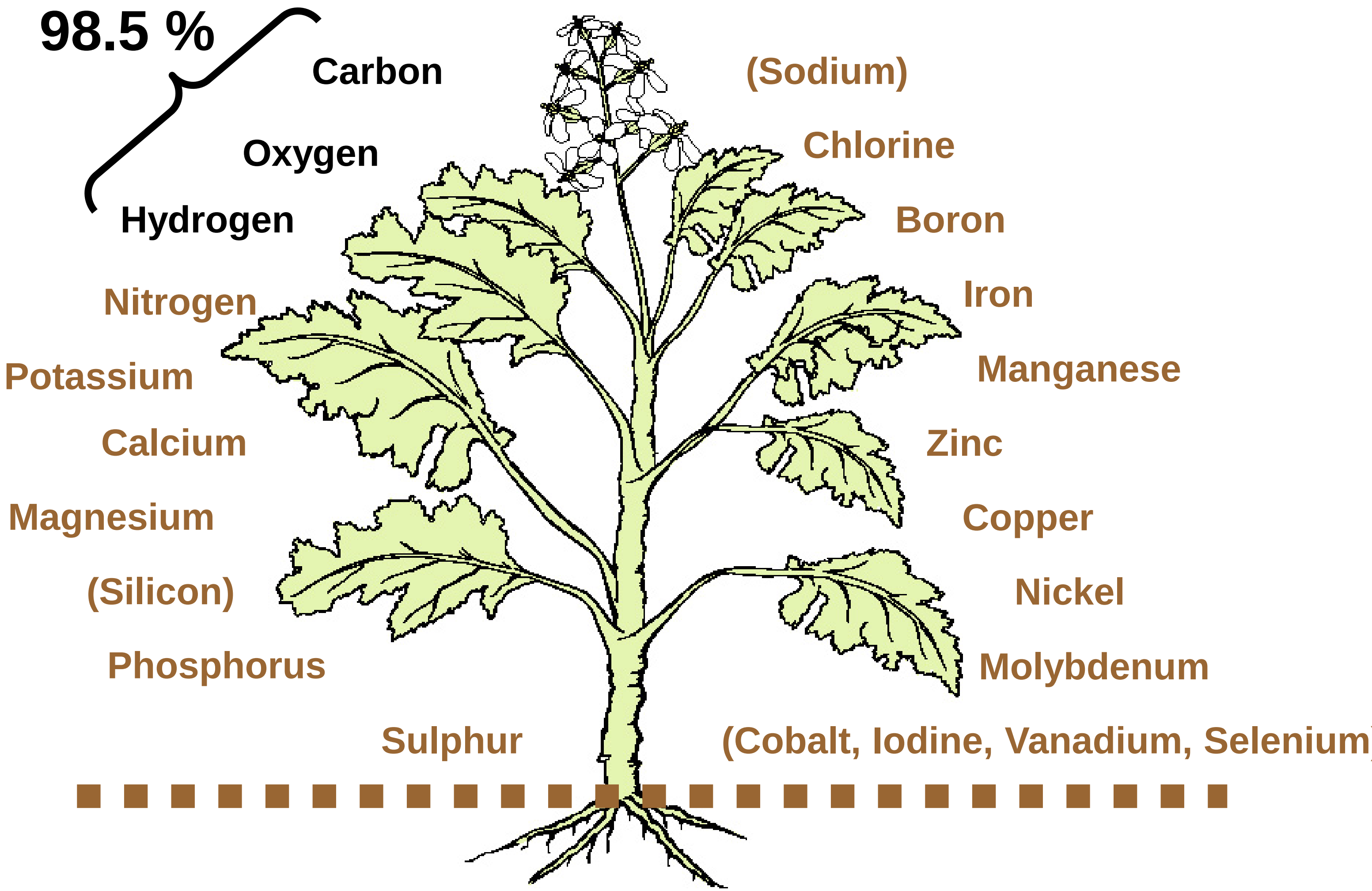
Effects of Genotype and Environment on the Plant Ionome

Philip J. White
Martin R. Broadley

and many others

FertBio2014
18th September 2014

Ionomics is the Study of the Elemental Composition of Plants



...and every other element in the periodic table available in the environment

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

AN ORDINAL CLASSIFICATION FOR THE FAMILIES OF FLOWERING PLANTS

The Angiosperm Phy

Abstract

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

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

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

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), Bromeliacae, 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 eurosids I), Bonnetiaceae, Ctenolophonaceae, Elatinaceae, Ixonanthaceae, Lophopyxidaceae, Podostemaceae (Malpighiales), Paracryphiaceae (unplaced in euasterid II), Sladeniaceae, Pentaphylacaceae (Ericales) and Cardiopteridaceae (Aquifoliales). Several major families are recircumscribed. 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 recircumscribed 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 Ruscaceae (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.

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

: compiled by Birgitta Bremer, Kåre Bremer,
las E. Soltis, Pamela S. Soltis and Peter F.
ı alphabetical order only, with contributions
Olmstead, Paula J. Rudall, Kenneth J.
Xiang and Sue Zmarzty (in alphabetical
ıt the Royal Swedish Academy of Sciences, PO
Vice Chancellor, Stockholm University, SE-106
Laboratory, Royal Botanic Gardens, Kew,
ıiley Hortorium, Department of Plant Biology,
'53-4301, USA; D. E. Soltis, Department of
11–8525, USA; P. S. Soltis, Florida Museum of
rida, 32611–7800, USA; and P. F. Stevens,
and Missouri Botanical Garden, PO Box 299,

2009

ering plants is provided. Many recent studies have
ırmerly unplaced families, resulting in a number of
les, Bruniales, Buxales, Chloranthales, Escalloniales,
ramniales, Trochodendrales, Vitales and Zygophylla-
included here in orders, greatly reducing the number
ıaeales), Haptanthaceae (Buxales), Peridiscaceae
ıfflesiaceae (both Malpighiales), Aphloiaceae, Geisso-
Picramniaceae (Picramniales), Dipentodontaceae
s), Balanophoraceae (Santalales), Mitrastemonaceae
ıember of lamiid clade). Newly segregated families
gnized families include Petermanniaceae (Liliales),
eae (both Brassicales), Schoepfiaceae (Santalales),
ıe and Talinaceae (all Caryophyllales) and Linder-
ıketed families is abandoned because of its unpopu-
tained; these include Amaryllidaceae, Asparagaceace
pighiales), Primulaceae (Ericales) and several other
with a new linear order for APG, subfamilial names
lidaceae *s.l.*, Asparagaceace *s.l.* and Xanthorrheaceae
s.l. (all Asparagales) and a formal supraordinal classification for the flowering plants. © 2009 The Linnean Society
iety, 2009, **161**, 105–121.

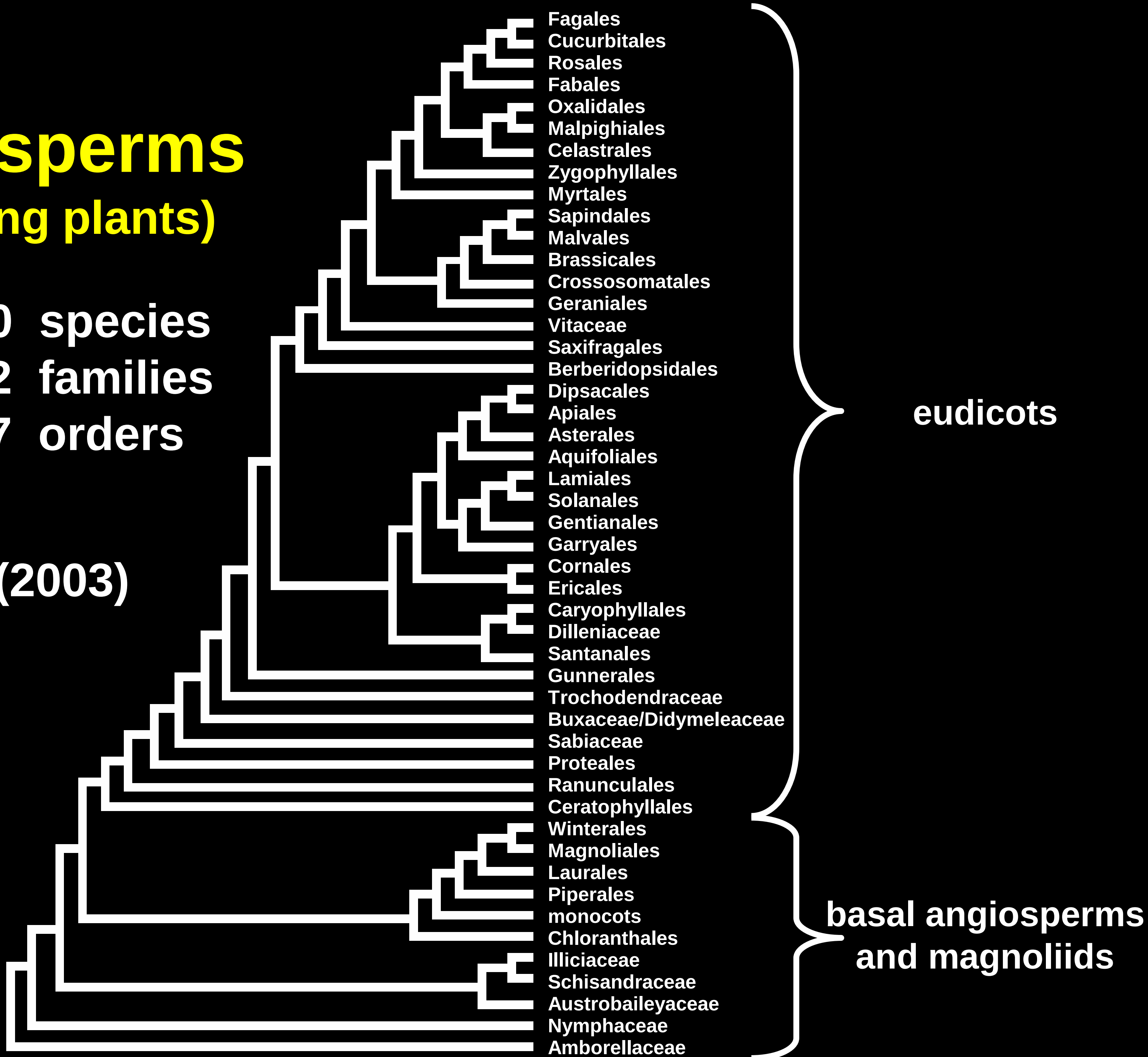
sification – phylogenetic classification – DNA phylogenetics –

The Angiosperm Phylogeny Group (1998, 2003, 2009)

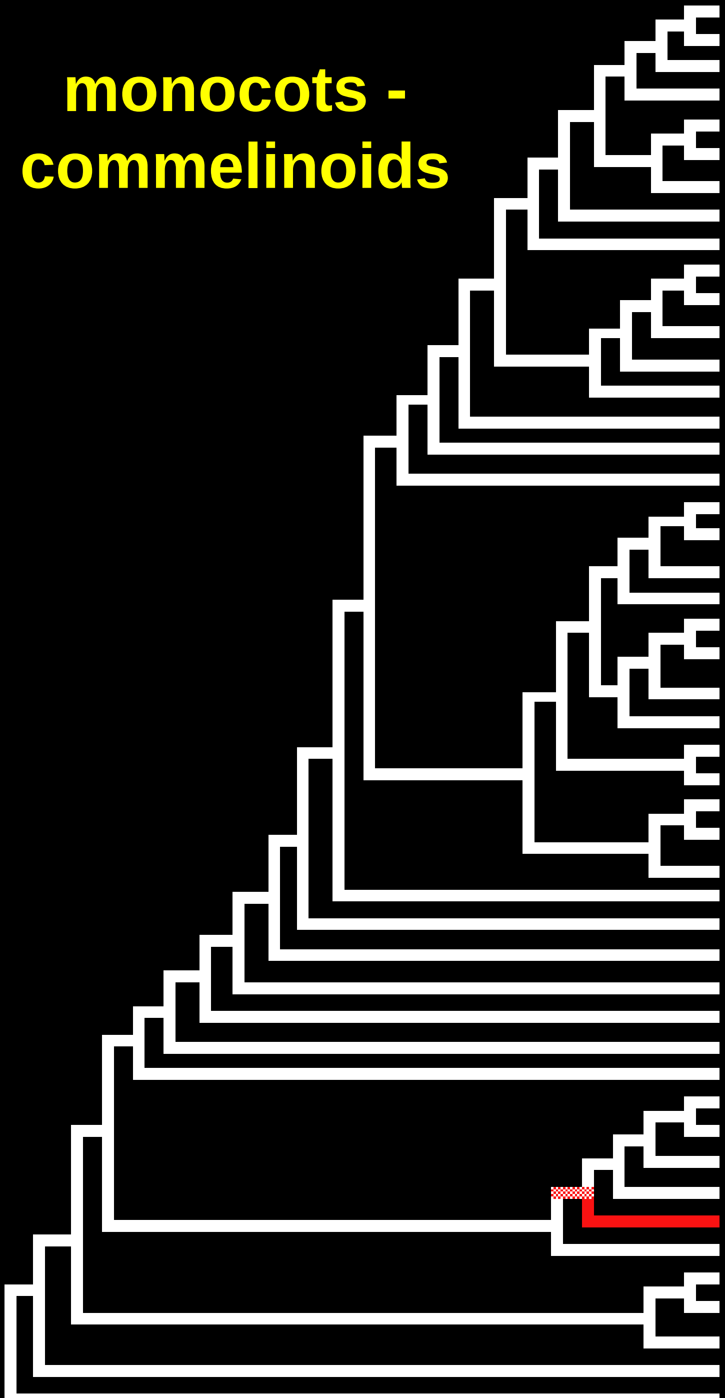
Angiosperms
(flowering plants)

250,000 species
462 families
47 orders

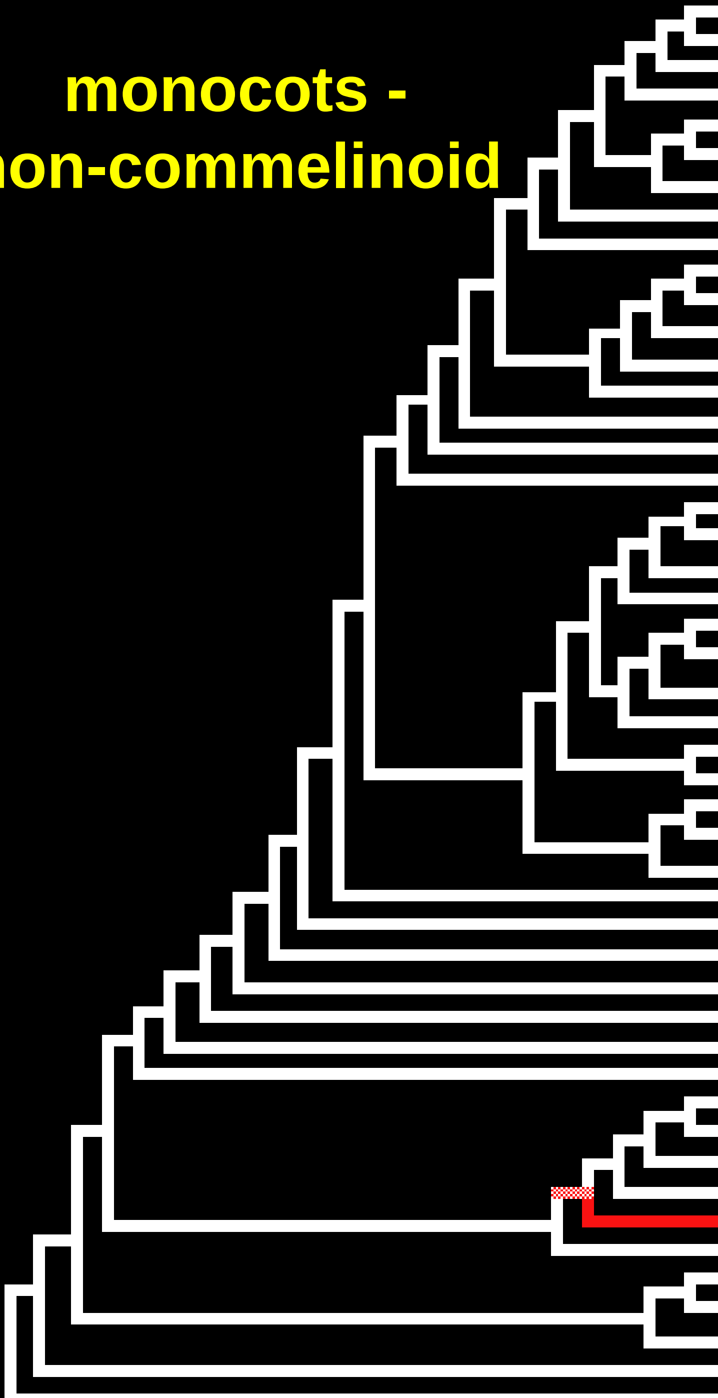
APG II (2003)



