Wurzelexsudate

Rhizosphäre und Bulkerde

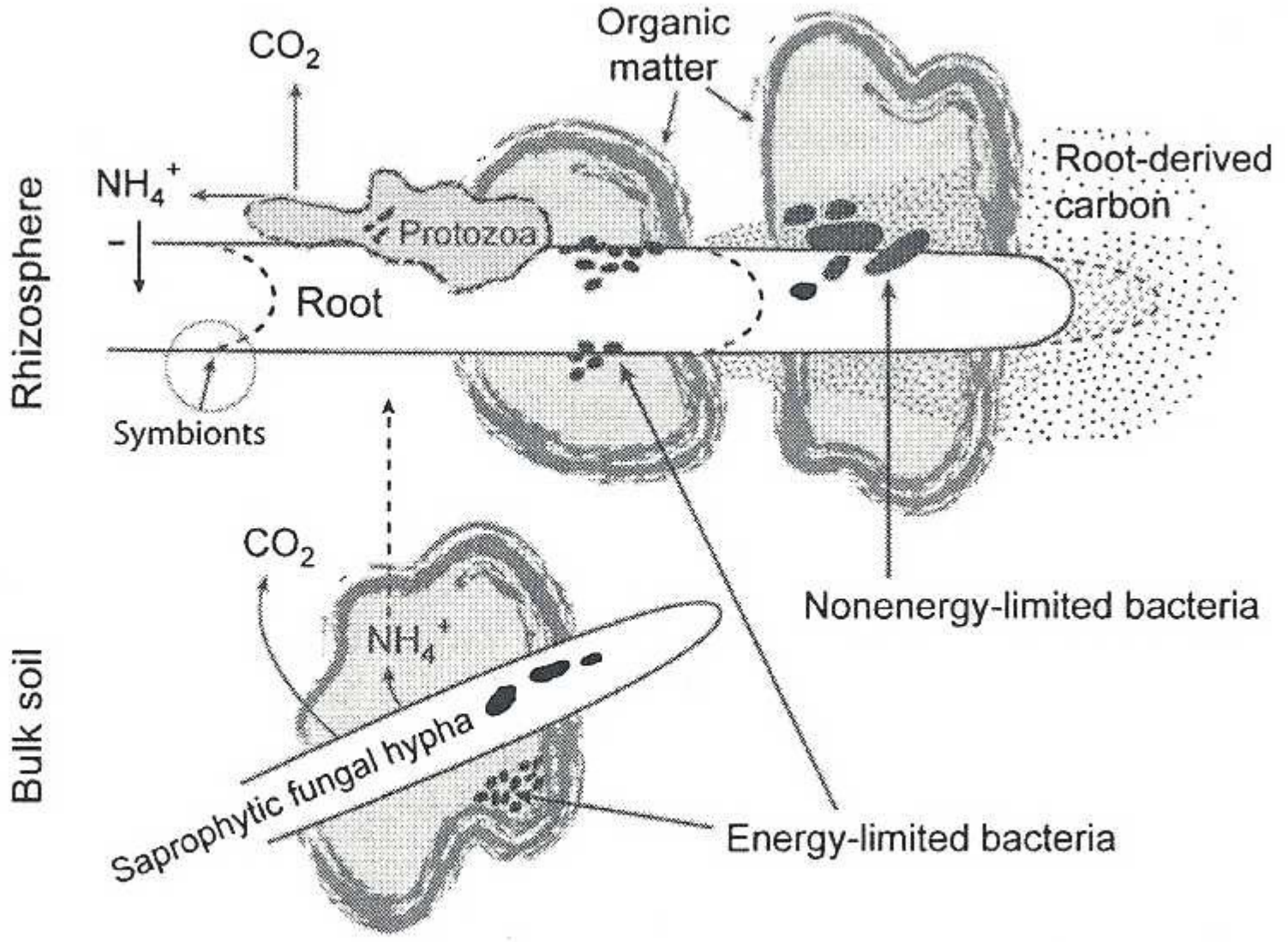
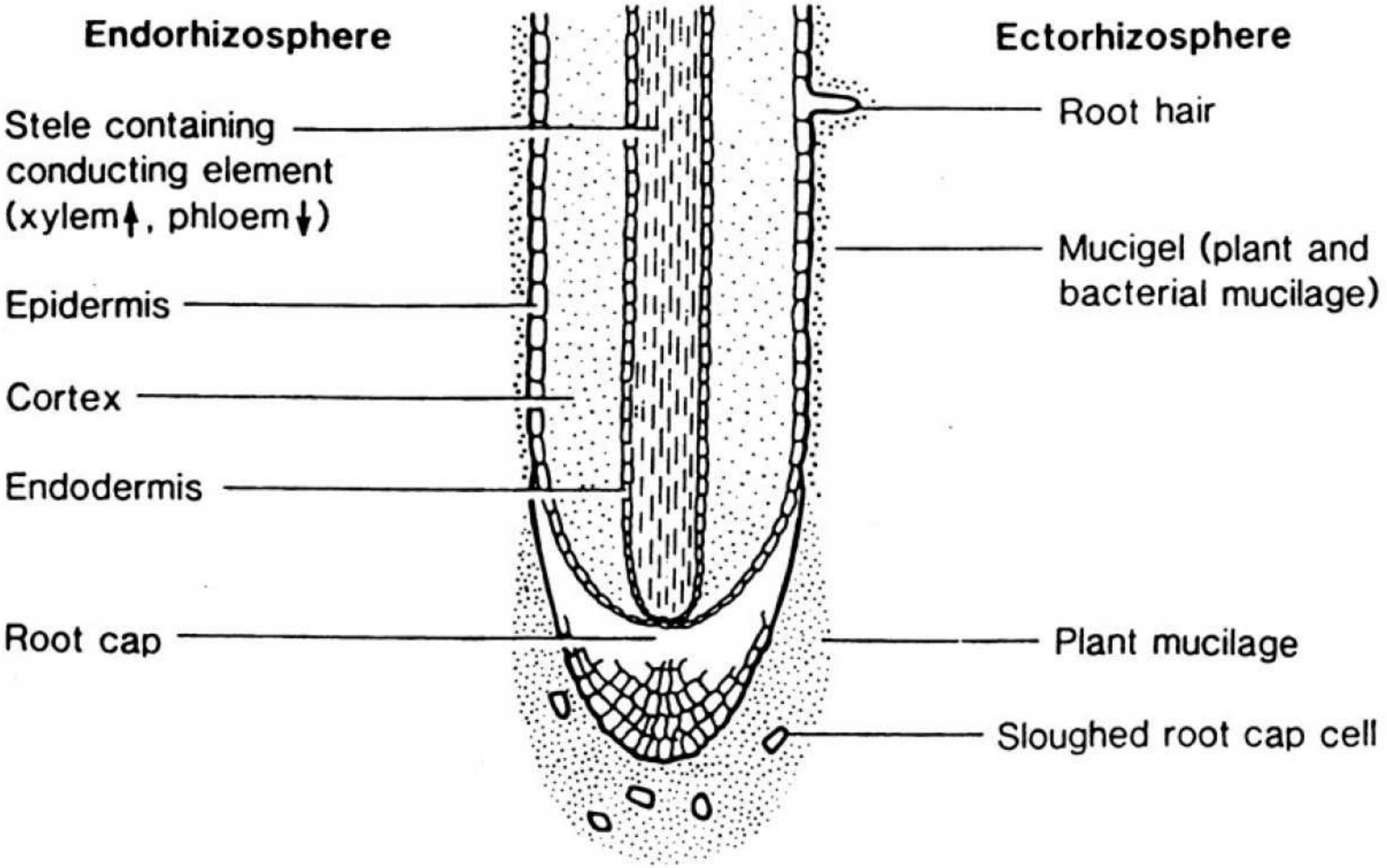


