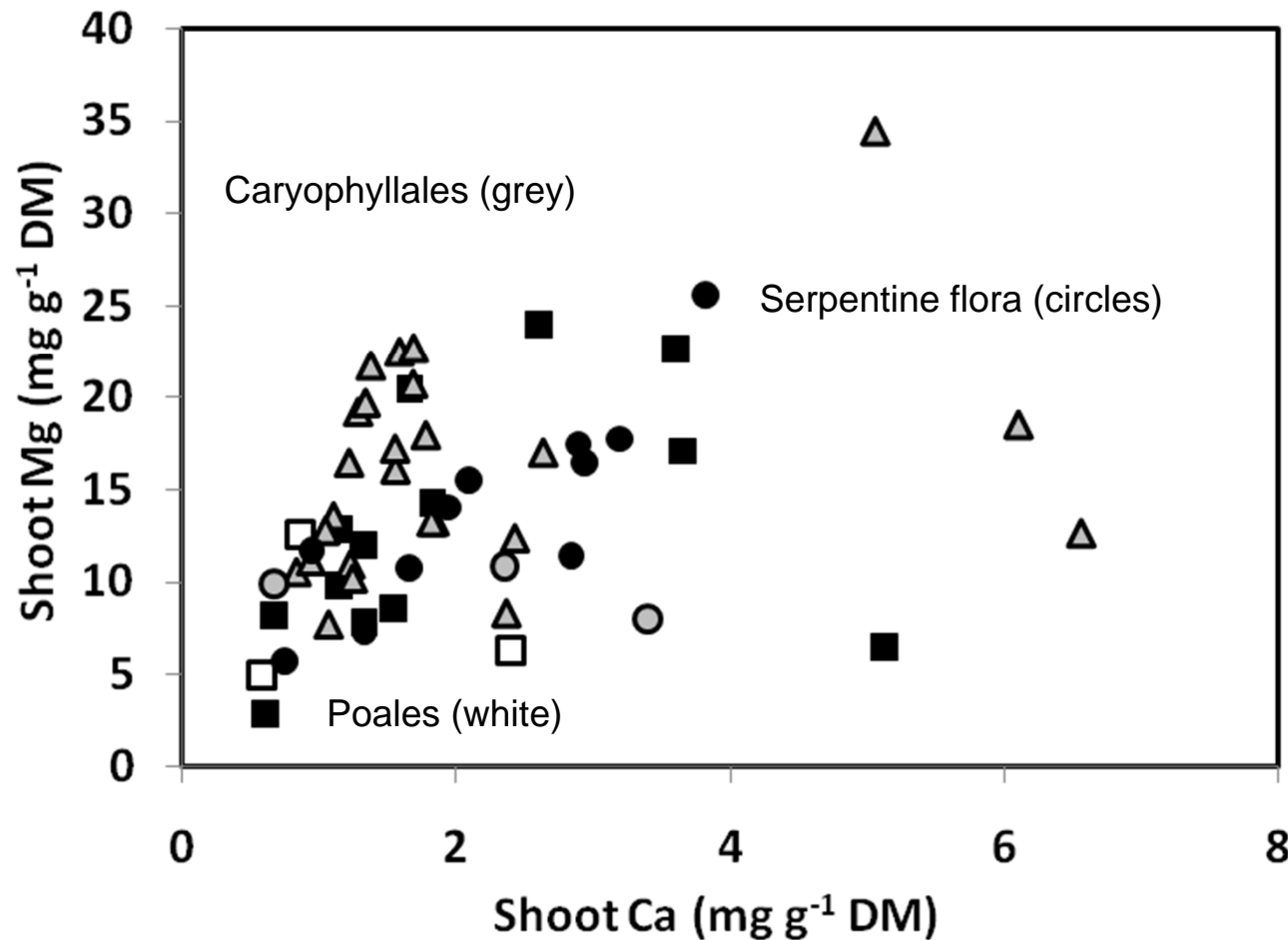
Shoot Mg : Ca Ratios

In Plants Supplied Non-Serpentine Solution