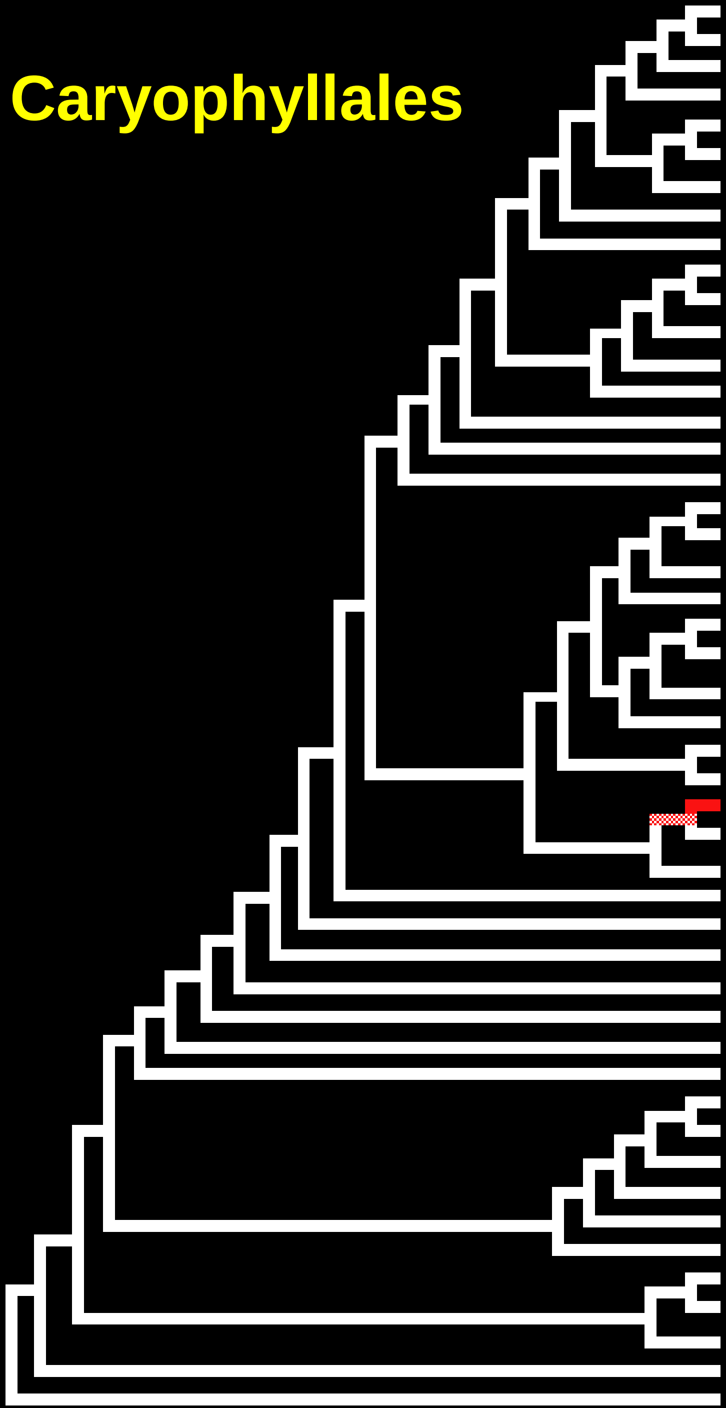
monocots - commelinoids



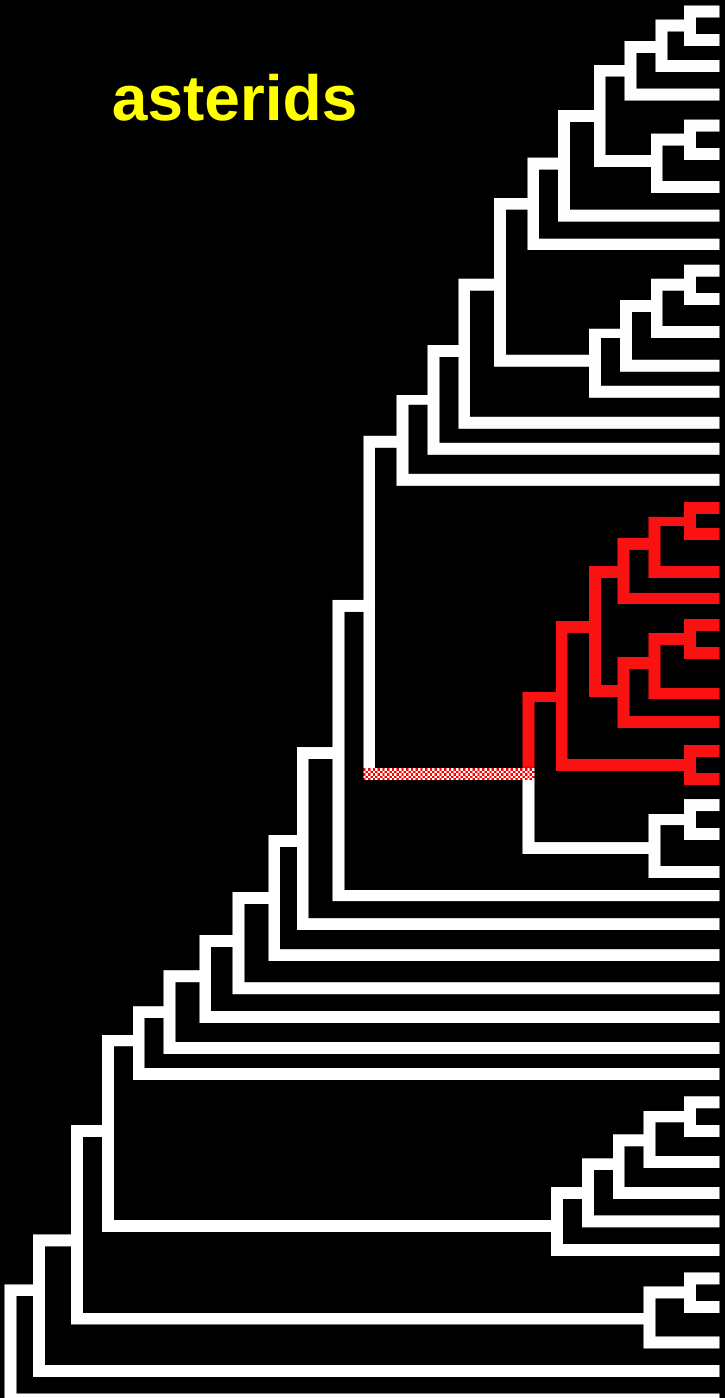
monocots -
non-commelinoid



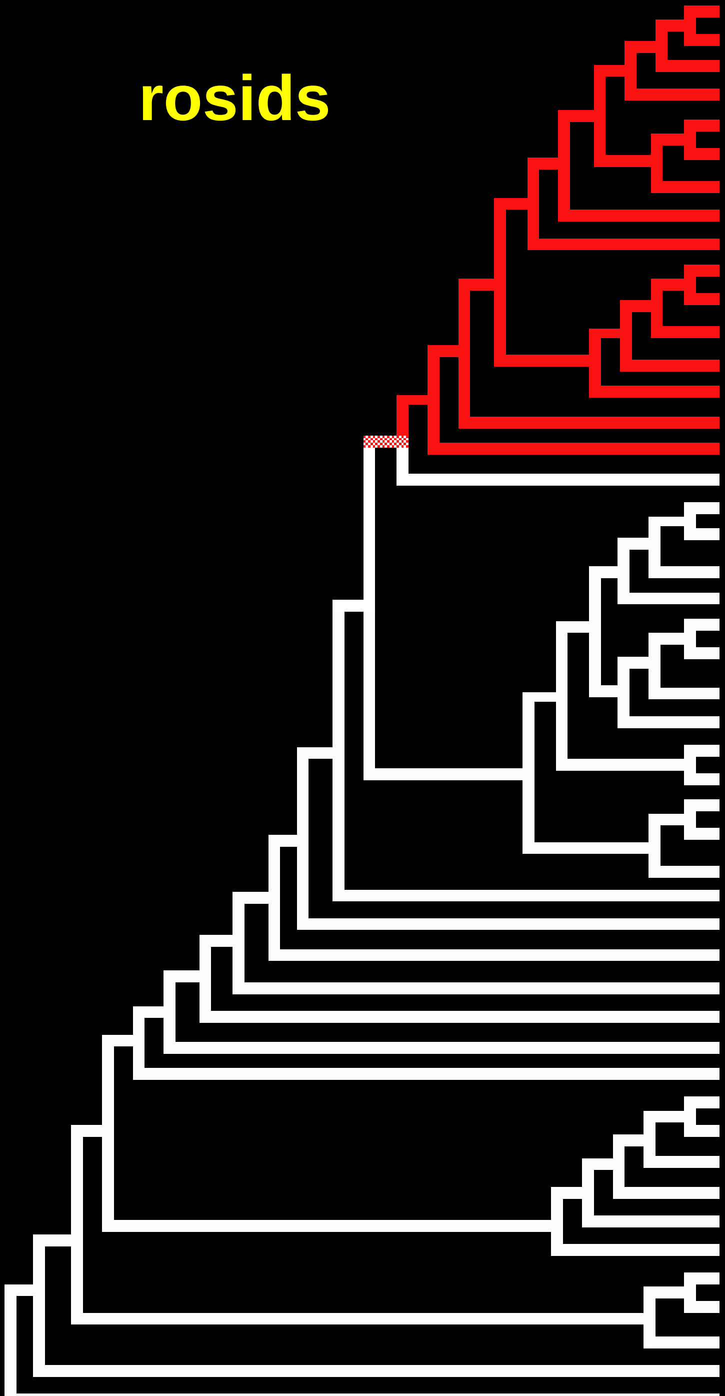
Caryophyllales



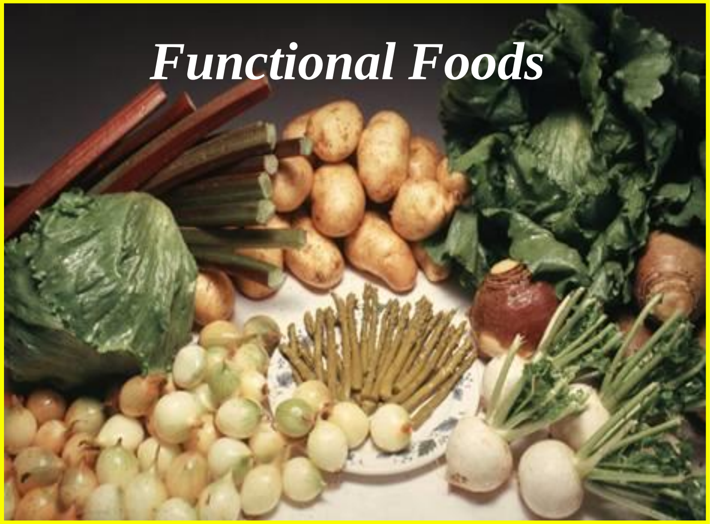
asterids

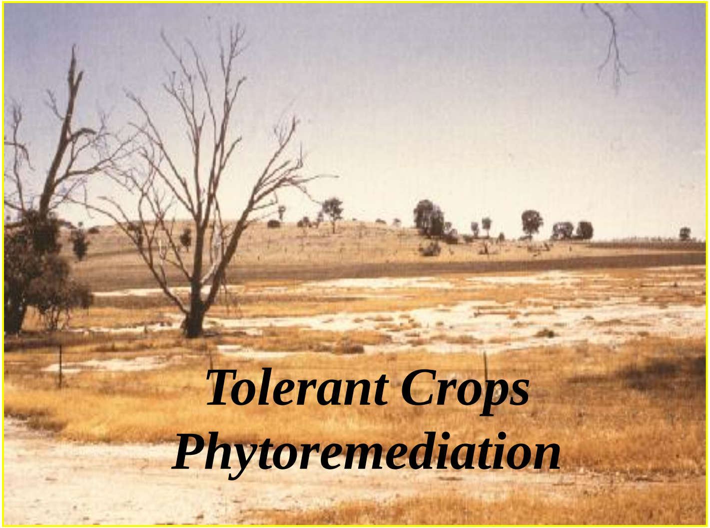


rosids



Plant Species Differ in Their Ionome





Evolution of the Angiosperm Ionome
Selected Examples

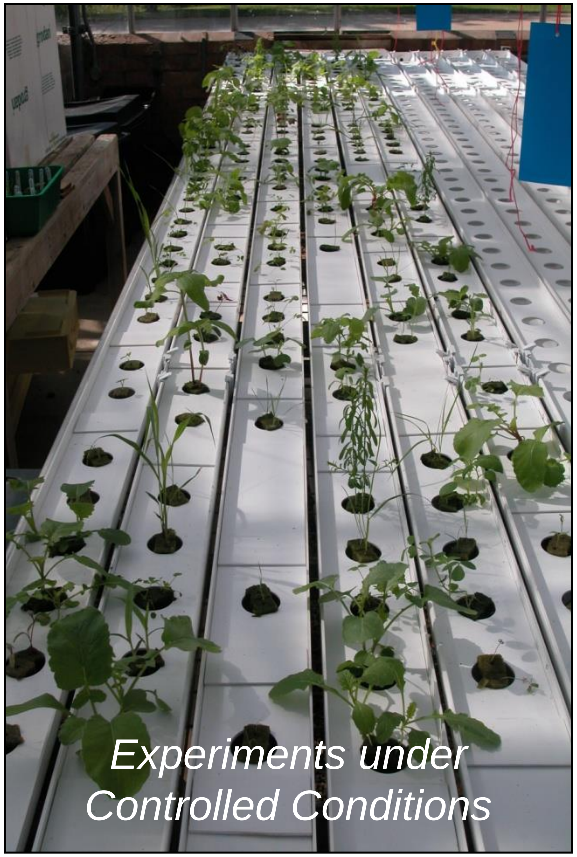
(1) Calcium, Strontium & Magnesium

(2) Silicon

(3) Sodium (in nonsaline environments)

(4) Rothamsted Park Grass Experiment

Evolution of the Angiosperm Ionome
Data Sources



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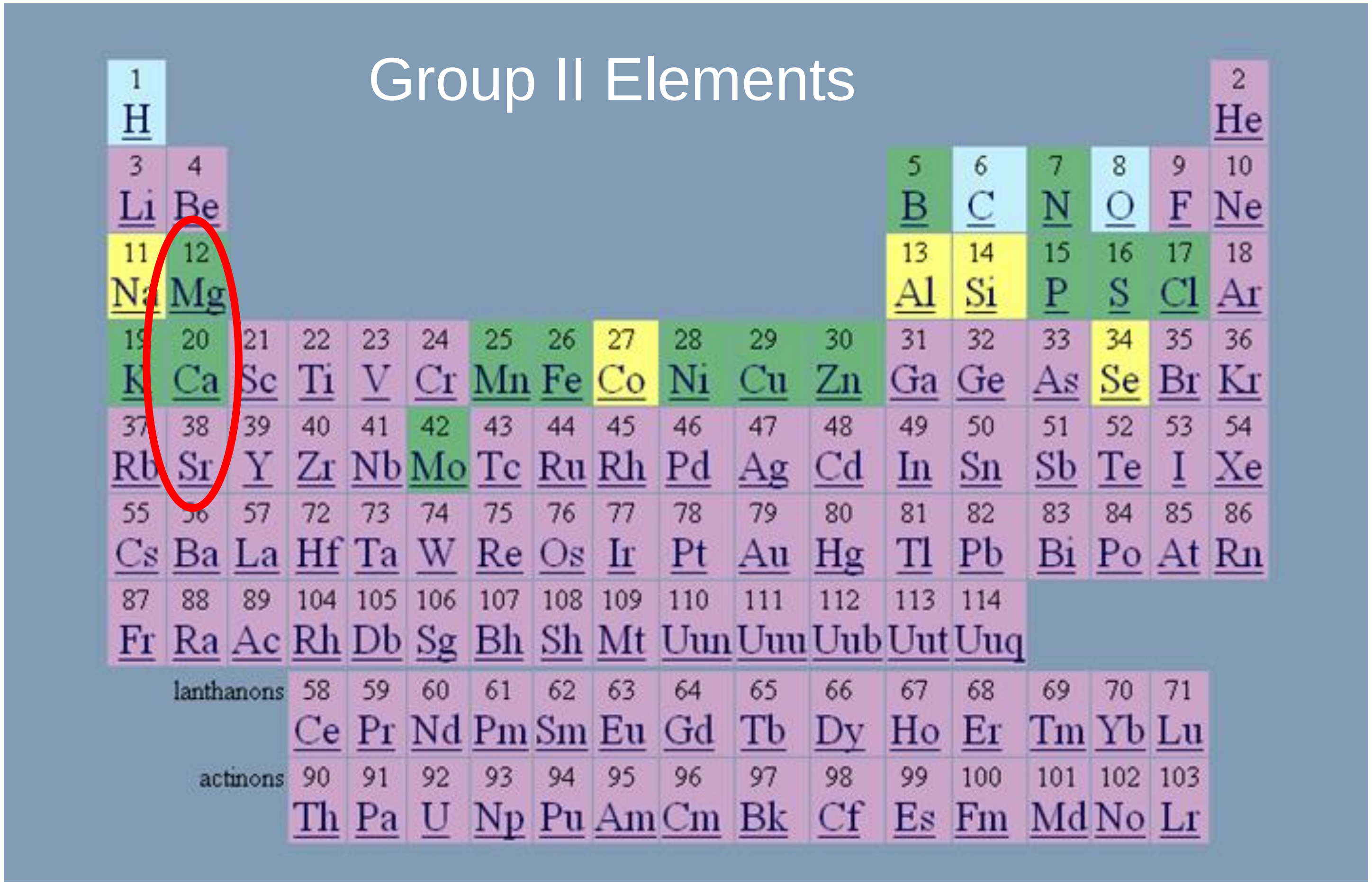
A Botanical Journey Through The Periodic Table