FIGURE 3.3 Model of proposed interactions in the rhizosphere and in the bulk soil.

Rhizosphäre



Ca. 20% des photosynthetisch fixierten Kohlenstoffs werden über die Wurzeln exudiert; 64-86% werden davon durch Mikroorganismen abgebaut.

What lies beneath

More creatures live in soil than any other environment on Earth. But what are they all doing there? **Amber Dance** reports on the world's widest biodiversity.

Ecosystems aren't green; they are black and brown, at least in the colour palette favoured by Diana Wall. Wall, a soil ecologist at Colorado State University in Fort Collins, spends her days digging into the world's underground ecosystems. These beiges, ochres and charcoals reflect a three-dimensional mosaic of micro-environments, each with its unique set of inhabitants.

But very little is known about these inhabitants. Understanding soil is a matter of rising urgency. A July report from the US National Research Council listed soil quality as the biggest barrier to higher crop yields for farmers in sub-Saharan Africa and south Asia. And knowing what myriad organisms live in the soil, and how they interact, is crucial to creating a healthy ecosystem.

For those scientists who are willing to crouch down and dig, the diversity of soil denizens beats any above-ground system, even that of a tropical rainforest. A handful of soil from one spot may house a very different community from soil just a metre away, because of variations in the availability of water or nutrients. For example, the ground under a decaying plant or animal is a different environment from soil lacking such enrichment. And around plant roots, specialized organisms inhabit the rhizosphere, a thin layer where roots and soil organisms interact in myriad ways. Large animals such as moles contribute, changing and aerating the underground landscape by tunnelling. Even a small clump of soil has a gradient of oxygen from its edges to the centre, and each oxygen concentration may make the perfect habitat for different kinds of creatures. "It is the most incredible zoo," says Wall.

Take that view to a larger scale, and it is possible to appreciate just how complicated the world's soil ecosystems are. In one ongoing study, not yet published, Wall and her colleagues scooped soil cores from two sites in Alaska, one in the tundra and one in the taiga forest. Although the sites were only 400 kilometres apart, the species living there were radically different: only 18 invertebrate taxa out of an estimated 1,300 appeared in both locations. "That just blew me away," says Wall.

> **"My dream is that you take a DNA sample from the soil, and then explain what species are there, and what benefits."**
> — Wim van der Putten

And that's just looking at invertebrates, not including microbes. "As far as I know, there is no environment on Earth that is more biologically diverse, per unit area, than soil," says Eric Triplett, a microbiologist at the University of Florida in Gainesville. Thanks to faster, cheaper DNA sequencing, scientists are now getting a grip on what is down there and what those organisms might be doing. That information, in turn, could help improve soil management for agriculture and forest management for conservation.