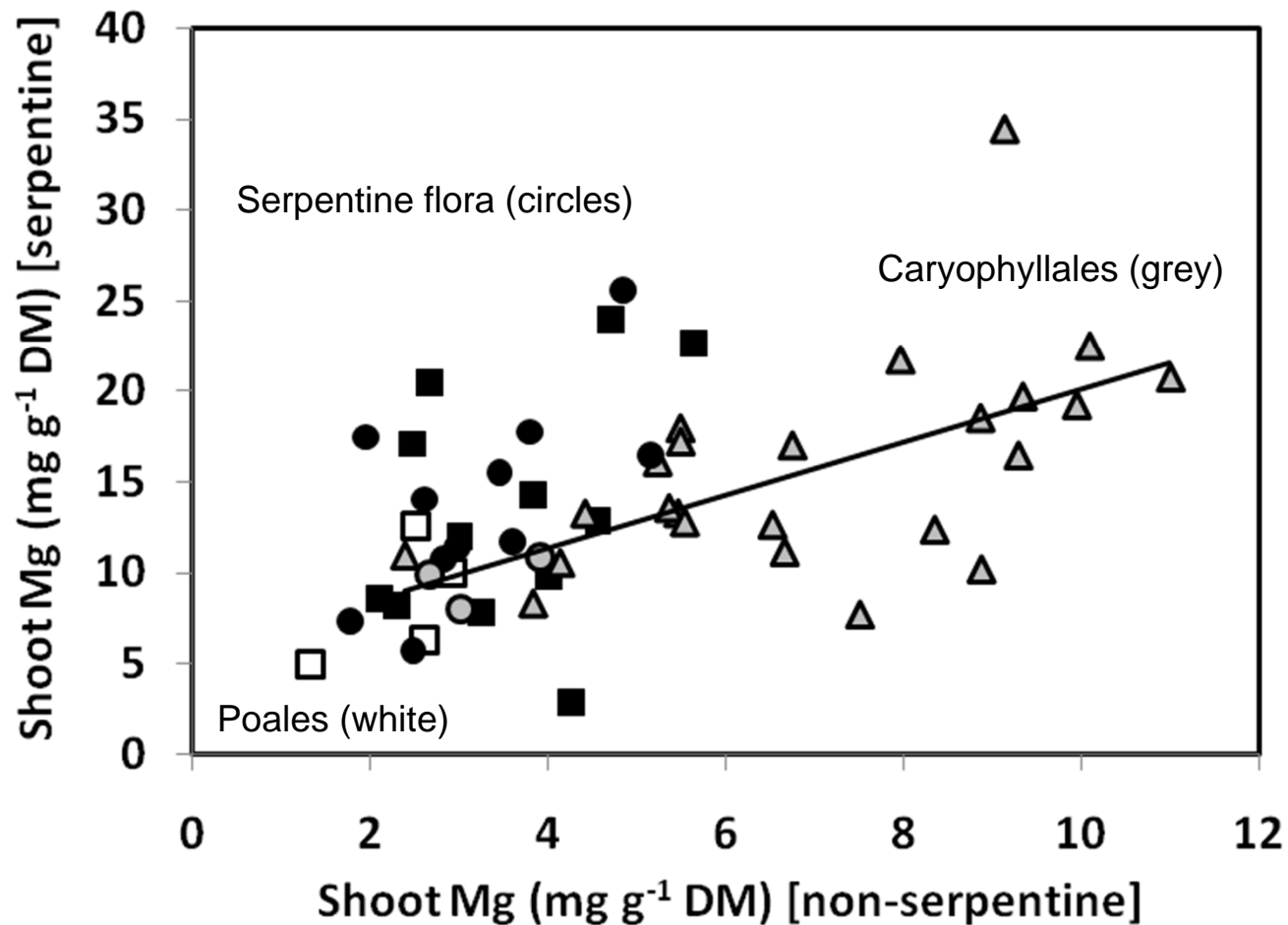
White, Shaw, Thompson & Wright, unpublished data