Broadley et al. (2003) J. Exp. Bot. 54, 1431-1446
Broadley et al. (2004) J. Exp. Bot. 55, 321-336

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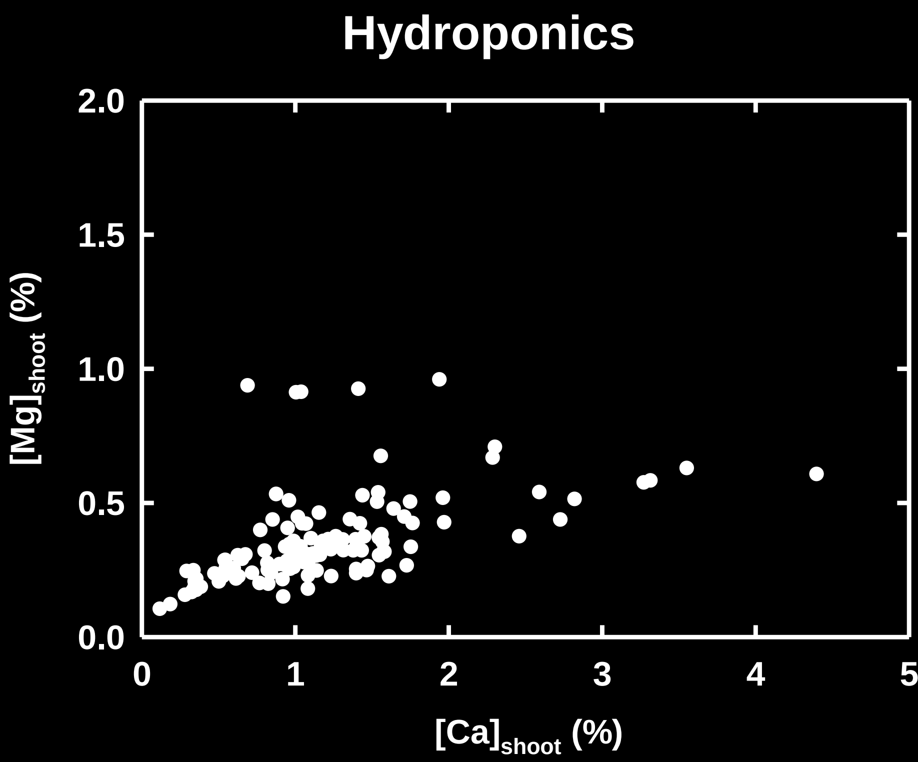
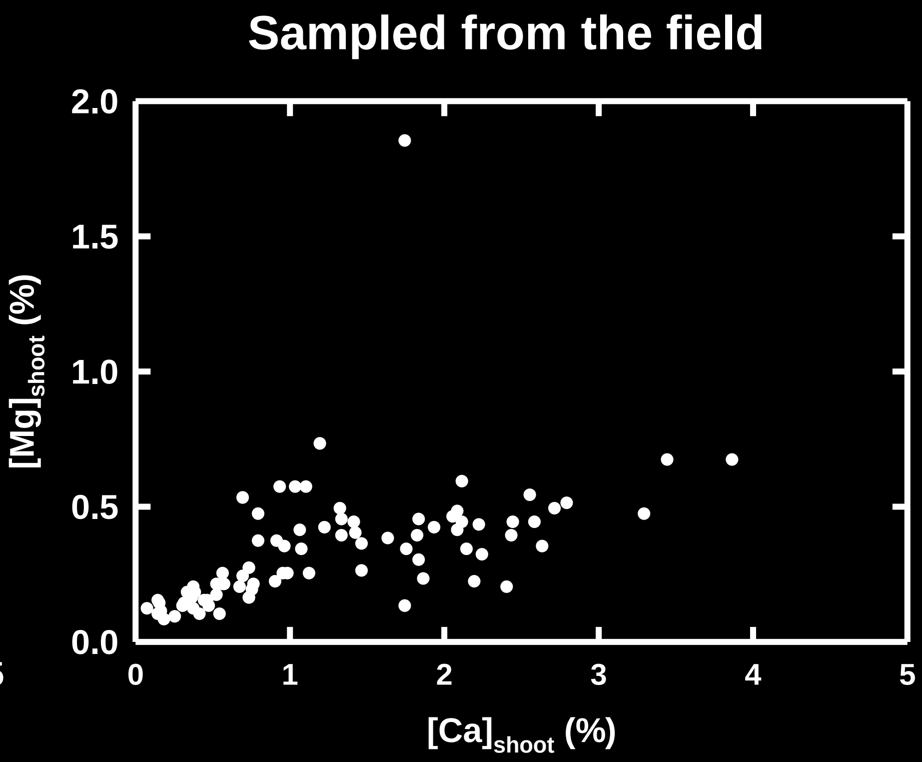
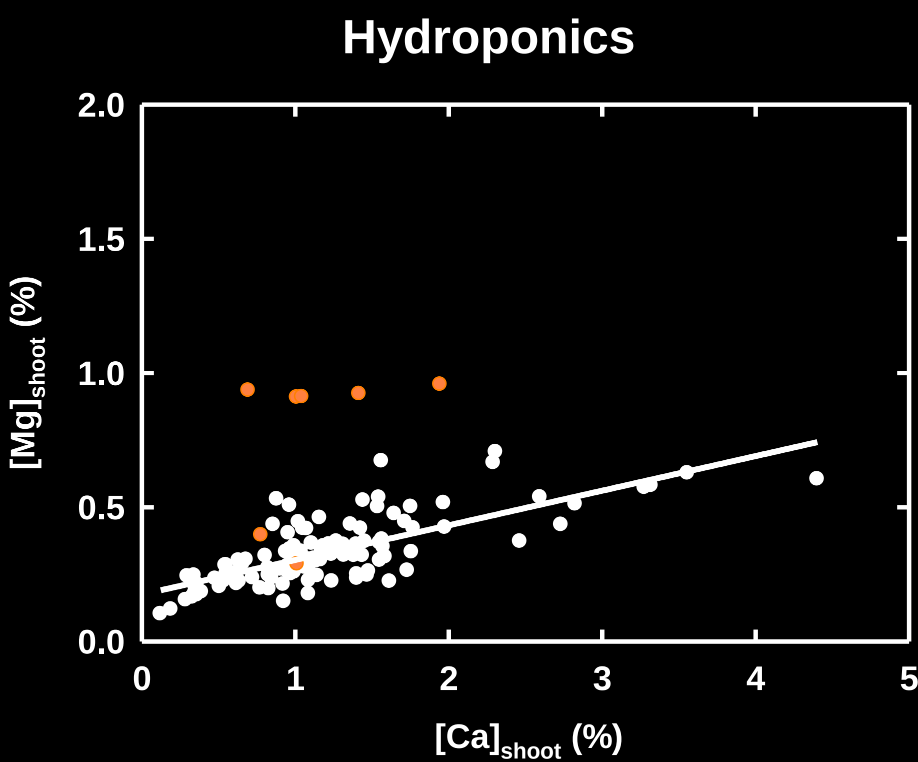
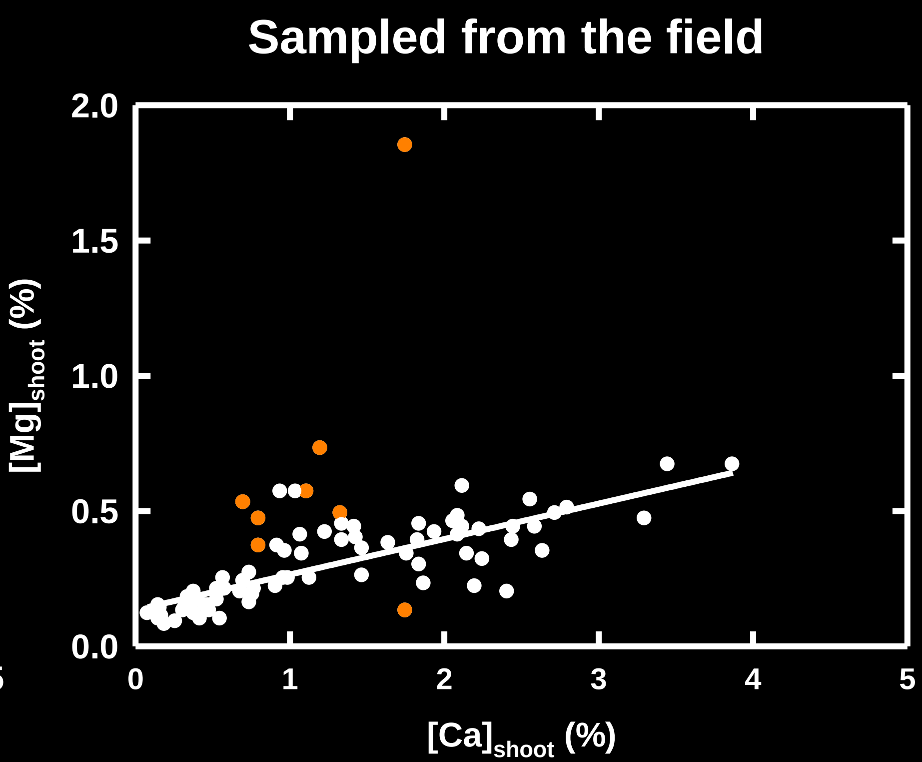
Magnesium : Calcium Ratios in Shoot Tissues





Magnesium : Calcium Ratios in Shoot Tissues



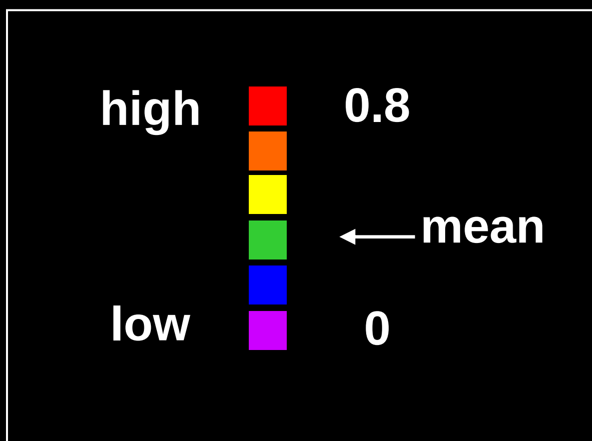


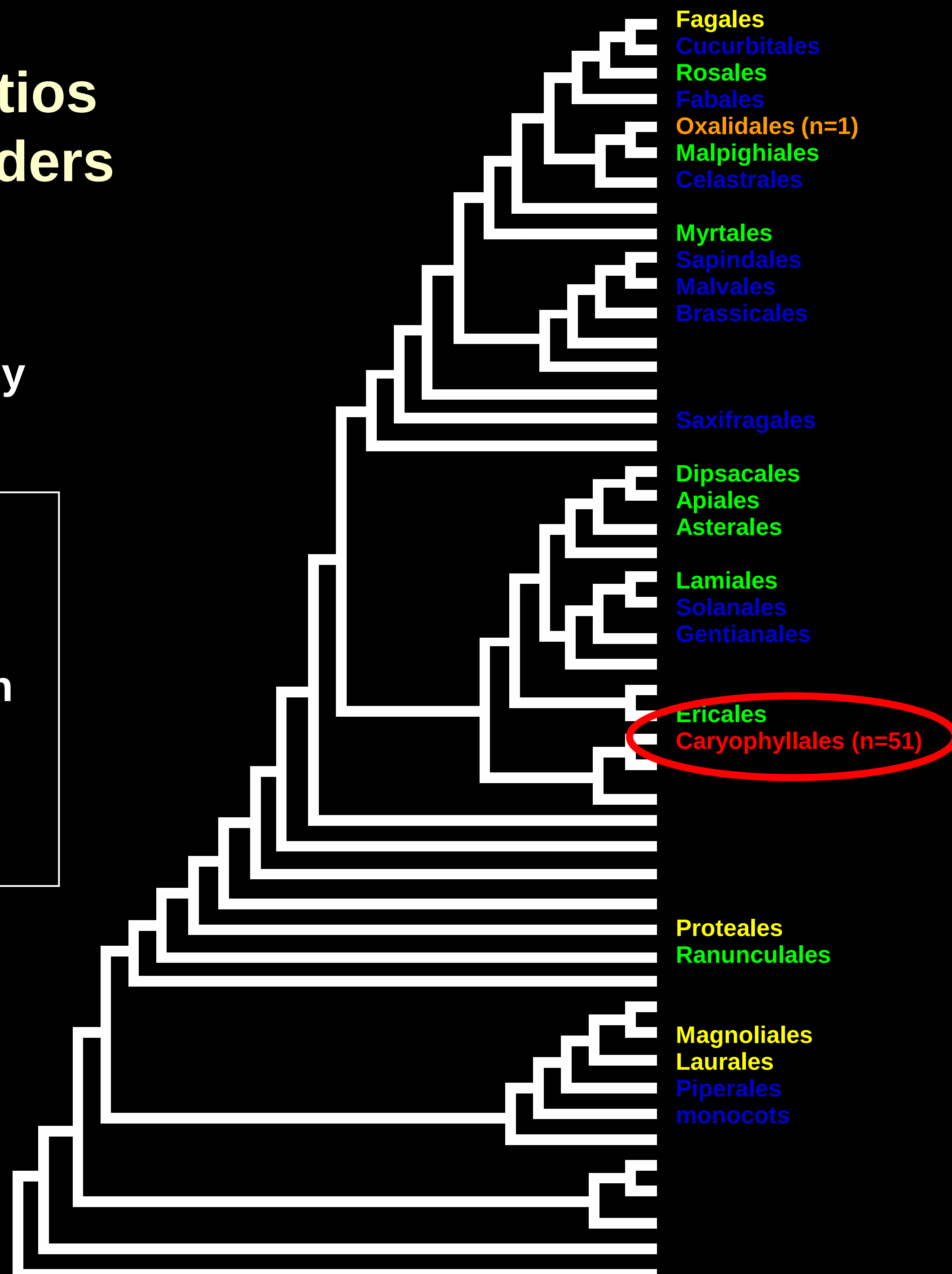
- All other taxa
- Caryophyllales (e.g. sugar beet, carnation)