At this point, scientists don't even agree on how many creatures they are looking for. The first DNA-based estimate of soil microbial biodiversity, published in 1990, counted about 4,000 different bacterial genomes per gram of soil[1]. Since then, various studies and models have pushed the number up as high as 830,000 species per gram[2], down to 2,000 (ref. 3), and back up again. Most recently, Triplett and his colleagues ran 139,000 individual sequences — more than other studies have used — and came up with an estimate of 10,000 to 50,000 species per gram of soil[4]. Complicating the matter is the fact that, because so few of these species have been described, researchers have to group similar organisms within 'operational taxonomic units', which correspond roughly but not precisely to species designations.

EYE OF SCIENCE/SPL

A. SYRED/SPL

Valuable species

Quantifying such diversity illustrates just how much remains to be discovered, and soil scientists are teaming up to tackle the challenge. The Tropical Soil Biology and Fertility (TSBF) Institute, run by the International Center for Tropical Agriculture and headquartered in Nairobi, has united more than 300 scientists in seven countries to survey soil organisms. The project, which began in 2002, aims to identify living indicators for fertile or poor soil, and has already identified some novel organisms that could be useful to humans.

In the Veracruz rainforest, for instance, Mexican scientists have discovered *Acaulospora*, a mycorrhizal fungus that entwines with lily roots and provides water and mineral nutrients. Last spring the researchers injected *Acaulospora* into the soil of test lily plots in Benigno Mendoza, a community in Veracruz where lily bulbs are an important cash crop. As a result, this year's harvest consists of big, first-quality bulbs that match the yields gained through using inorganic fertilizer with none of the downsides of chemical treatments. Isabelle Barois, a soil ecologist at the Institute of Ecology in Xalapa and coordinator of the TSBF Mexican team, says that the fungus could eventually help replace the expensive nitrogen fertilizer and harsh agrochemicals that farmers apply to their land five or six times a year.

Global soils contain a bounty of unusual and potentially useful organisms such as *Acaulospora* — more, theoretically, than they should. Although some species are common, there are also countless taxa found in vanishingly small numbers. Many species also seem to be redundant, eating the same foods and fulfilling the same ecosystem jobs, so scientists don't quite understand why they're there at all. "There is some debate about how many species need to be present in the soil to make an ecosystem," says Wim van der Putten, an ecologist at the Netherlands Institute of Ecology in Heteren.

Heikki Setälä, an ecologist at the University of Helsinki, took on this question with experiments in which he controlled the number of animal or microbial species in artificial ecosystems. In one study[5], he set up soil microcosms in glass jars and added fungal species: only one in some jars, and up to 43 in others. Diverse systems decomposed more organic matter — demonstrated by higher carbon dioxide production — and produced more nitrogen compounds in the soil. But that relationship held true only at the lower end of the spectrum. Six species were better than one, but 43 weren't any better than six. "It was kind of a bummer," Setälä says. "It would be nice to tell the audience that we need all the species to make the planet green and sustain it."

The explanation for the wealth of soil biodiversity, then, remains an open question. Maybe the multitudinous creatures are simply adapted for niches that humans don't yet understand. Alternatively, they could literally be waiting for a rainy day; some organisms spring into action after a storm, fire or other disturbance, and so make the ecosystem more resilient. Or perhaps those organisms are truly redundant. "We know virtually nothing about what controls the diversity of soil communities," says soil ecologist Richard Bardgett of Lancaster University, UK.

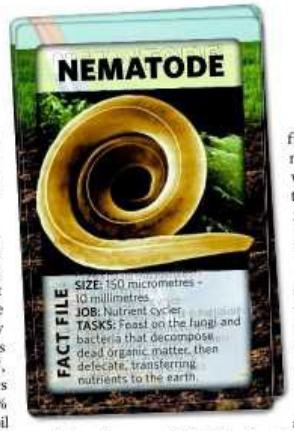
Triplett disagrees. "I don't think it's a vast unknown," he says. "I think there are some dominant genera out there that we could learn about pretty fast." In a follow-up to his soil biodiversity survey[6], Triplett and his colleagues found that up to around 65% of the DNA samples from soil microbes fell into known genera, which makes those genera prime candidates for further study. For example, *Chitinophaga* was prevalent in the four distinct soils tested, from Canada, Illinois, Florida and Brazil. But a PubMed search for the genus finds only ten papers on the genus (and one of those is Triplett's), highlighting the lack of work that has been done in this area.

"My dream for the future would be that you would just take a DNA sample from the soil, and then explain what species are there, and what benefits," van der Putten says. But this kind of quick DNA test is years in the future.

Setting microbes to work

For some scientists, just defining the diversity isn't enough. Triplett, for instance, wants to alter it. He envisions harnessing the nitrogen-fixing power of bacteria that form nodules on the roots of some plants, such as legumes, and convert nitrogen from the air into a form the plants can use. He thinks he could insert some of the nitrogen-fixing (nif) genes from the bacteria into agricultural crops — which could then collect their own nitrogen from the atmosphere and eliminate the use of artificial nitrogen fertilizer. It has already been shown that some nif genes can function in plants[7]. A nitrogen-fixing plant would require at least ten new genes, making the task difficult, Triplett says, but not impossible.

B. P. KENT/PHOTOLIBRARY.COM



LONDON SCHOOL HYG. TROP. MED./SPL

Policy-makers are slowly starting to pay attention to the problem of soils. In 2006 the European Union agreed that soils need protection from erosion, landslides and salinisation, but has not yet finalized the laws that would ensure this happens. Some countries, including France, would prefer to see individual countries regulate soil. "I'm pretty confident that the politicians will swallow the hook sooner or later," Setälä says.