Shoot Mg : Ca Ratios In Plants Supplied Serpentine Solution



White, Shaw, Thompson & Wright, unpublished data

Shoot Magnesium Concentration In Plants Supplied Non-Serpentine Solution



White, Shaw, Thompson & Wright, unpublished data

Phylogenetic Effects On Shoot Magnesium Concentrations

Species differ in their shoot Mg and Ca concentrations

Differences attributed to ancient evolutionary events

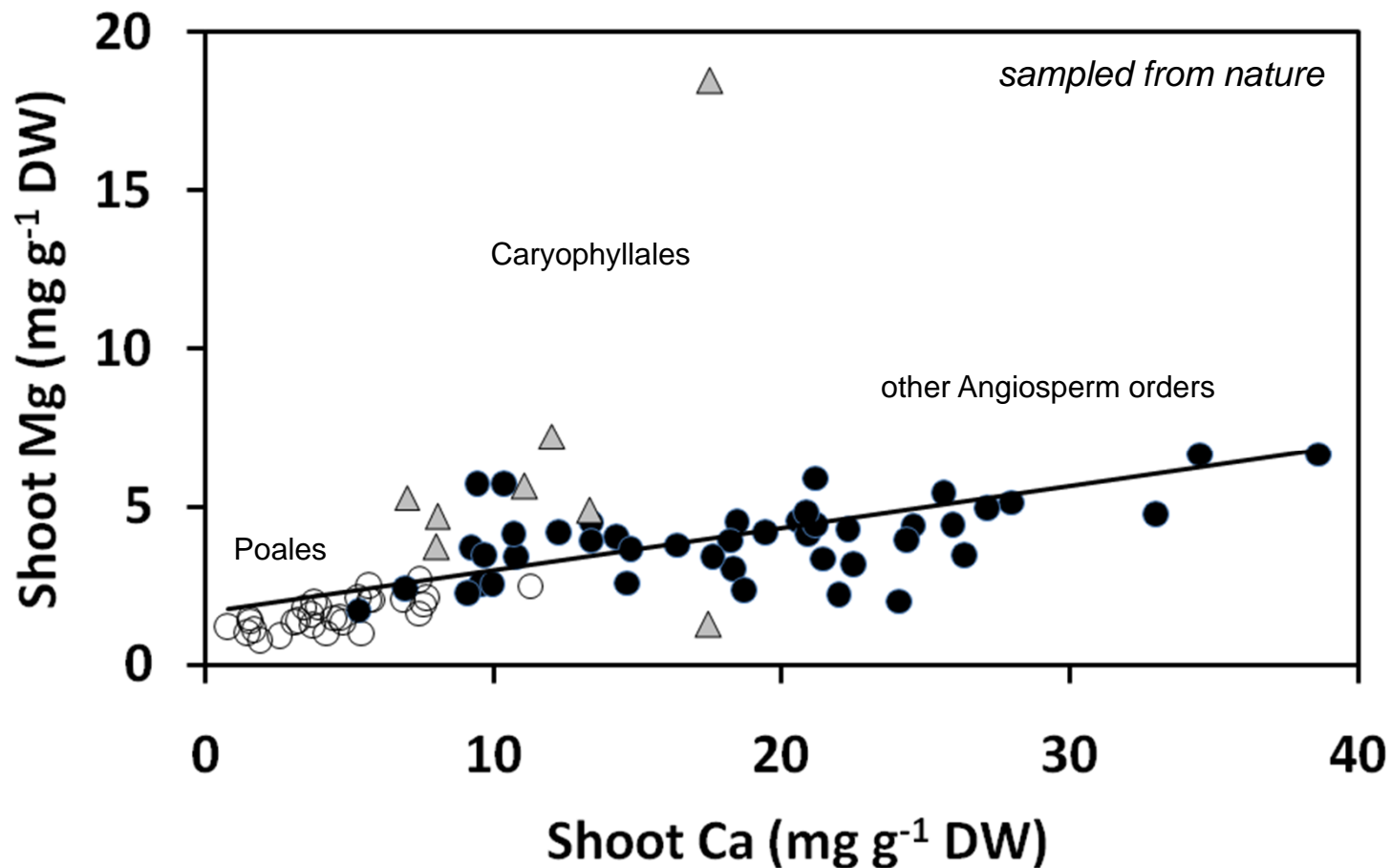
Shoot Mg and Ca concentrations are correlated
among many species

Commelinoid monocots - low shoot Mg and Ca concentrations

Caryophyllales - high Mg / Ca quotients

(Phylo)genetic variation can exceed environmental variation

Calcium : Magnesium Ratios In Plants Sampled From An Herbaceous Flora



Thompson et al. (1997) *New Phytologist* 136: 679-689