Shoot Mg / Ca Ratios of Angiosperm Orders

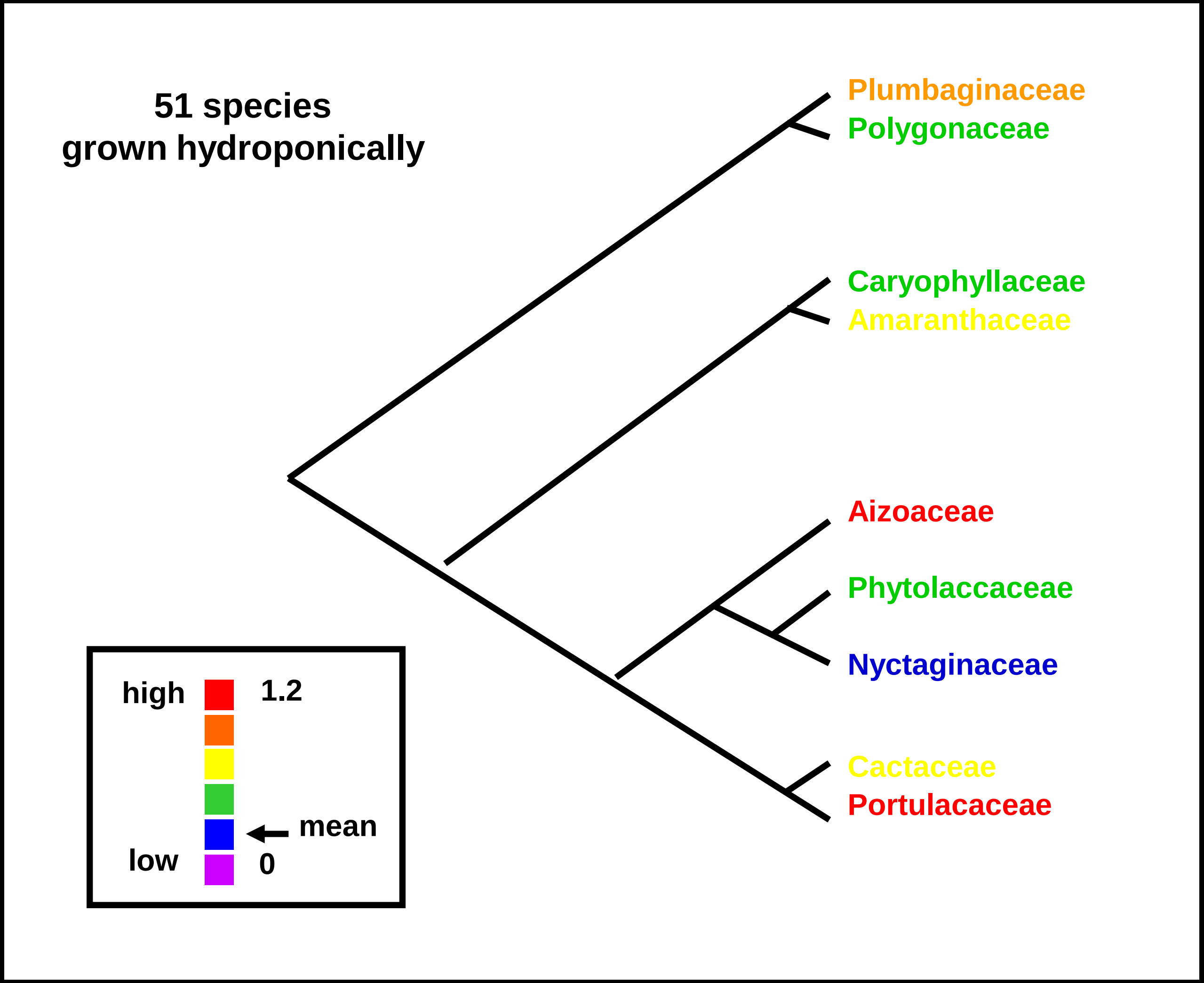
> 200 species

grown hydroponically





Shoot Mg / Ca Ratios in the Caryophyllales



Ecological Implications - Serpentine Flora

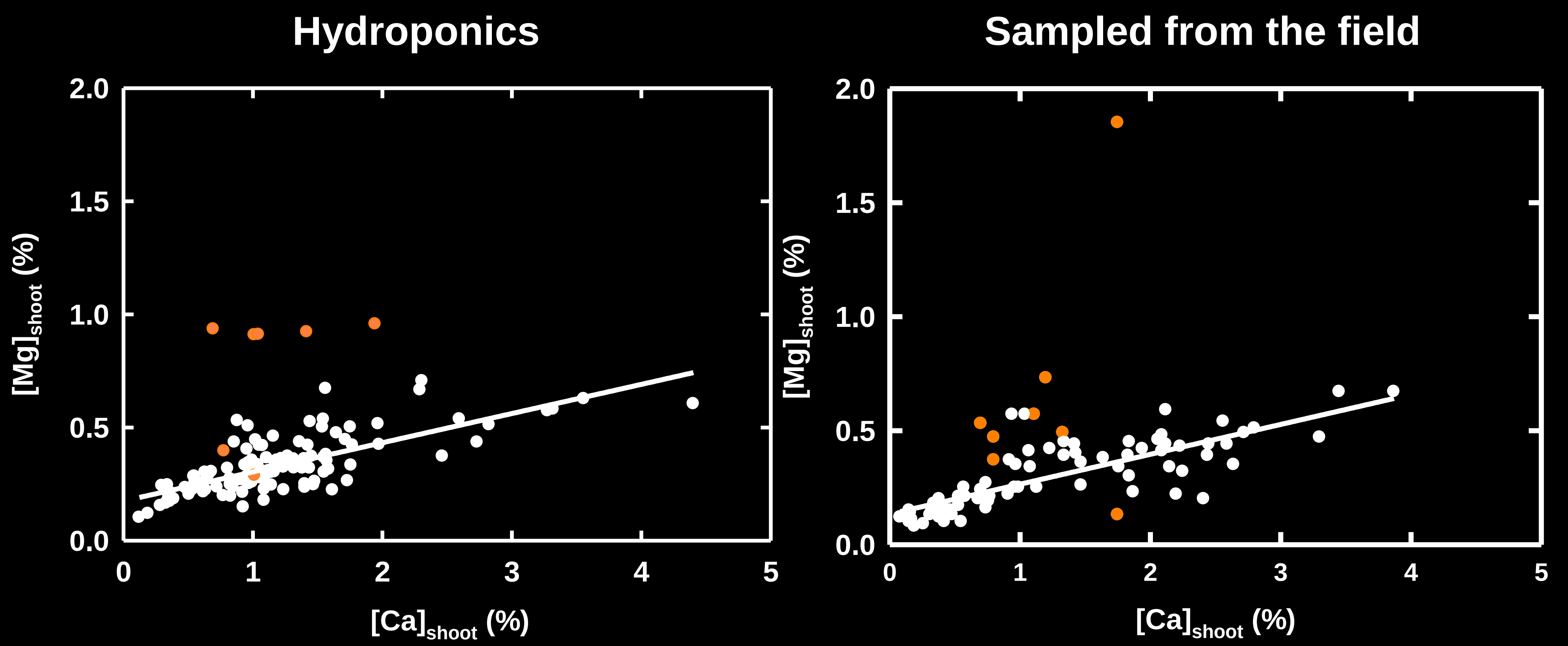
name is derived from the mineral serpentine
($(Mg,Fe)_3Si_2O_5(OH)_4$)

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

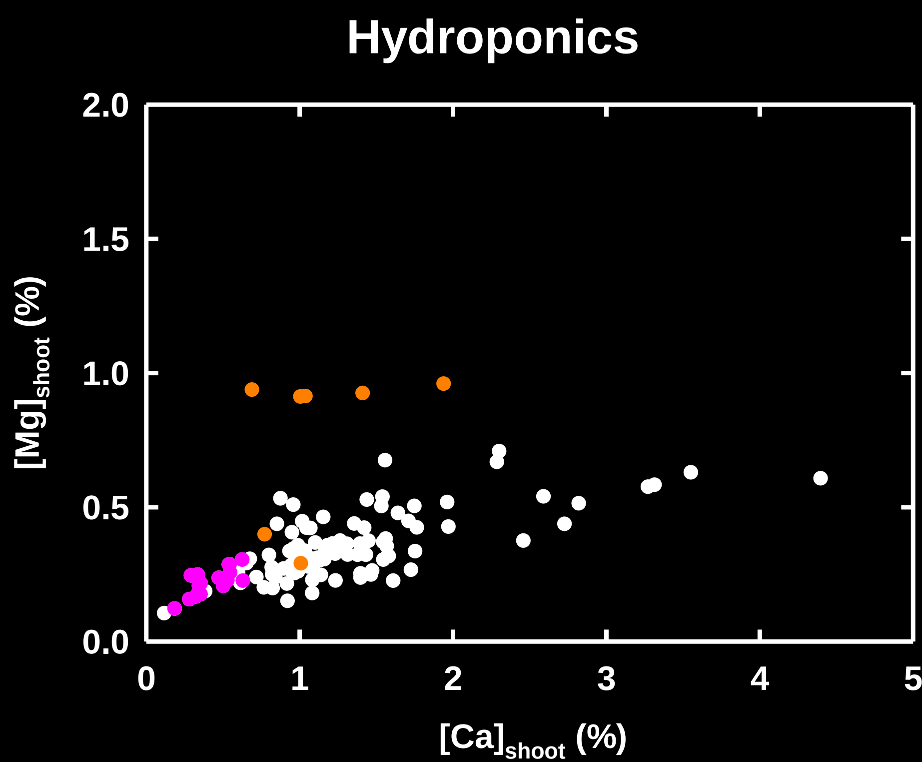
Proctor J (1999) Toxins, nutrient shortages and droughts: the serpentine challenge.
***Trends in Ecology and Evolution*, 14, 334-335**

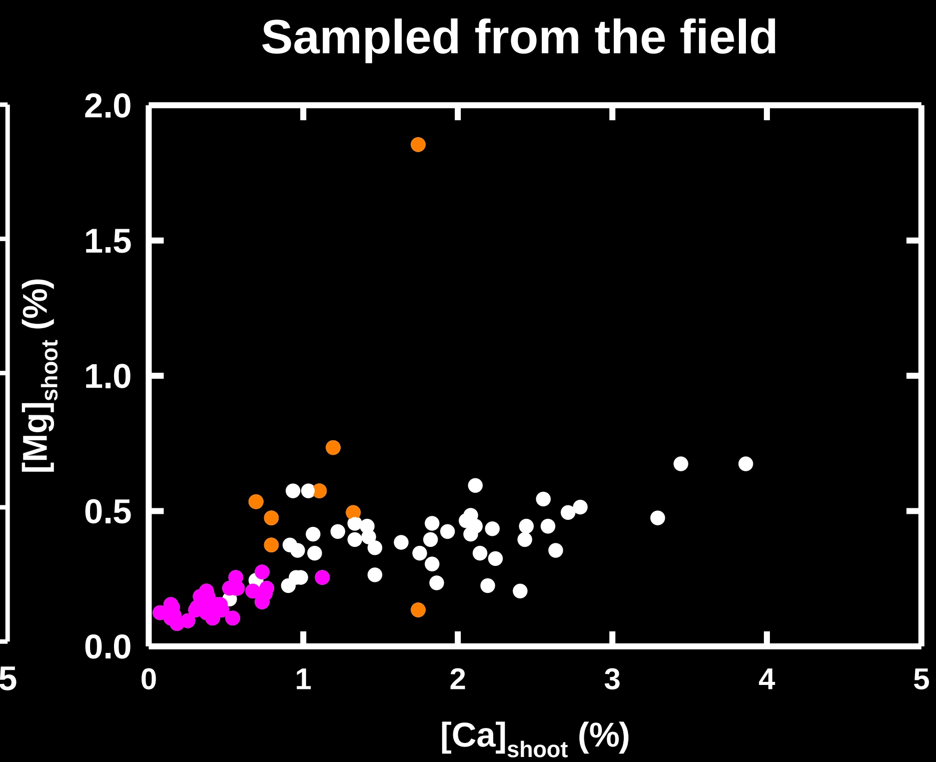
Magnesium : Calcium Ratios in Shoot Tissues



- All other taxa
- Caryophyllales (e.g. sugar beet, carnation)

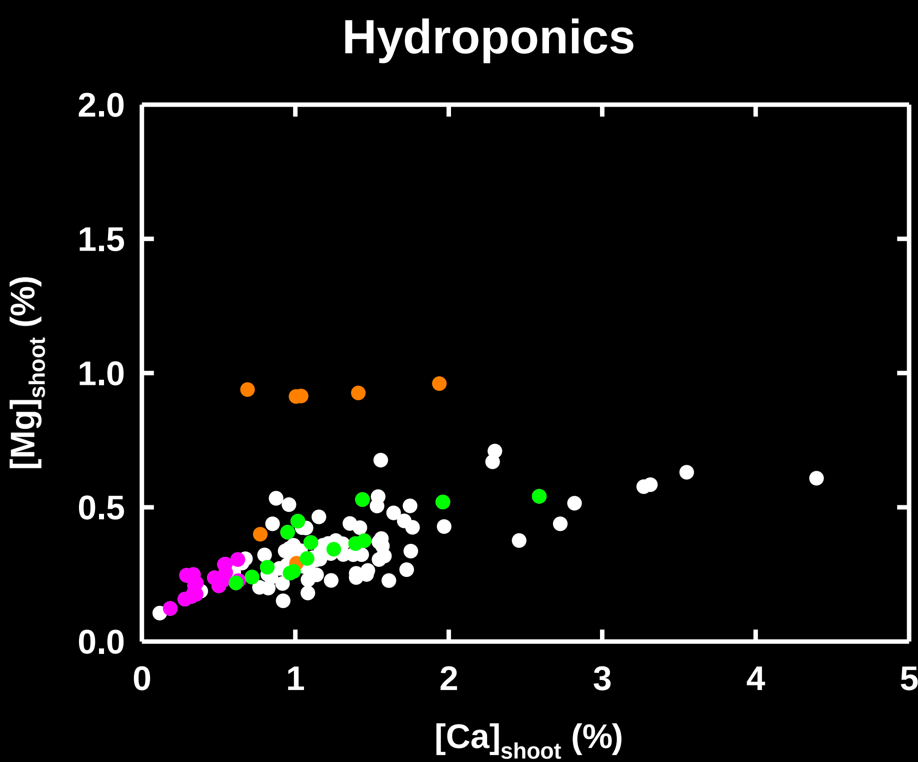
Magnesium : Calcium Ratios in Shoot Tissues

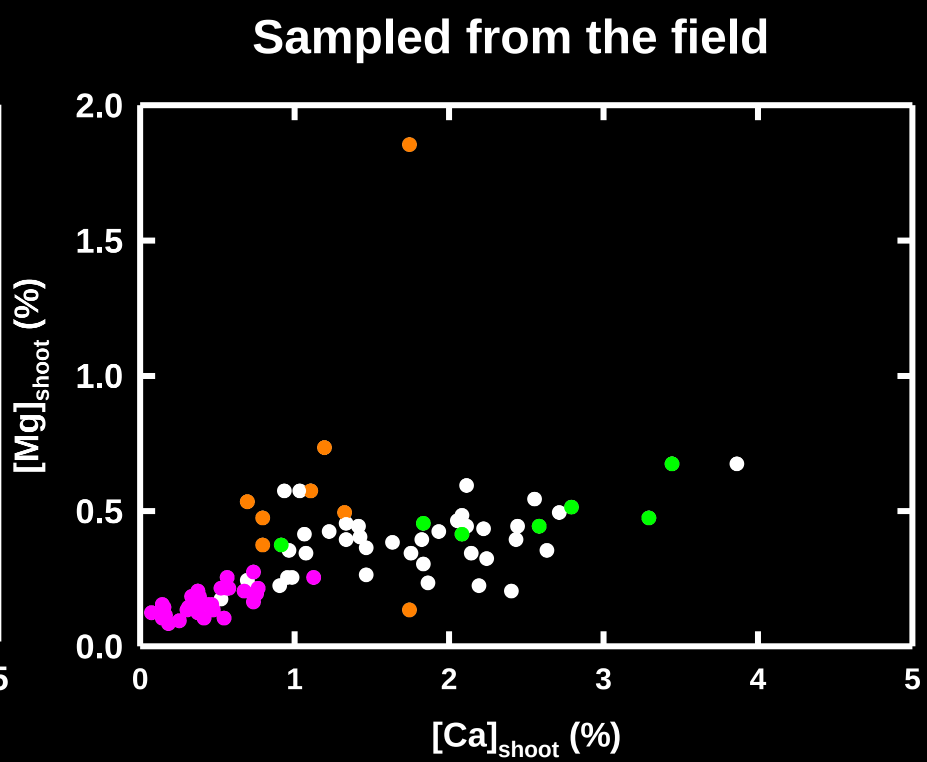




- All other taxa
- Caryophyllales (e.g. sugar beet, carnation)
- Poales (e.g. the grass / cereal family, Poaceae)