Avoiding that hook comes with a price tag: one estimate valued the free services provided by the world's soil biota at US$1.5 trillion or more each year[8]. Soils are also important as a carbon sink; soil stockpiles 1,500 gigatonnes of organic carbon, more than Earth's atmosphere and all the plants on the planet, according to the United Nations Food and Agriculture Organization. If soils remain degraded and their many denizens disappear, the world might lose access to organisms that improve crop yields, degrade toxins, or make useful by-products such as drugs — before they're even discovered. ■

Amber Dance is a freelance science writer based in the Los Angeles area, and a former News intern with *Nature*.

1. Torsvik, V., Goksøyr, J. & Daae, F. L. *Appl. Environ. Microbiol.* **56**, 782–787 (1990).
2. Gans, J., Wolinsky, M. & Dunbar, J. *Science* **309**, 1387–1390 (2005).
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4. Roesch, L. F. *et al. ISME J.* **1**, 283–290 (2007).
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6. Fulthorpe, R. R., Roesch, L. F., Riva, A. & Triplett, E. W. *ISME J.* **2**, 901–910 (2008).
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8. Brussaard, L., de Ruiter, P. C. & Brown, G. G. *Agric. Ecosyst. Environ.* **121**, 233–244 (2007).

J. DE MEESTER/ARDEA.COM

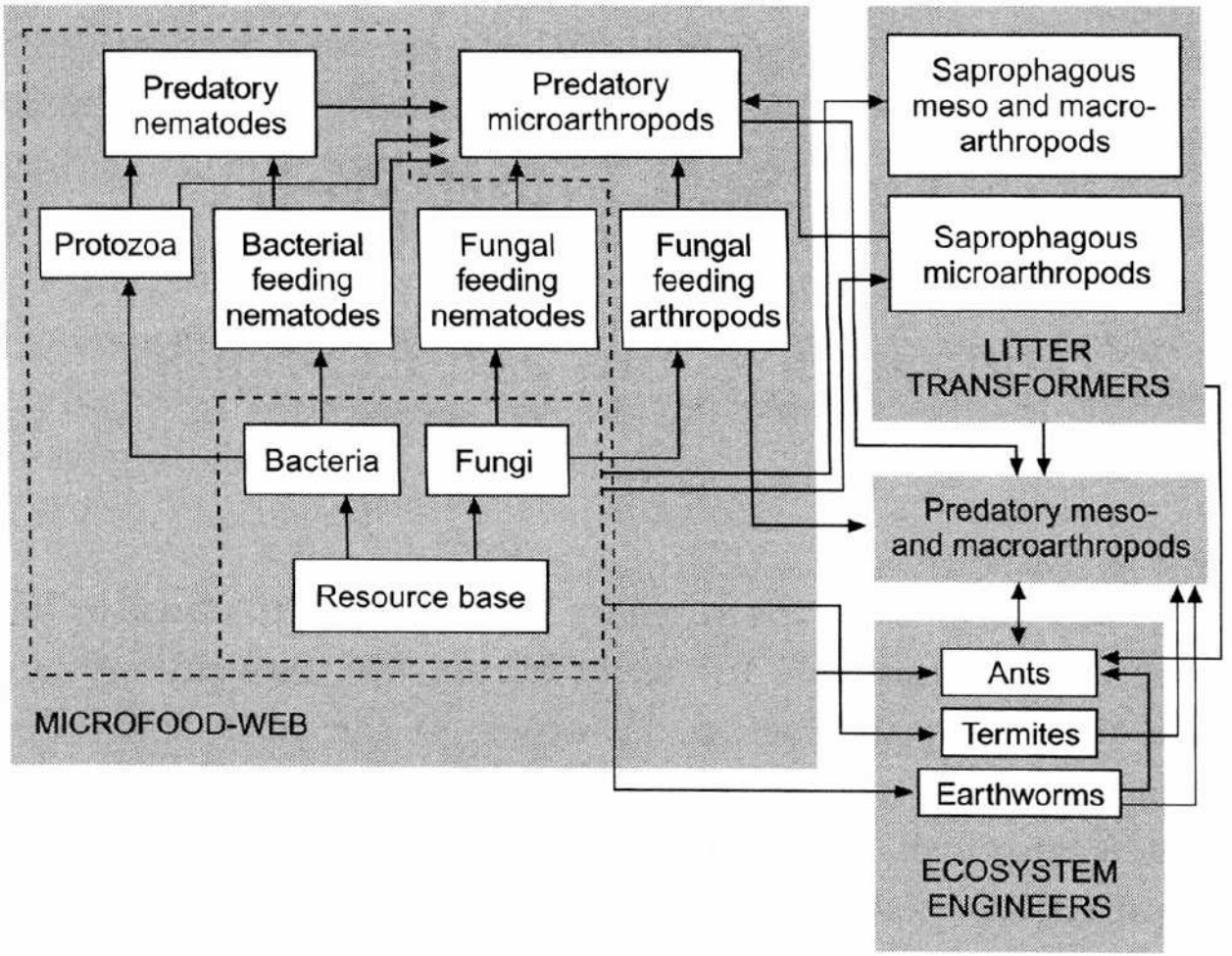
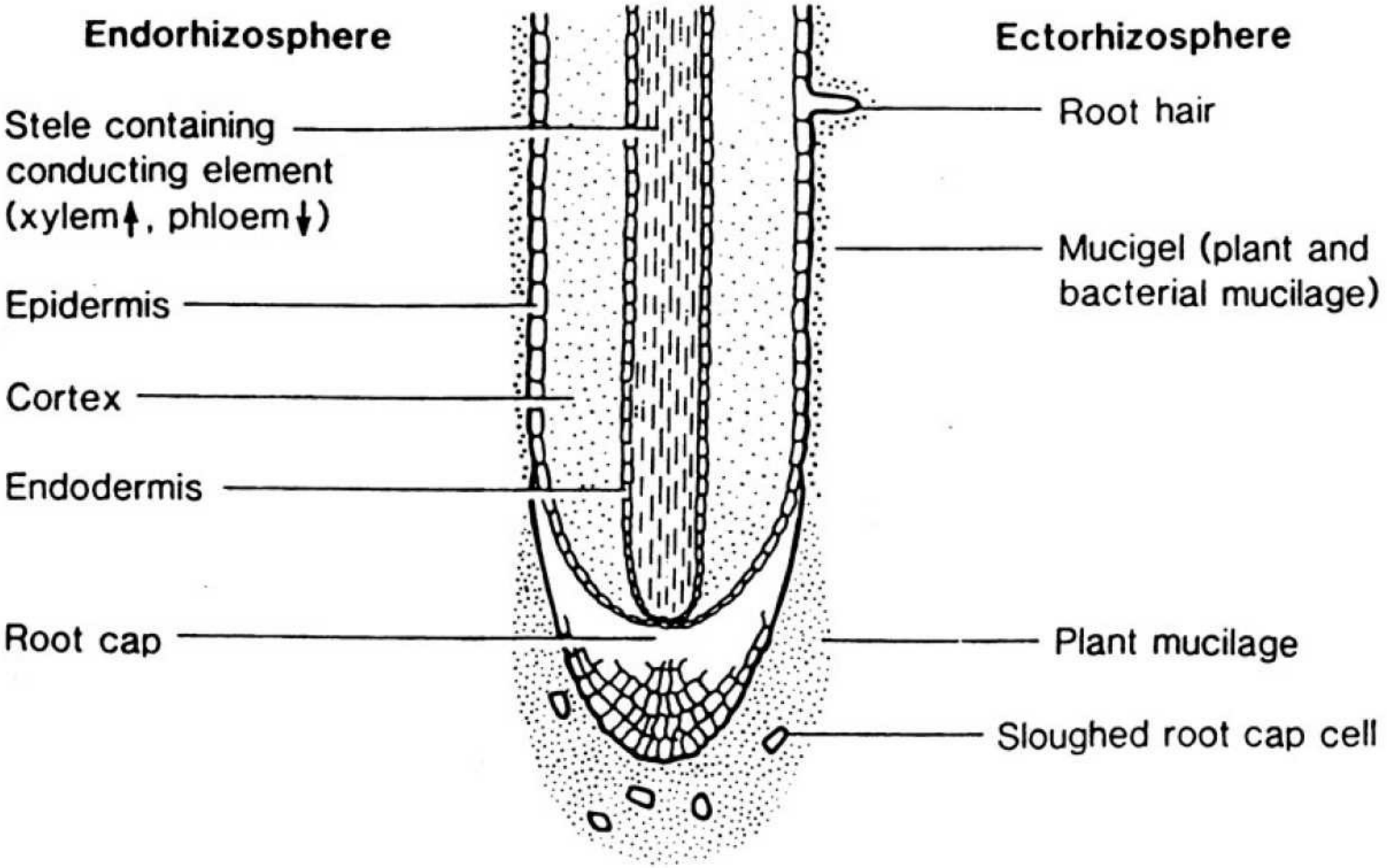


FIGURE 2.1. Structure of the soil food web. Only major groups of organisms and well-established linkages are shown. Arrows indicate direction of energy flow. The microfood-web, litter transformer, and ecosystem engineer categories are derived from Lavelle et al. (1995). Note that the groups of organisms represented in this diagram are only those that have been the most extensively studied; a more complete description of the feeding habits of other, less well-studied fauna, which may nevertheless be ecologically important (e.g., burrowing vertebrates, bacterial-feeding rotifers and tardigrades) is given in Petersen and Luxton (1982).

Rhizosphäre



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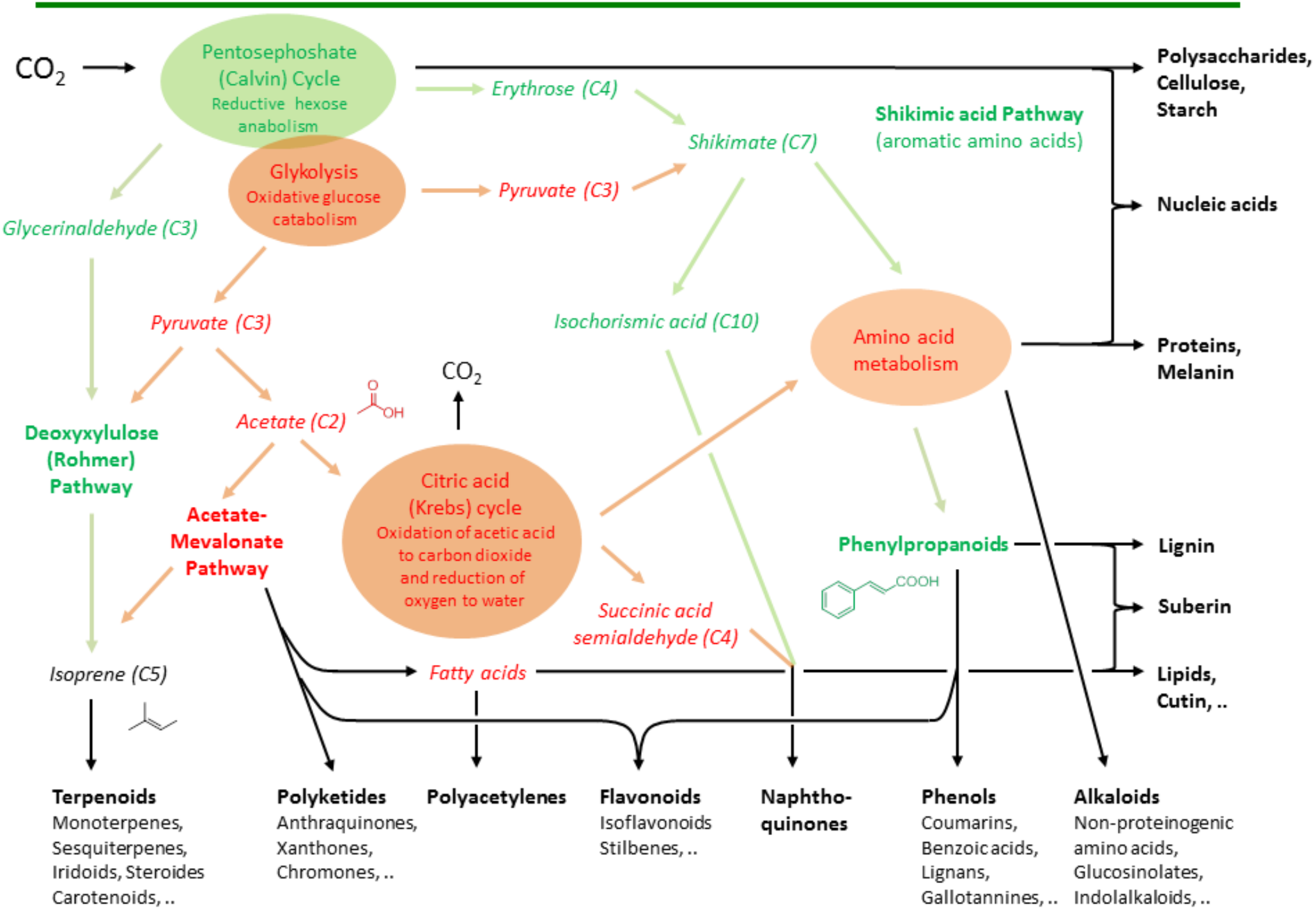
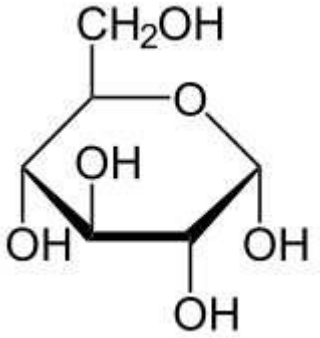
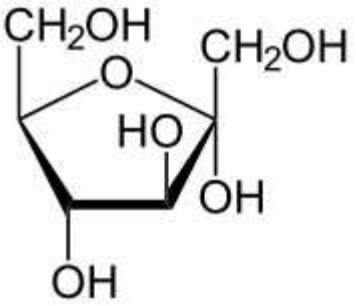
Primary and Secondary Plant Metabolism