Magnesium : Calcium Ratios in Shoot Tissues

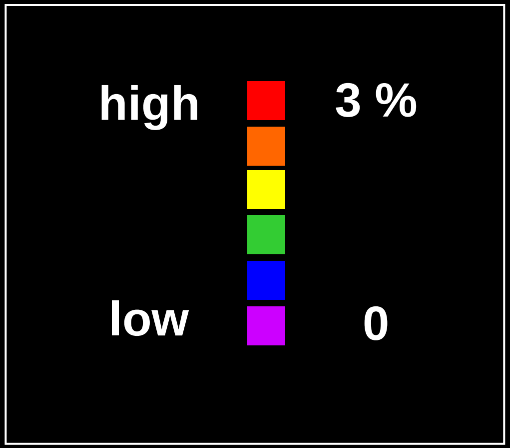


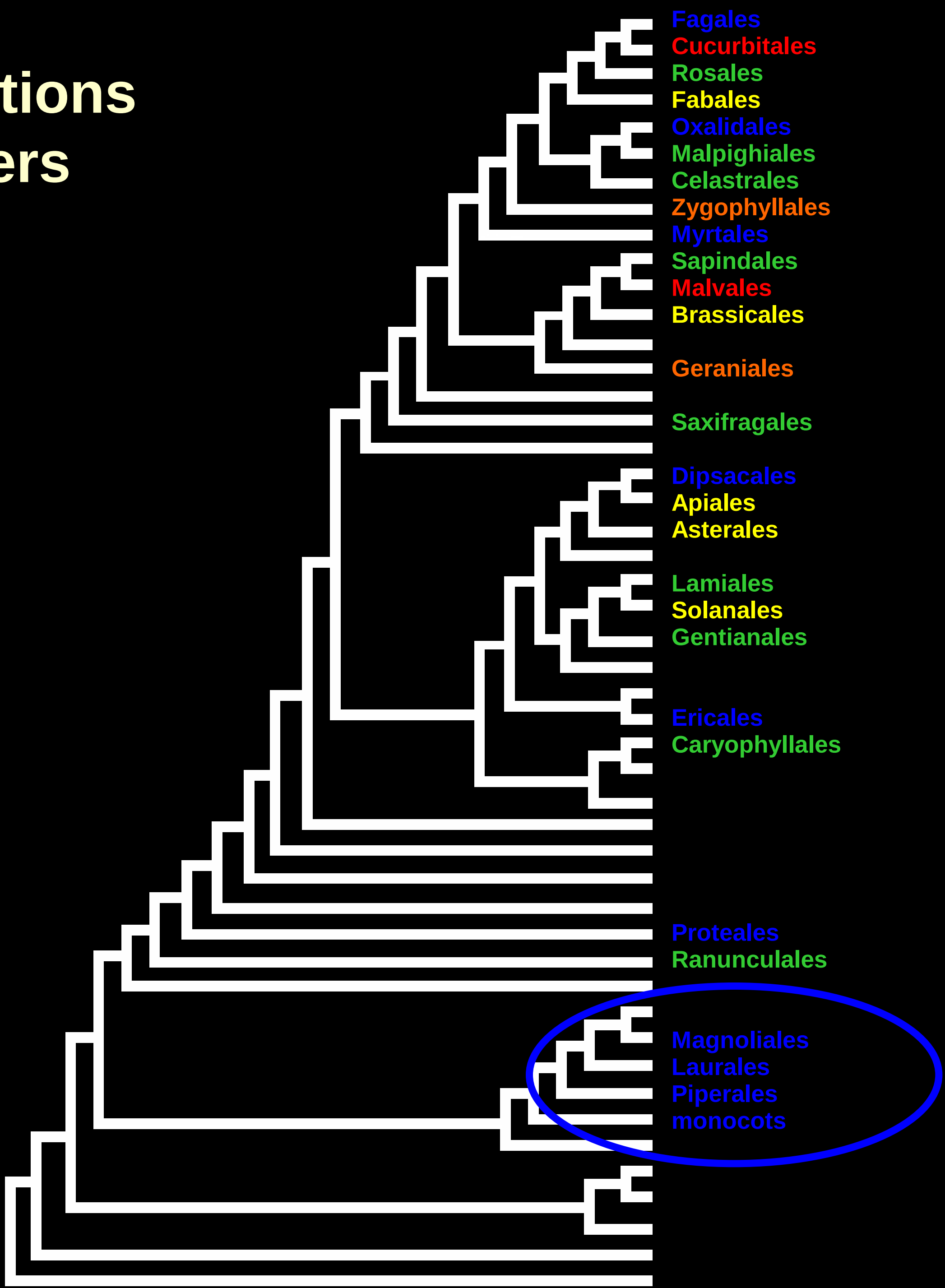


- All other taxa
- Caryophyllales (e.g. sugar beet, carnation)
- Poales (e.g. the grass / cereal family, Poaceae)
- Asterales (e.g. the daisy / sunflower family Asteraceae)

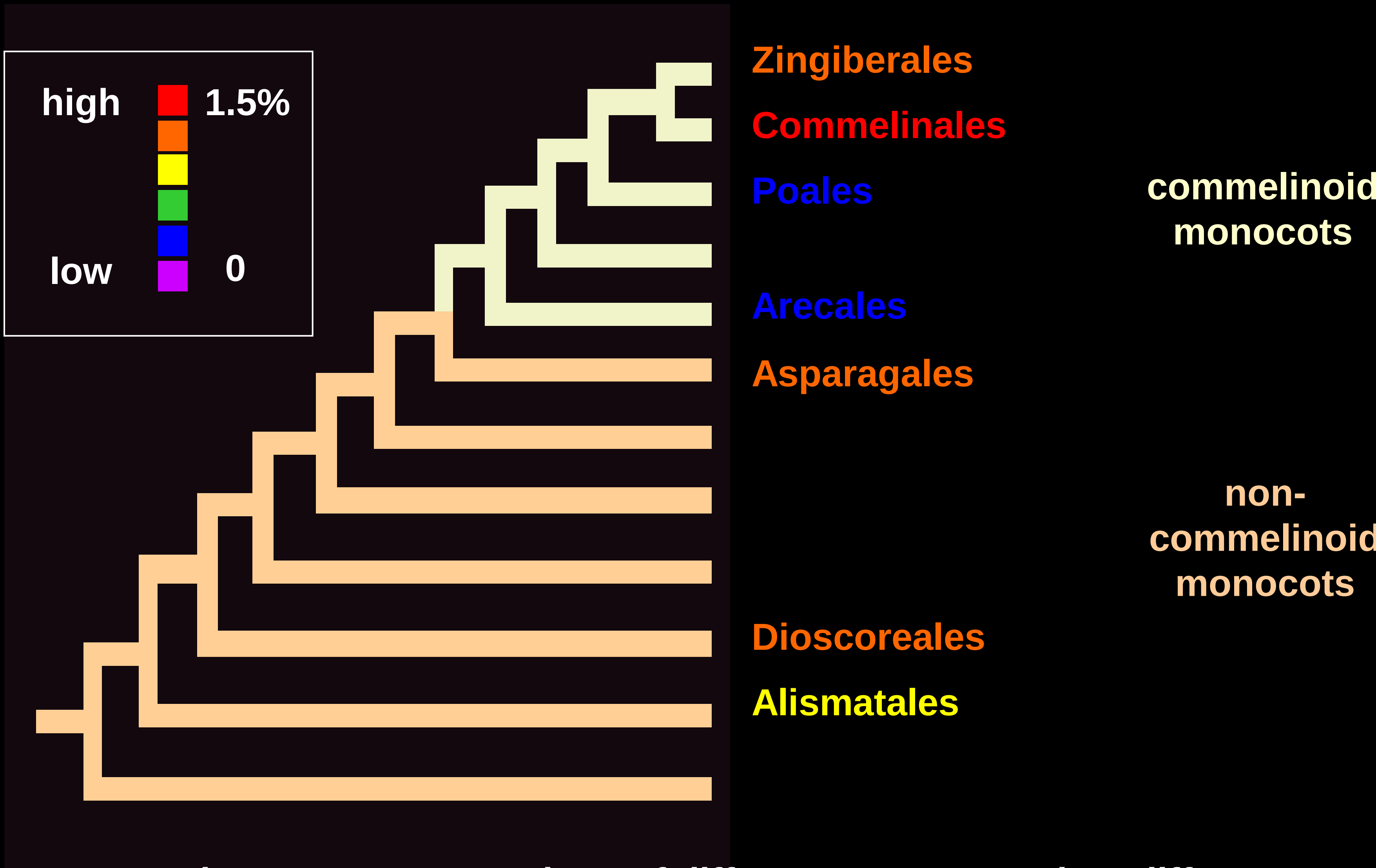
Shoot Ca Concentrations of Angiosperm Orders

Eudicots > monocots





Shoot Calcium Concentrations of Monocot Orders

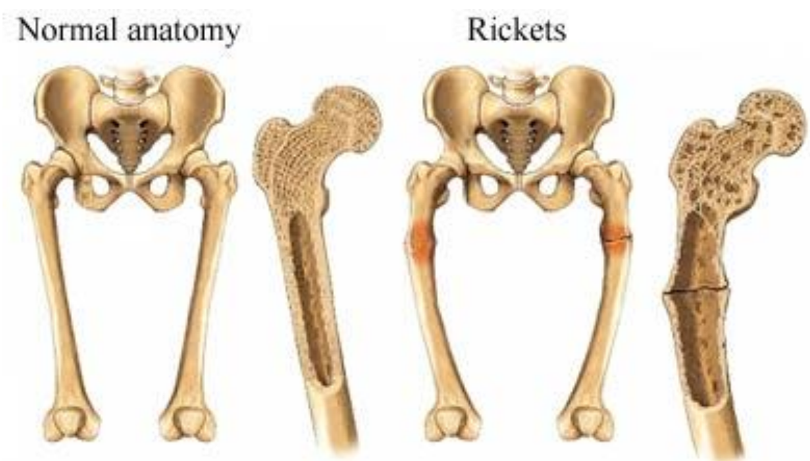


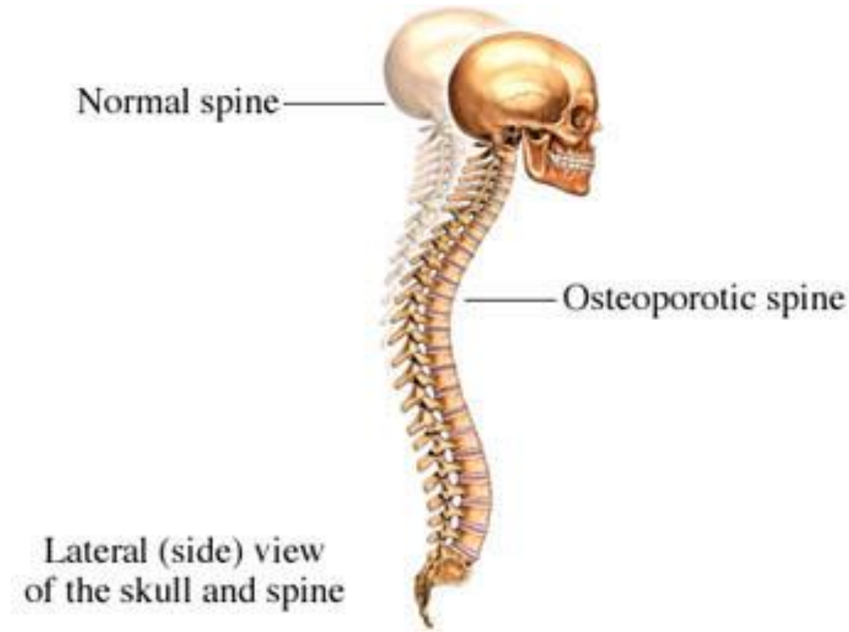
shoot Ca concentrations of different monocot orders differ

non-commelinoid monocots > commelinoid monocots (Poales, Arecales)

Plant Calcium - Dietary Consequences

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





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

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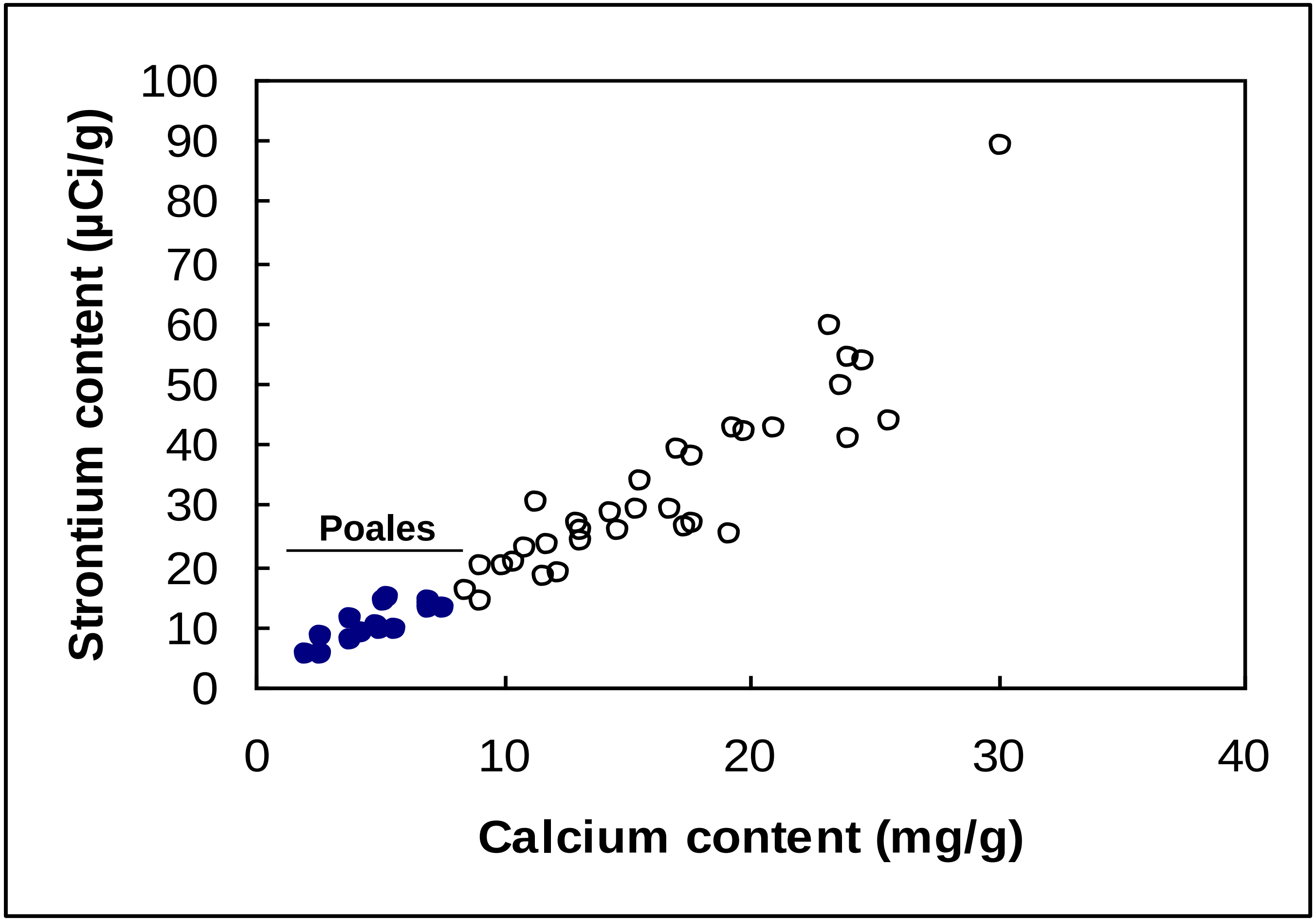
Strontium : Calcium Ratios

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

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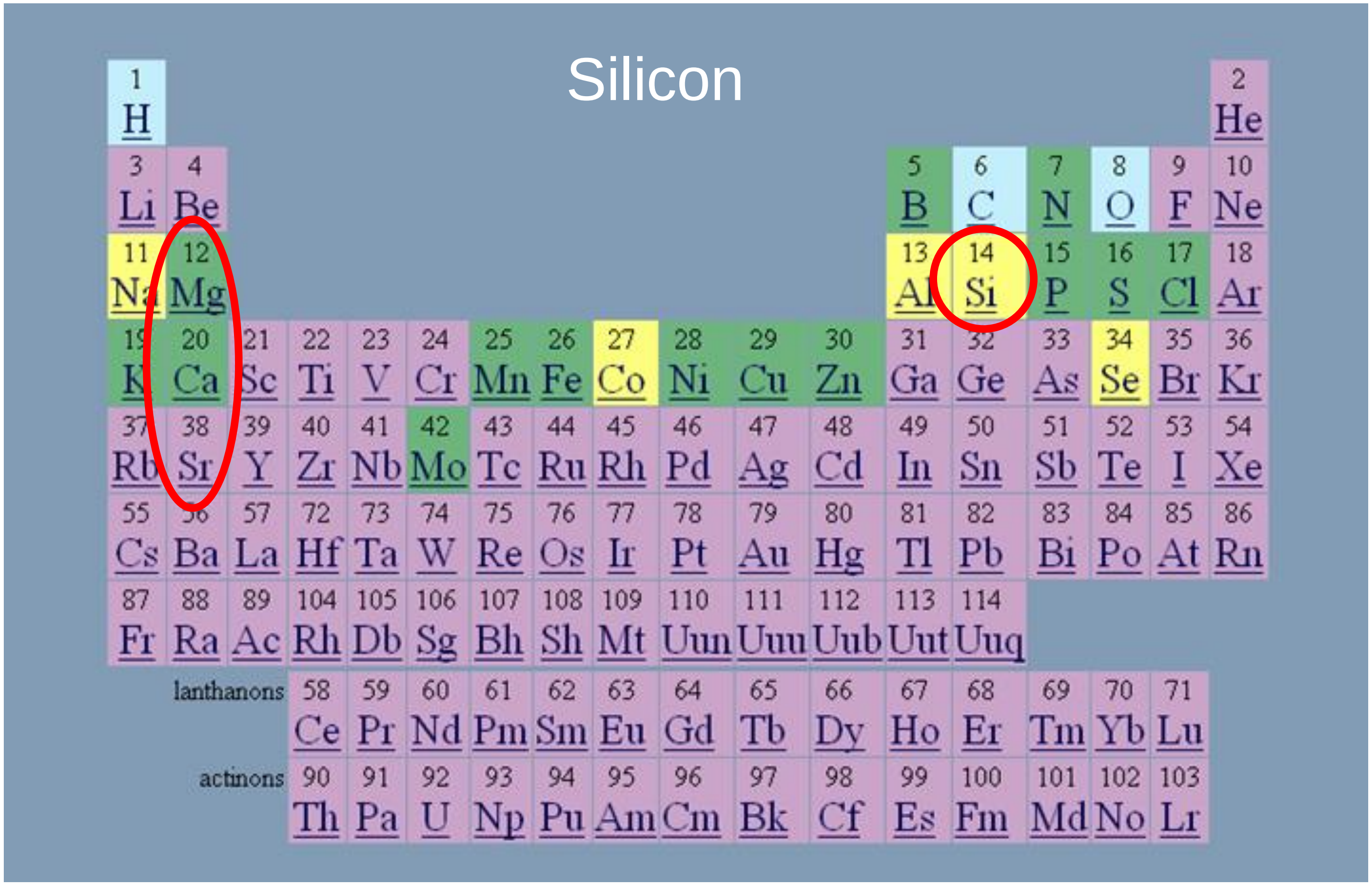
A Botanical Journey Through The Periodic Table



Hodson et al. (2005) Ann. Bot. 96, 1027-1046

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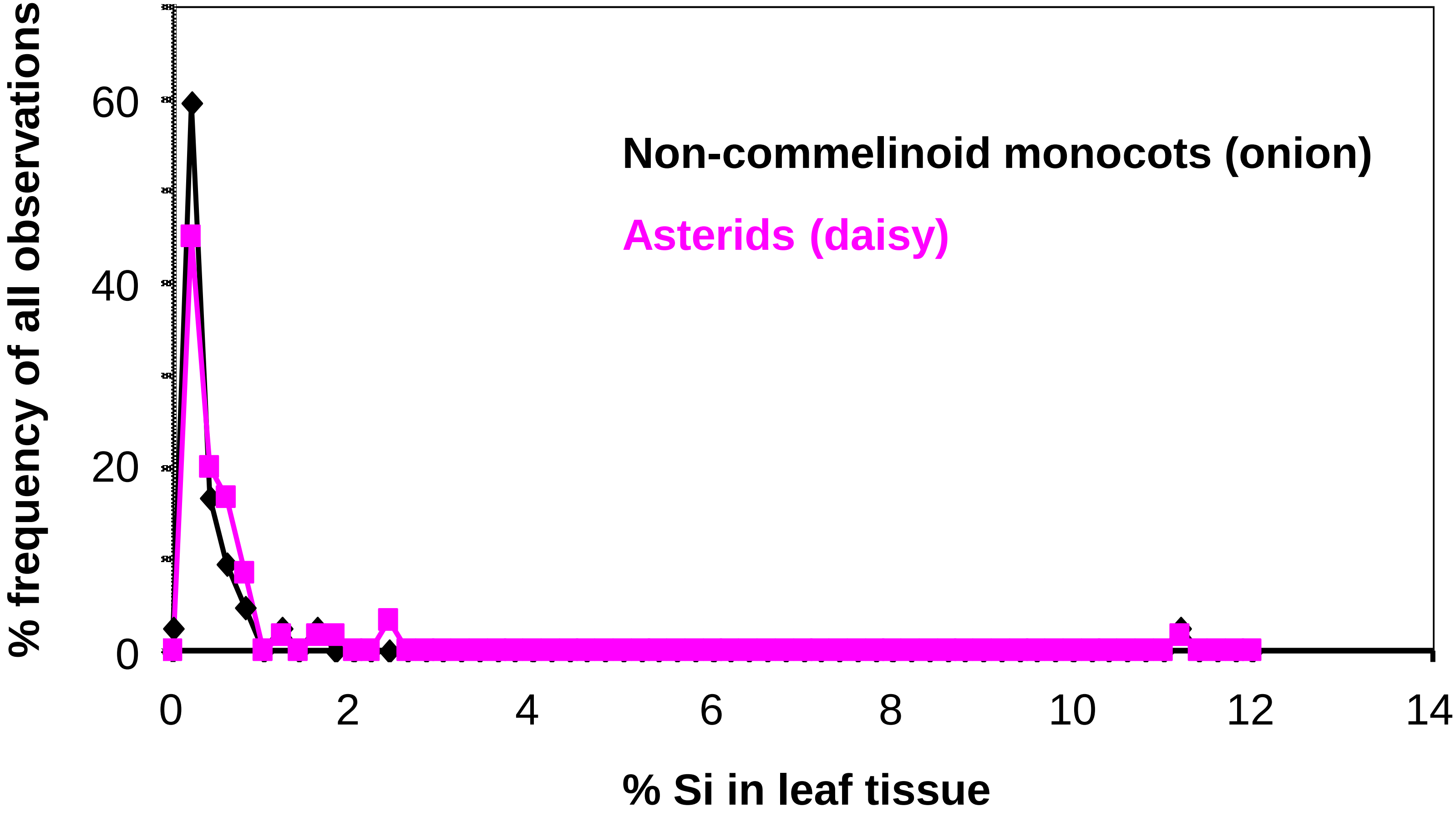
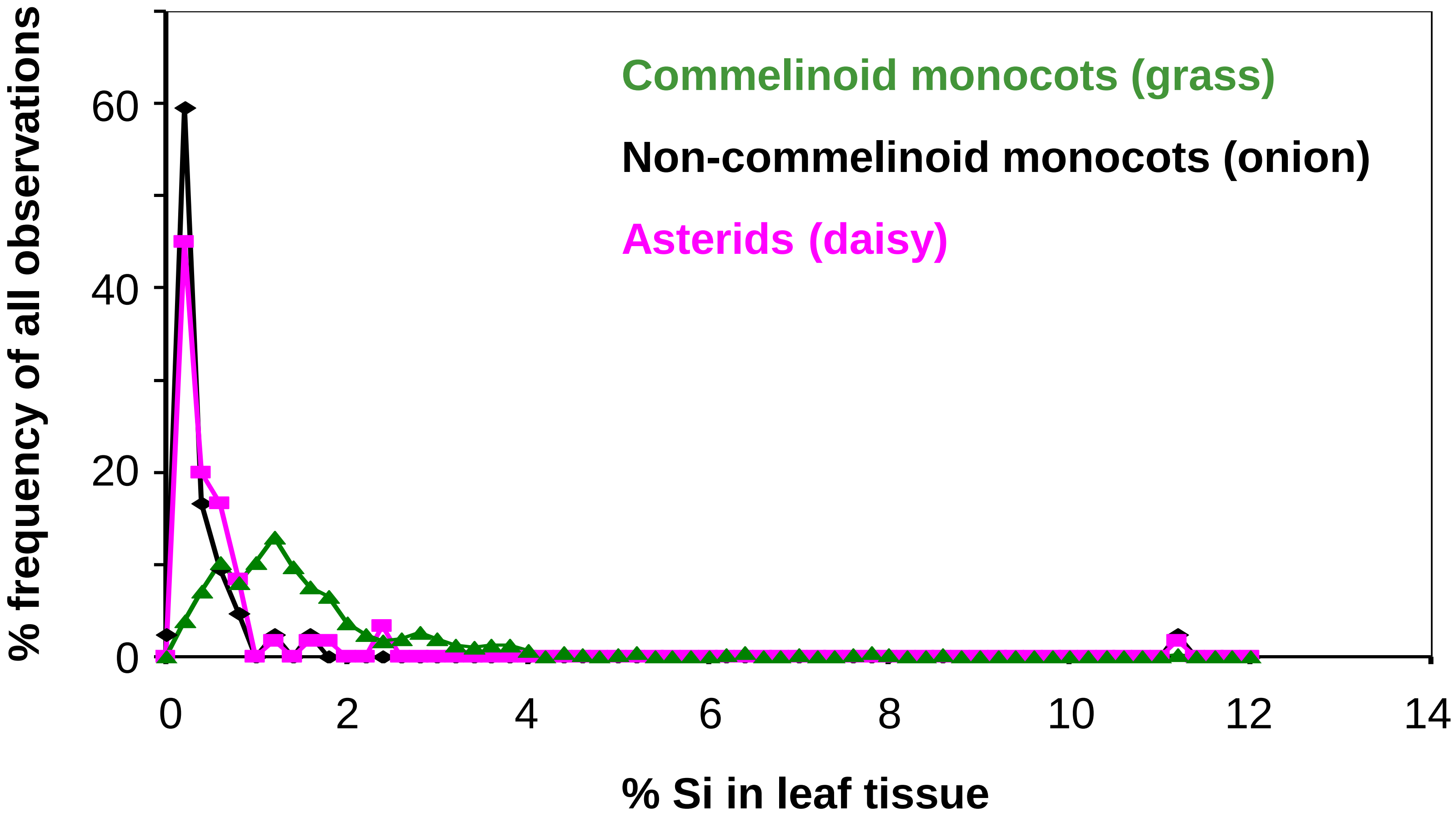
Silicon in Plants



Hodson et al. (2005) Ann. Bot. 96, 1027-1046

Silicon in Plants



Hodson et al. (2005) Ann. Bot. 96, 1027-1046

Silicon in Plants

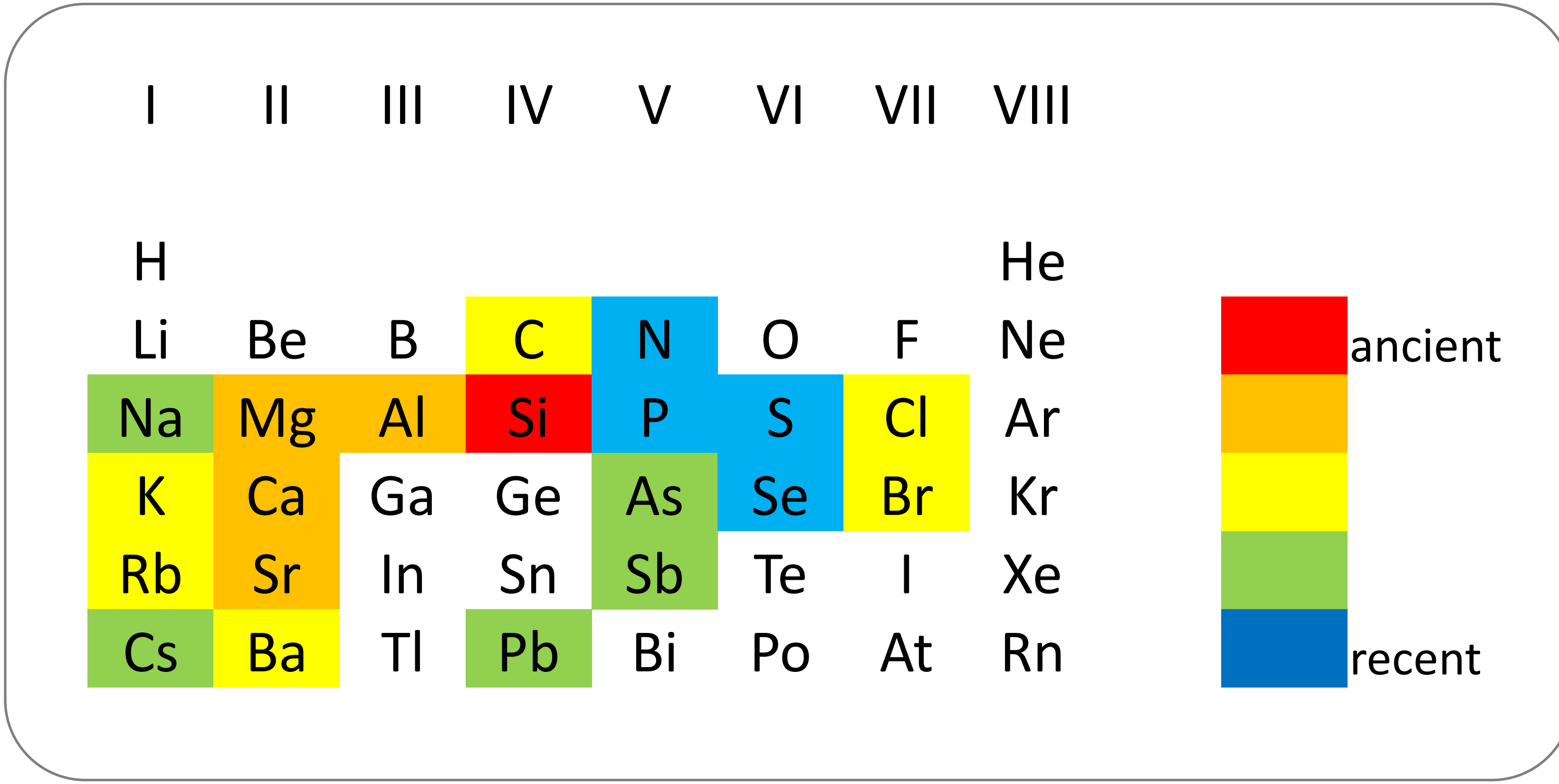
	Proportion of genetic variation			
	Ca	Mg	Sr	Si
order and above (%)	64	65	76	80
within order (%)	36	35	24	20

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

Ca, Mg, Sr : eudicots ≥ non-commelinoid monocots > commelinoid monocots

Si : eudicots ≤ non-commelinoid monocots < commelinoid monocots

Variation in Ionomes of Angiosperm Species



Watanabe et al. (2007) New Phytol. 174, 516-523

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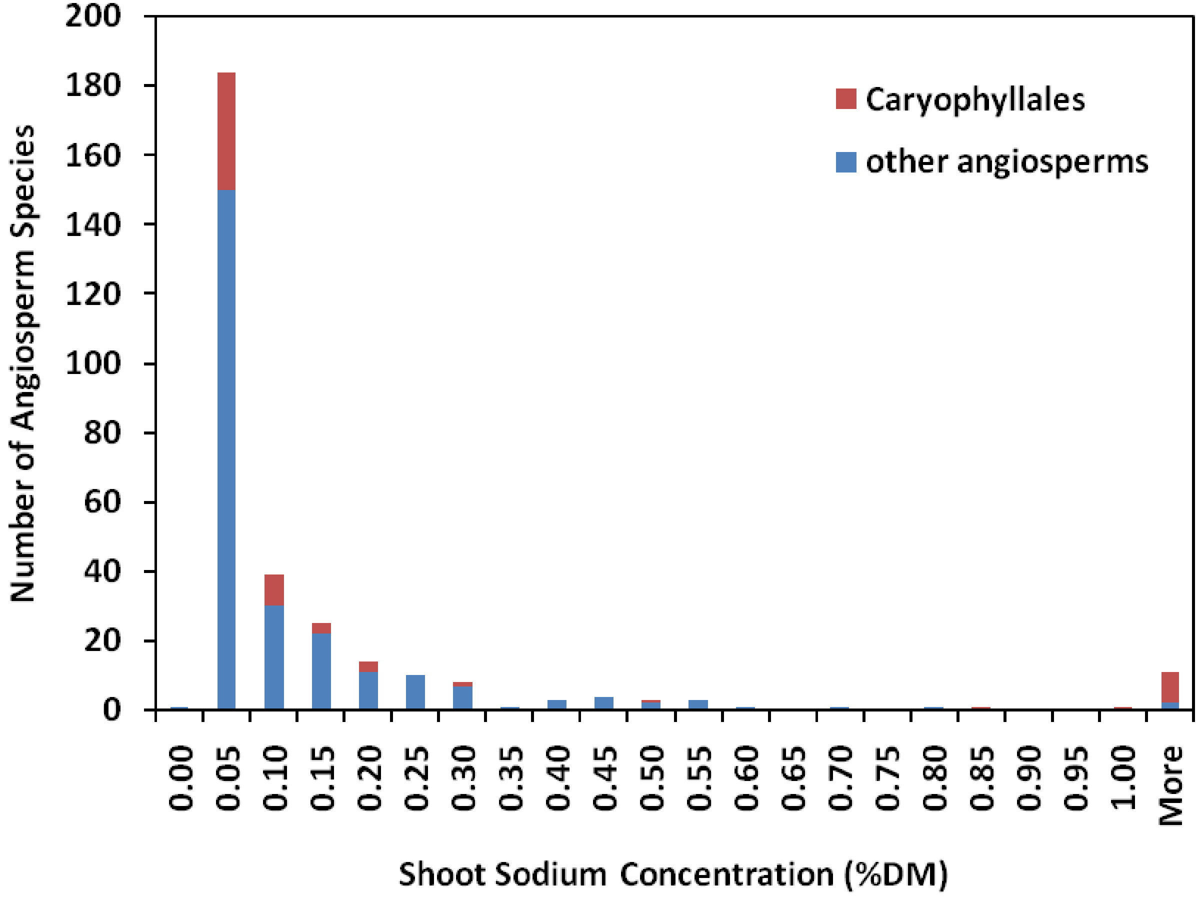
Distribution of Leaf Sodium Concentrations Among Angiosperm Species