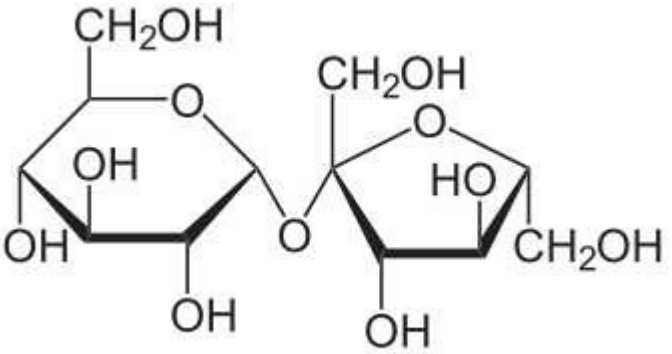
Zucker



Glukose

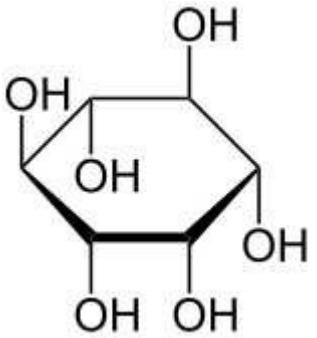


Fruktose



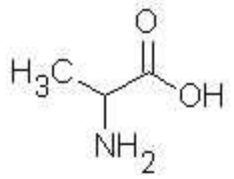
Saccharose

Zuckeralkohole

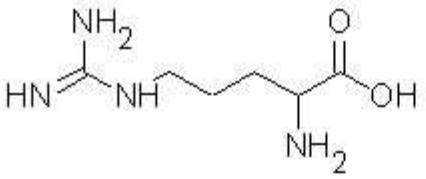


myo-Inosit

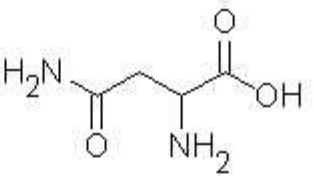
Proteinogene Aminosäuren



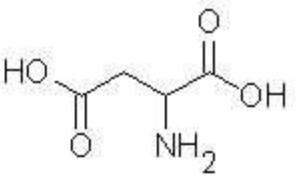
Alanin **(Ala)**



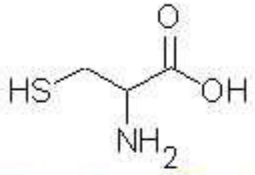
Arginin **(Arg)**



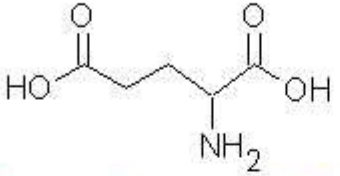
Asparagin **(Asn)**



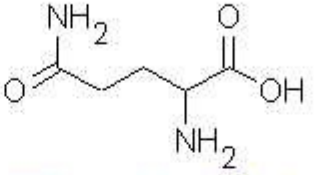
Asparaginsäure **(Asp)**



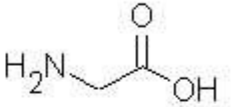
Cystein **(Cys)**



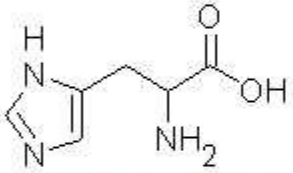
Glutaminsäure **(Glu)**



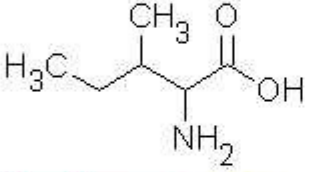
Glutamin **(Gln)**



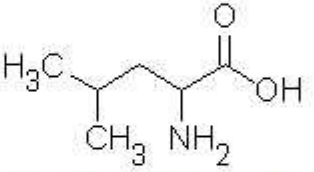