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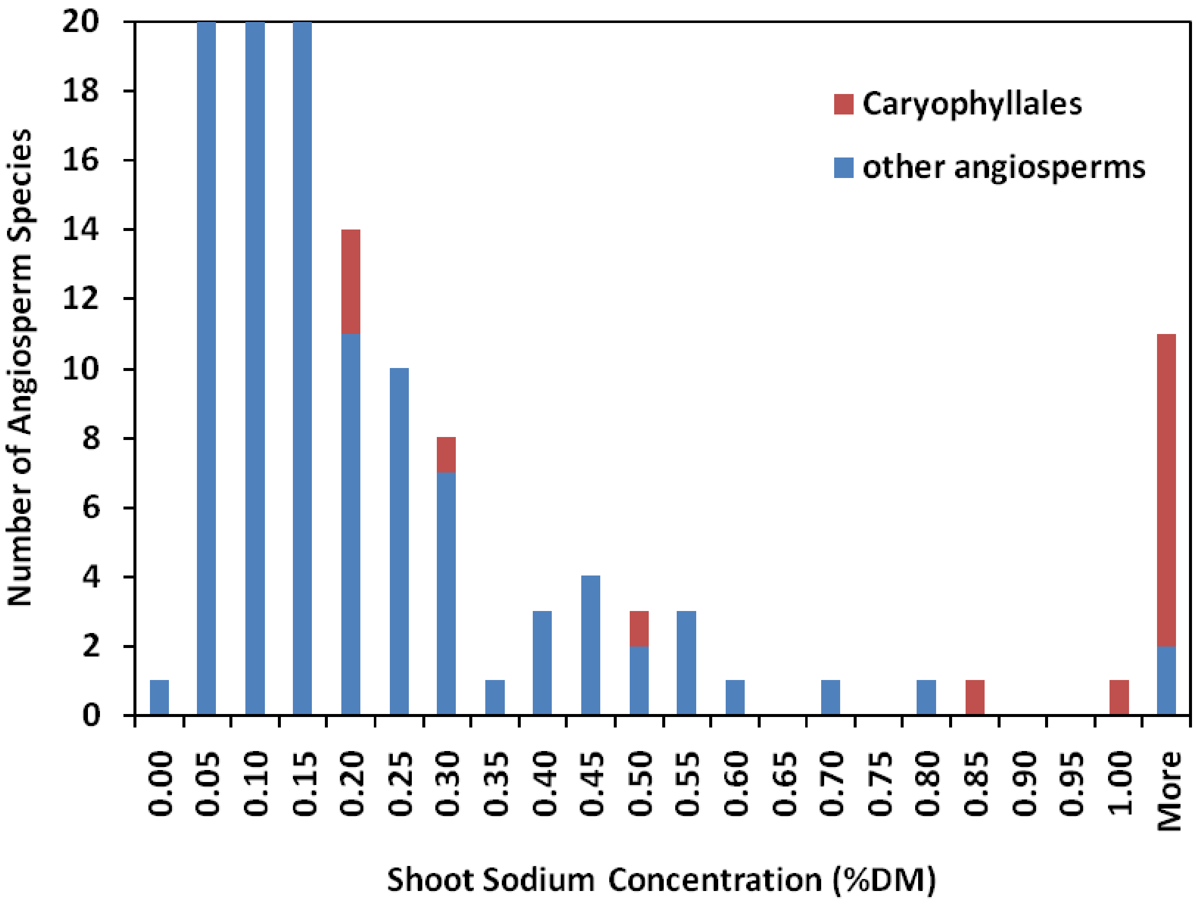
Distribution of Leaf Sodium Concentrations Among Angiosperm Species



Evolution of Sodium Accumulation in the Caryophyllales

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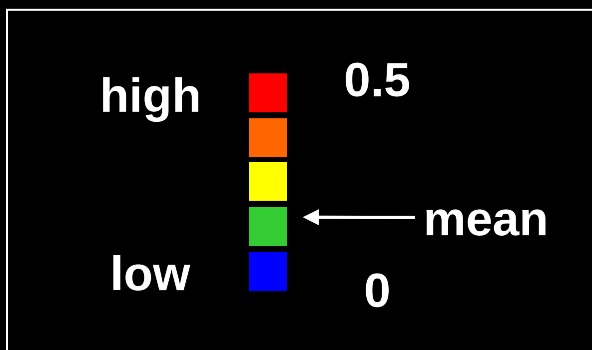
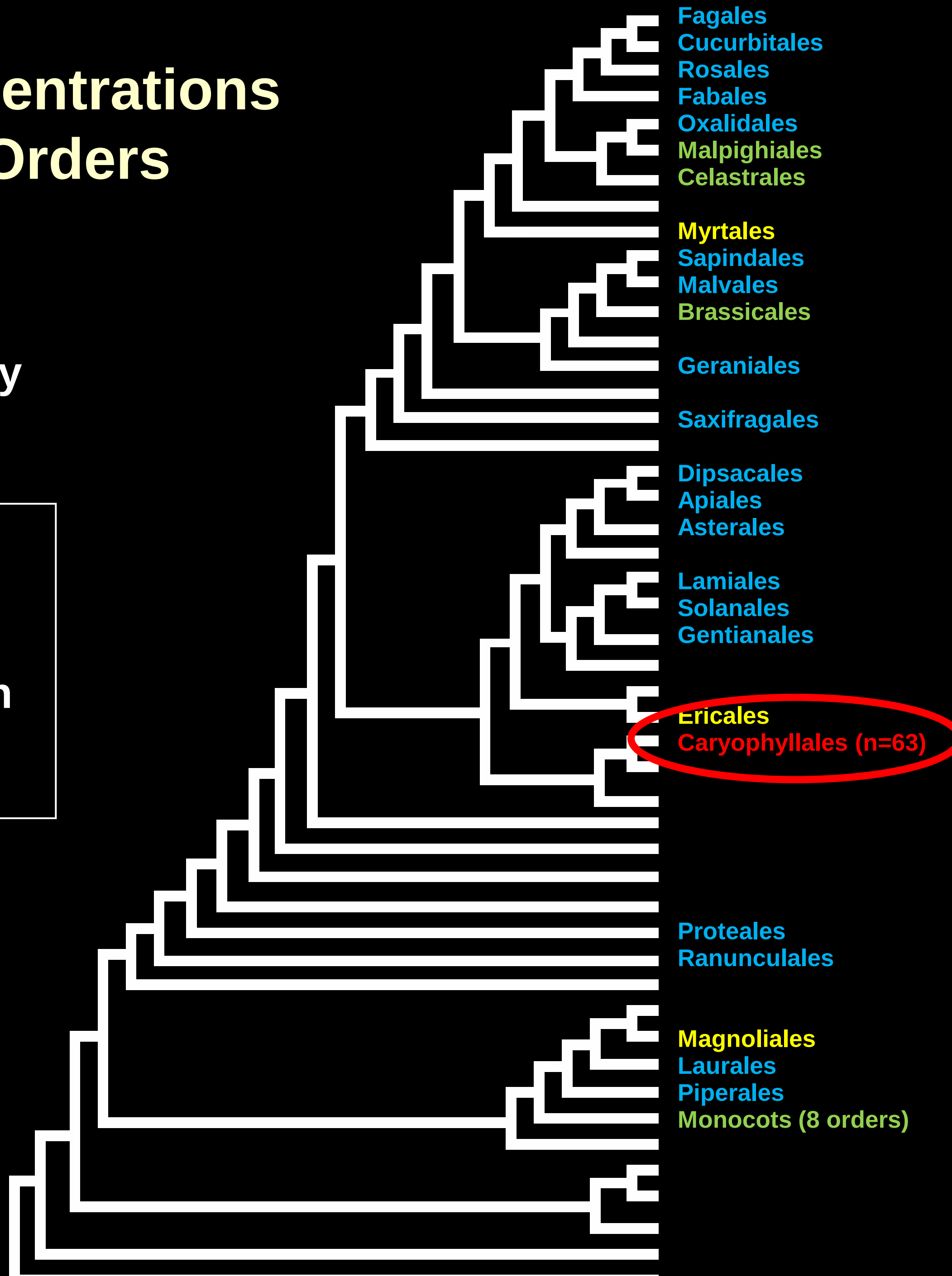
Shoot Sodium Concentrations of Angiosperm Orders

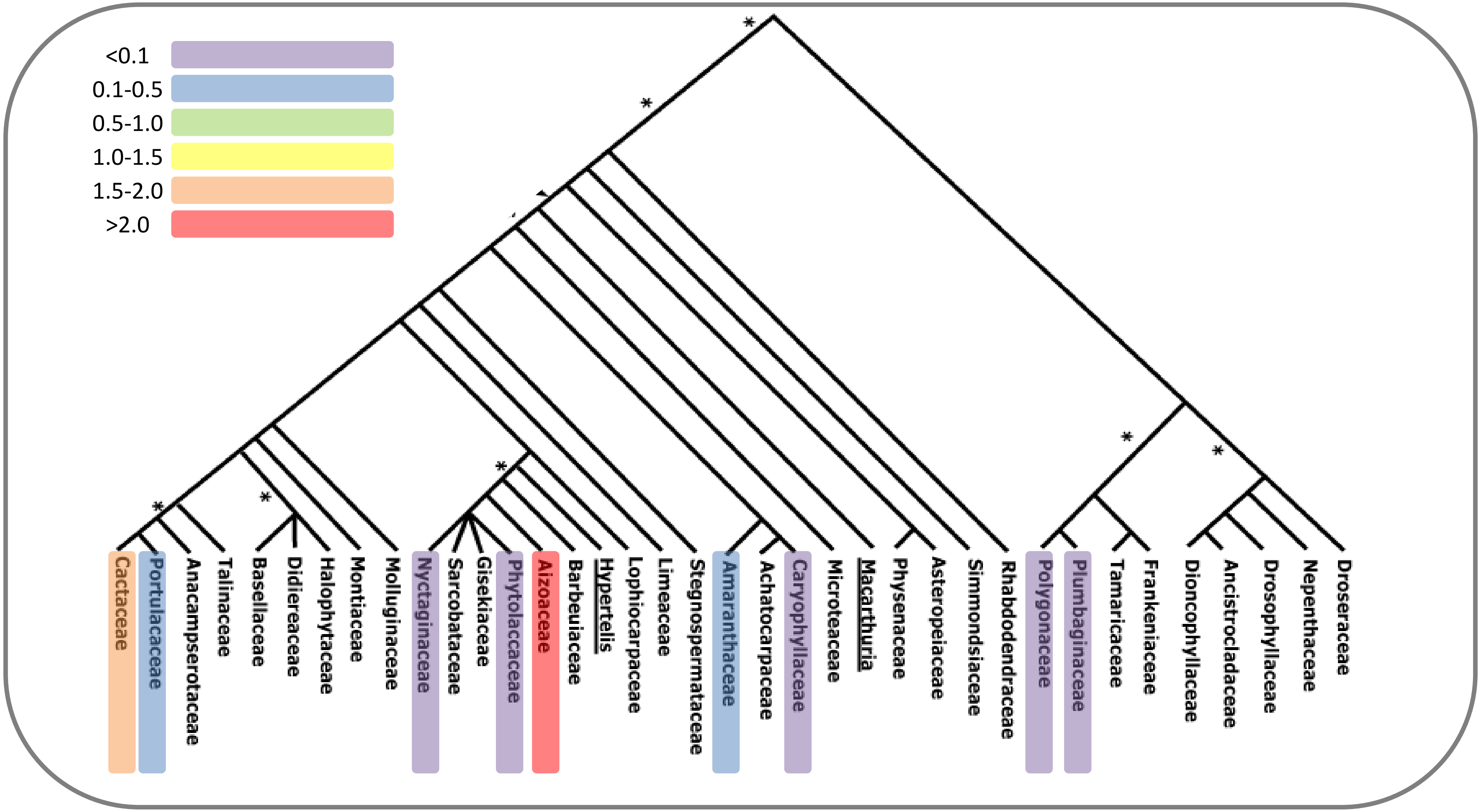
311 species

grown hydroponically



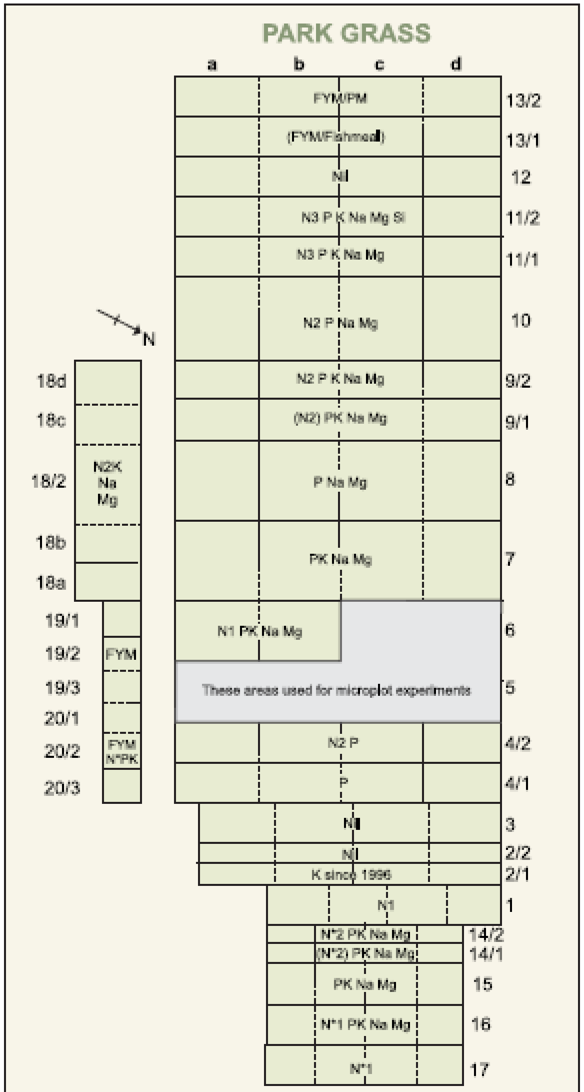


Phylogenetic Effects on the Plant Ionome



Evolution of Sodium Accumulation in the Caryophyllales

Phylogenetic and Environmental Effects on the Plant Ionome



Park Grass, Rothamsted
1856-2014

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

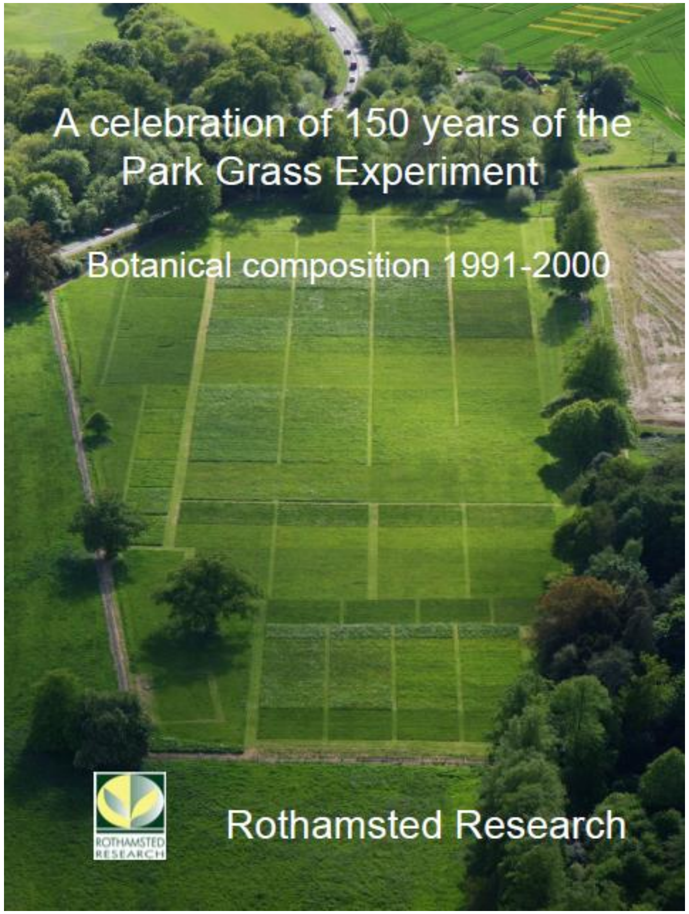


Table 3. Species comprising at least 10% of herbage, and total number of species; mean 1991-2000.

Treatment	Plot	Soil pH 1995-02	AC	AP	AO	AE	DG	FR	HP	HL	LoP	LaP	TP	AS	CN	HS	LH	PL	RaA	RuA	SM	Total no. of species
			Percentage of dry matter (Species names are listed below)																			
Nil	3a	7.2	10	+	+	+	+	30	+	+	+	+	+	−	10	+	15	+	+	+	10	38
	b	6.4	10	+	+	+	+	20	+	+	−	+	+	−	10	−	15	10	+	+	+	36
	c	5.3	30	−	+	−	+	30	+	+	−	+	+	−	+	+	15	+	+	+	+	37
	d	5.2	45	+	+	+	+	30	+	+	−	+	+	−	10	−	+	+	+	+	+	36
P	4/1a	6.9	+	+	+	+	+	30	+	+	+	+	10	−	+	+	15	10	+	+	+	34
	b	6.1	+	+	+	+	+	20	+	+	+	+	+	−	+	−	10	15	10	+	+	34
	c	5.2	30	+	+	+	+	25	+	+	+	+	+	−	+	−	10	+	+	+	+	29
	d	5.3	25	+	+	+	+	25	+	+	+	+	+	−	+	−	15	+	+	+	+	32
PKNaMg	15a	5.7	+	+	+	10	+	10	+	+	+	20	10	+	+	+	−	+	+	+	−	28
	b	5.9	+	+	+	15	+	10	+	+	+	+	30	+	+	+	+	10	+	+	−	27
	c	5.0	20	+	+	+	+	10	+	+	+	+	20	−	15	+	−	+	+	+	−	28
	d	4.9	40	+	+	+	+	10	+	+	+	+	10	−	+	+	+	+	+	+	−	27
N*1	17a	7.1	10	+	+	+	+	15	+	+	+	−	+	−	+	+	25	10	+	+	+	32
	b	6.4	15	+	+	+	+	+	+	+	+	+	−	−	+	+	30	15	+	+	+	34
	c	5.8	25	+	+	+	+	10	+	+	+	−	−	−	+	+	25	10	+	+	+	34
	d	5.8	25	+	+	+	+	10	+	+	+	−	+	+	10	+	10	+	+	+	−	34
N*2PKNaMg	14/2a	6.9	+	20	−	50	+	+	+	−	+	+	−	10	−	+	−	+	+	+	−	24
	b	6.4	+	30	+	40	+	+	−	+	+	−	+	10	−	+	−	−	+	+	−	24
	c	6.1	+	20	+	40	+	+	−	+	+	+	−	+	−	+	−	+	+	+	−	21
	d	5.9	+	25	−	30	10	+	+	+	+	+	−	+	−	10	−	+	+	+	−	22
N1	1a	7.1	+	+	+	+	10	25	10	+	−	+	+	−	+	−	10	+	+	+	+	33
	b	6.2	20	+	+	+	10	25	+	+	+	+	+	−	10	−	+	+	+	+	+	31
	c	5.3	35	−	+	+	+	45	+	+	+	+	+	−	+	−	−	−	+	+	−	33
	d	4.1	65	−	30	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	10
N2KNaMg	18a	7.1	15	+	+	+	10	15	+	+	+	−	+	−	10	+	10	+	−	+	−	30
	b	6.3	30	+	+	+	+	15	+	+	+	−	−	−	25	+	+	+	−	+	−	29
	c	5.4	35	+	+	+	15	20	+	+	10	−	−	−	+	+	−	−	−	+	−	21
	d	3.6	60	−	20	+	−	−	−	+	−	−	−	−	−	−	−	−	−	+	−	6
N2P	4/2a	6.9	10	+	+	+	+	55	+	10	+	−	−	−	+	−	−	+	+	+	−	22
	b	6.2	15	10	+	+	+	65	+	10	+	−	−	−	−	−	+	−	−	+	−	14
	c	5.2	30	+	+	+	+	55	+	+	+	−	−	−	−	−	−	+	−	10	−	18
	d	3.7	30	−	70	+	−	+	−	+	−	−	−	−	−	−	−	−	−	+	−	10
N2PKNaMg	9/2a	6.9	+	15	+	25	10	+	−	15	+	+	+	+	−	10	−	+	+	+	−	22
	b	6.3	+	25	+	35	+	+	+	15	−	+	+	+	−	+	−	−	−	+	−	17
	c	5.0	30	10	10	+	+	15	−	+	−	+	+	+	−	+	−	−	−	+	−	18
	d	3.7	15	−	65	−	−	−	−	20	−	−	−	−	−	−	−	−	−	−	−	4
N3PKNaMg	11/1a	6.5	+	20	−	40	10	+	+	10	+	−	−	+	−	+	−	−	+	+	−	14
	b	6.2	+	20	+	35	20	+	+	10	+	−	−	+	−	+	−	−	−	+	−	15
	c	4.9	+	30	+	20	+	−	−	30	−	−	−	+	−	+	−	−	−	+	−	13
	d	3.6	−	−	+	−	−	−	−	100	−	−	−	−	−	−	−	−	−	−	−	3
FYM/PN	13/2a	6.8	30	+	+	+	10	15	+	+	10	−	−	−	+	+	−	−	−	+	−	28
	b	6.1	+	15	+	20	10	+	−	+	+	+	−	+	+	10	−	+	+	+	−	30
	c	5.3	20	+	+	+	+	+	+	10	−	+	+	+	+	+	+	10	+	+	−	32
	d	5.1	35	10	+	+	+	10	+	10	+	+	+	−	+	+	+	+	+	+	−	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 less than 10%; −, species not identified on that plot.
Species that do not occur at 10%, or more, on any one plot are not shown.

Grasses:	*Agrostis capillaris*	Common Bent
	Alopecurus pratensis	Meadow Foxtail
	Anthoxanthum odoratum	Sweet Vernal Grass
	Arrhenatherum elatius	False Oat Grass
	Dactylis glomerata	Cock's-foot
	Festuca rubra	Red Fescue
	Helictotrichon pubescens	Downy Oat-grass
	Holcus lanatus	Yorkshire Fog
	Lolium perenne	Perennial Ryegrass
Legumes:	*Lathyrus pratensis*	Meadow Vetchling
	Trifolium pratense	Red Clover
Forbs:	*Anthriscus sylvestris*	Cow Parsley
	Centaurea nigra	Common Knapweed
	Heracleum sphondylium	Hogweed
	Leontodon hispidus	Rough Hawkbit
	Plantago lanceolata	Ribwort Plantain
	Ranunculus acris	Meadow Buttercup
	Rumex acetosa	Common Sorrel
	Sanguisorba minor	Salad Burnet

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

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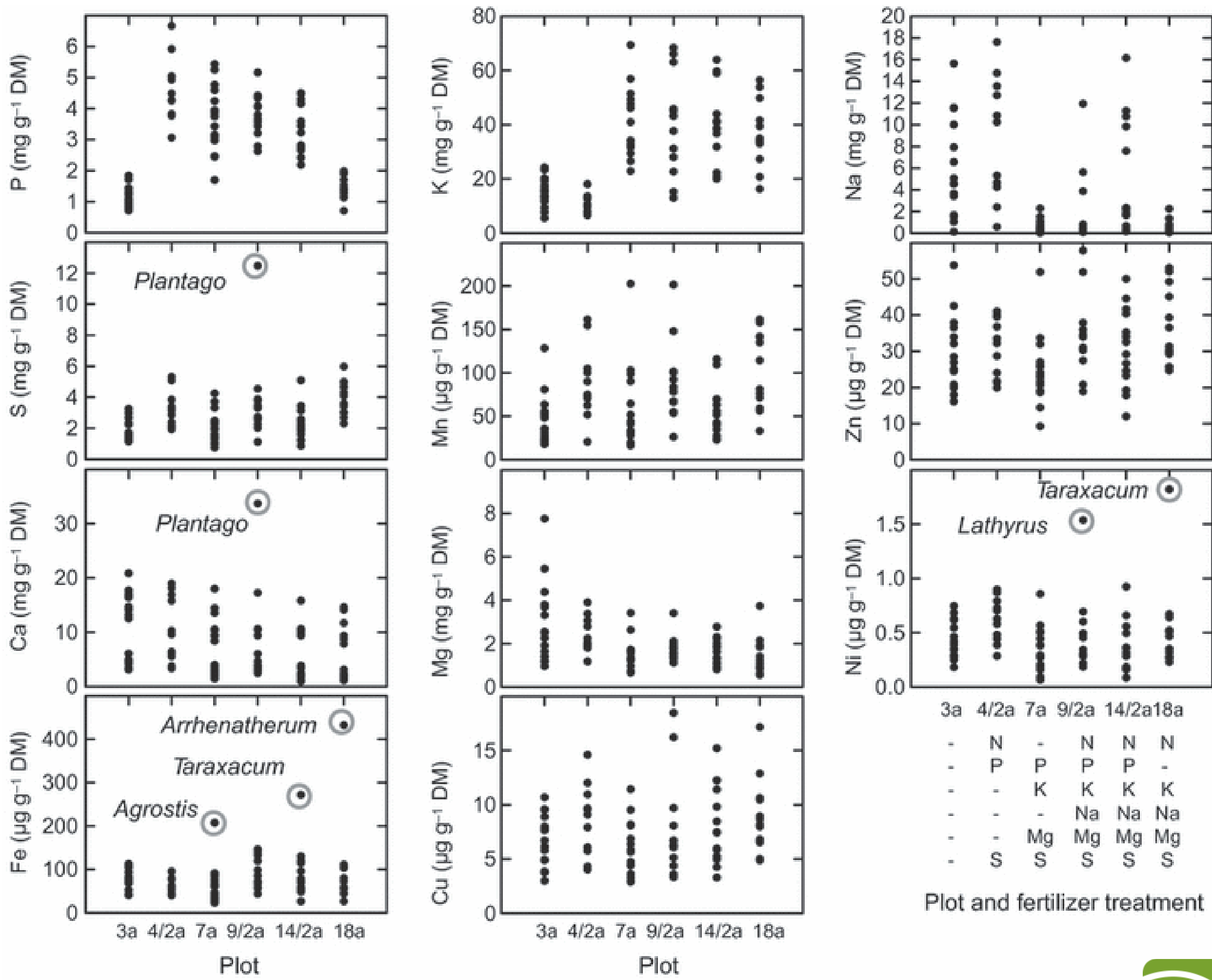
Phylogenetic and Environmental Effects on the Plant Ionome



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

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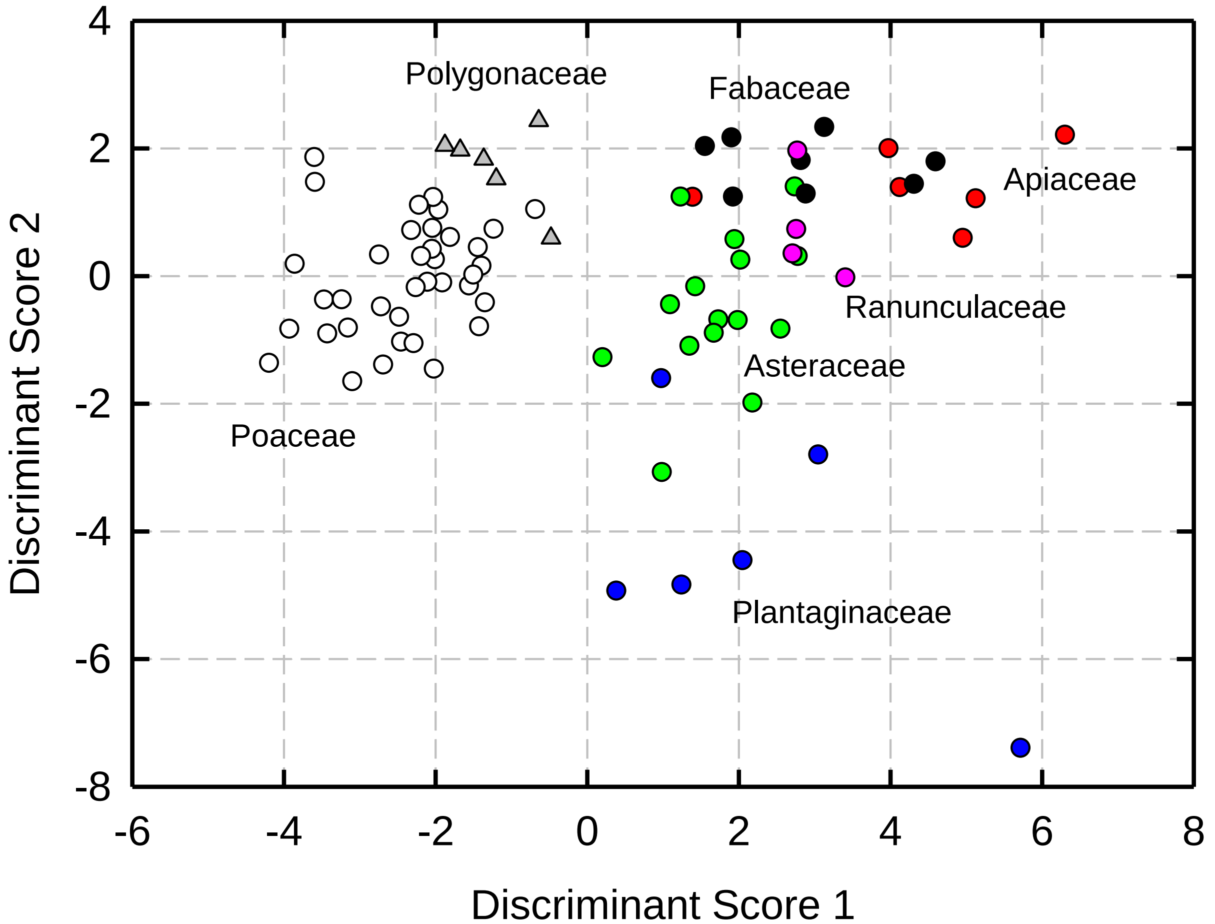
Plant Species Differ in Their Ionome



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

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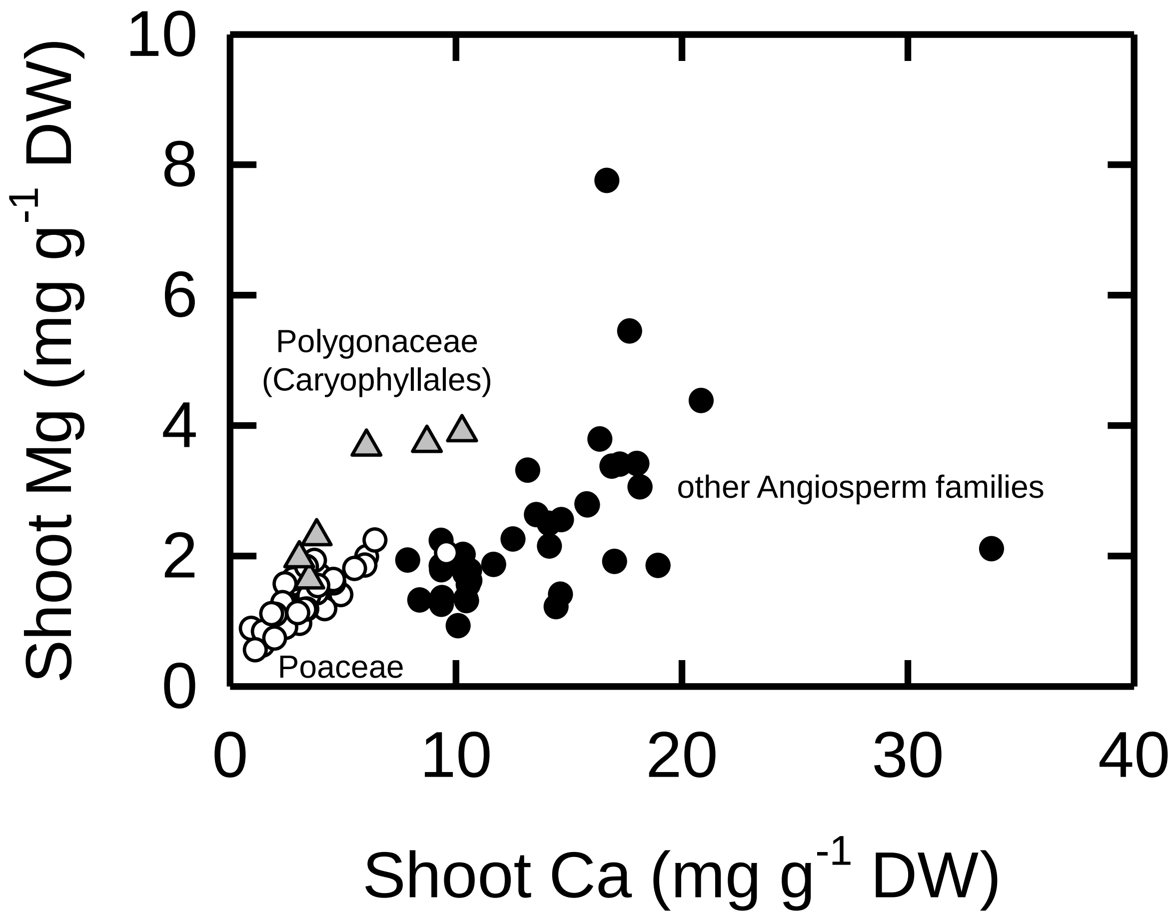
Calcium : Magnesium Ratios



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

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Phylogenetic and Environmental Effects on the Plant Ionome

	Mean	Variance	Species (%)	Treatment (%)	Residual (%)
Calcium	9.4	40.5	70.8	8.2	21.0
Zinc	31.5	124.2	64.3	13.4	22.3
Manganese	68.9	2096.2	36.3	23.4	40.3
Magnesium	2.0	1.3	32.8	19.9	47.3
Copper	8.0	11.5	30.8	6.6	62.6
Nickel	0.5	0.09	29.6	12.6	57.8
Sodium	3.8	23.7	24.8	37.8	37.4
Sulphur	2.8	2.6	24.8	27.5	41.3
Potassium	30.9	326.0	19.6	53.9	26.5
Phosphorus	3.1	2.6	10.7	77.0	12.3
Iron	79.4	3097.0	2.3	−0.7	98.4

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

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Evolution of the Angiosperm Ionome

Plant Species Differ in their Ionome

Differences Attributed to
Ancient and Recent Evolutionary Events

Commelinoid monocots - low Calcium, Magnesium, Strontium
Commelinoid monocots - high Silicon
Caryophyllales - high Magnesium / Calcium Ratios
Some Caryophyllales (hyper)accumulate Sodium

(Phylo)genetic Variation exceeds Environmental Variation
For some Elements

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