Glycin **(Gly)**



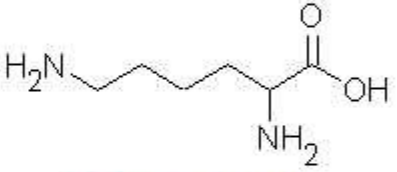
Histidin **(His)**



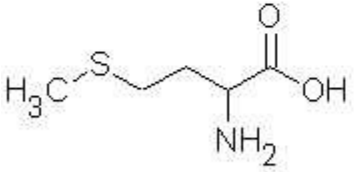
Isoleucin **(Ile)**



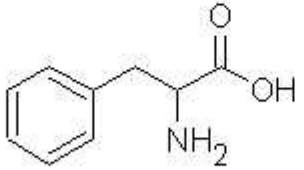
Leucin **(Leu)**



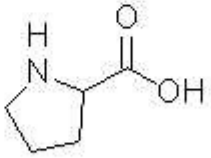
Lysin **(Lys)**



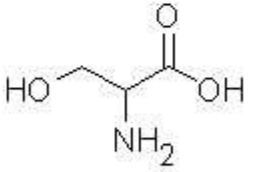
Methionin **(Met)**



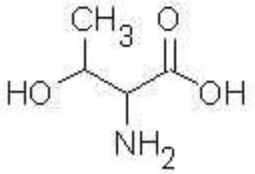
Phenylalanin **(Phe)**



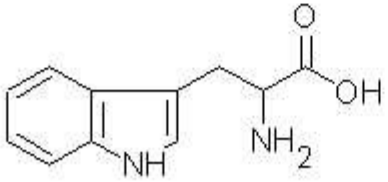
Prolin **(Pro)**



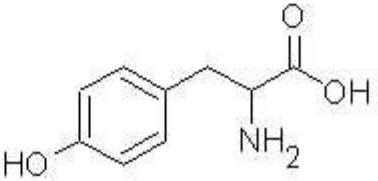
Serin **(Ser)**



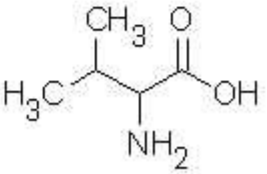
Threonin **(Thr)**



Tryptophan **(Trp)**

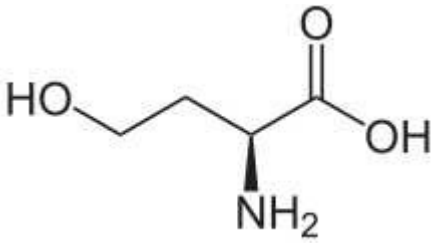


Tyrosin **(Tyr)**



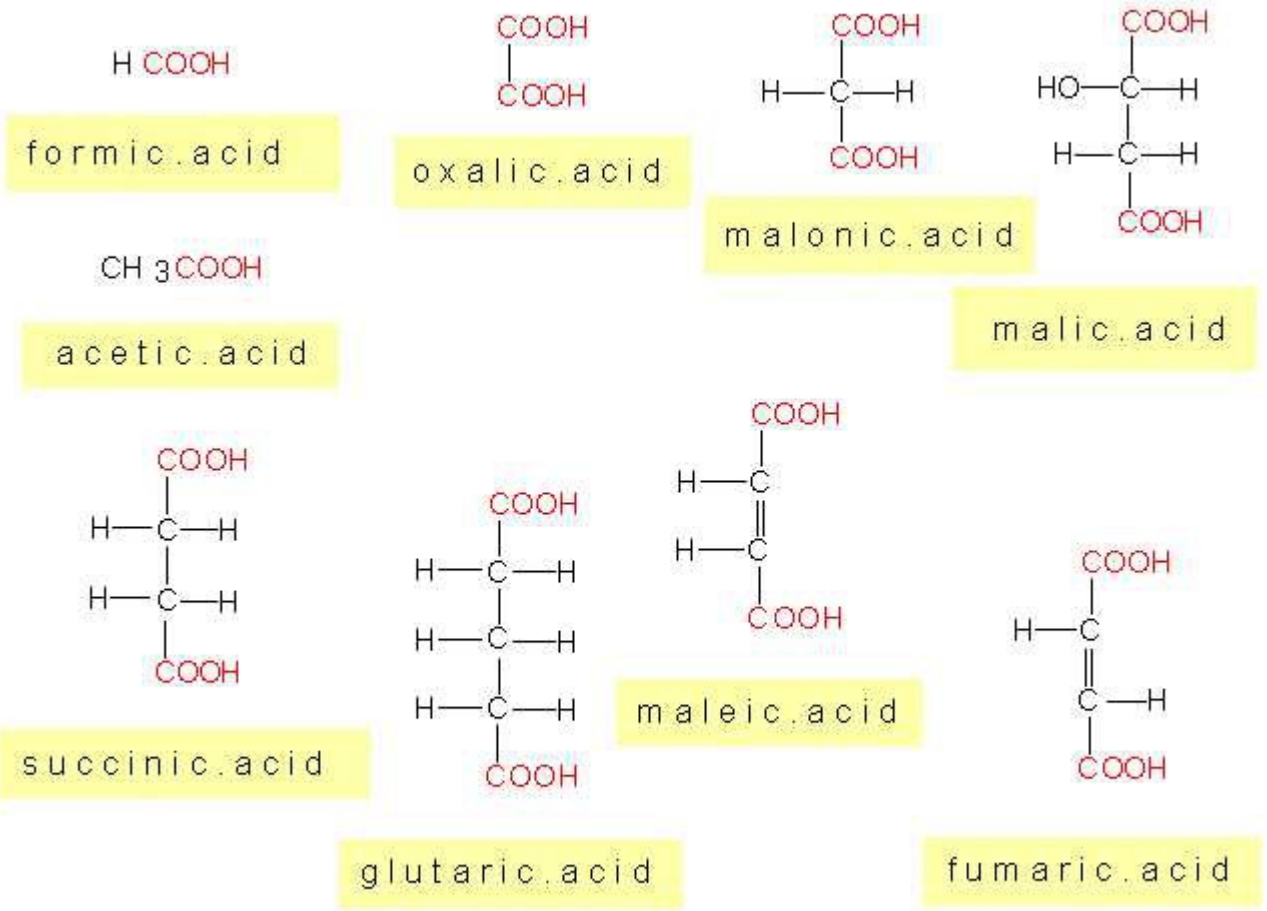
Valin **(Val)**

Nichtproteinogene Aminosäuren

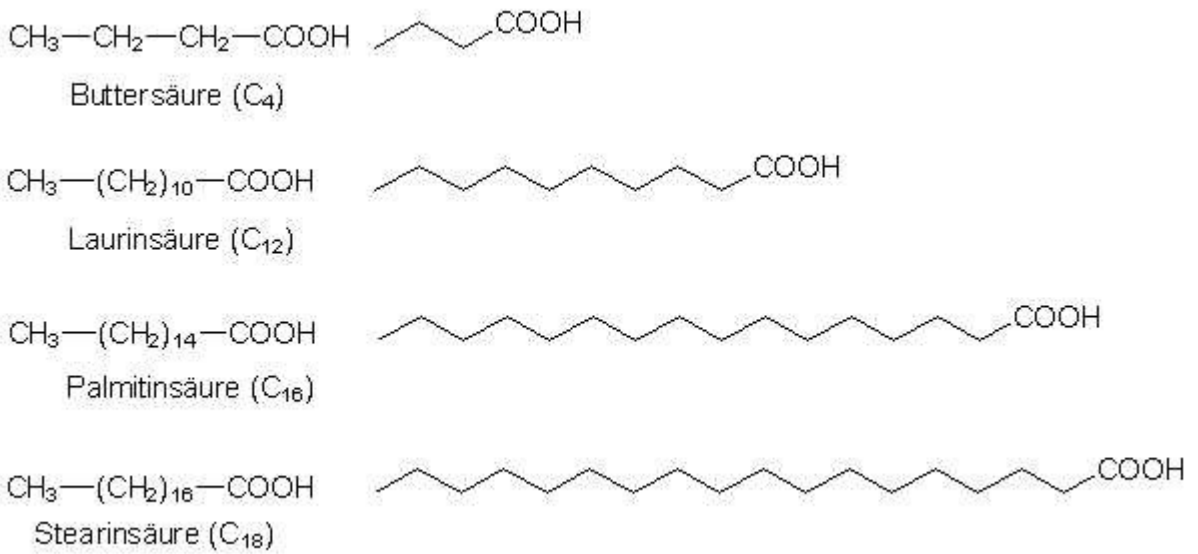


Homoserin

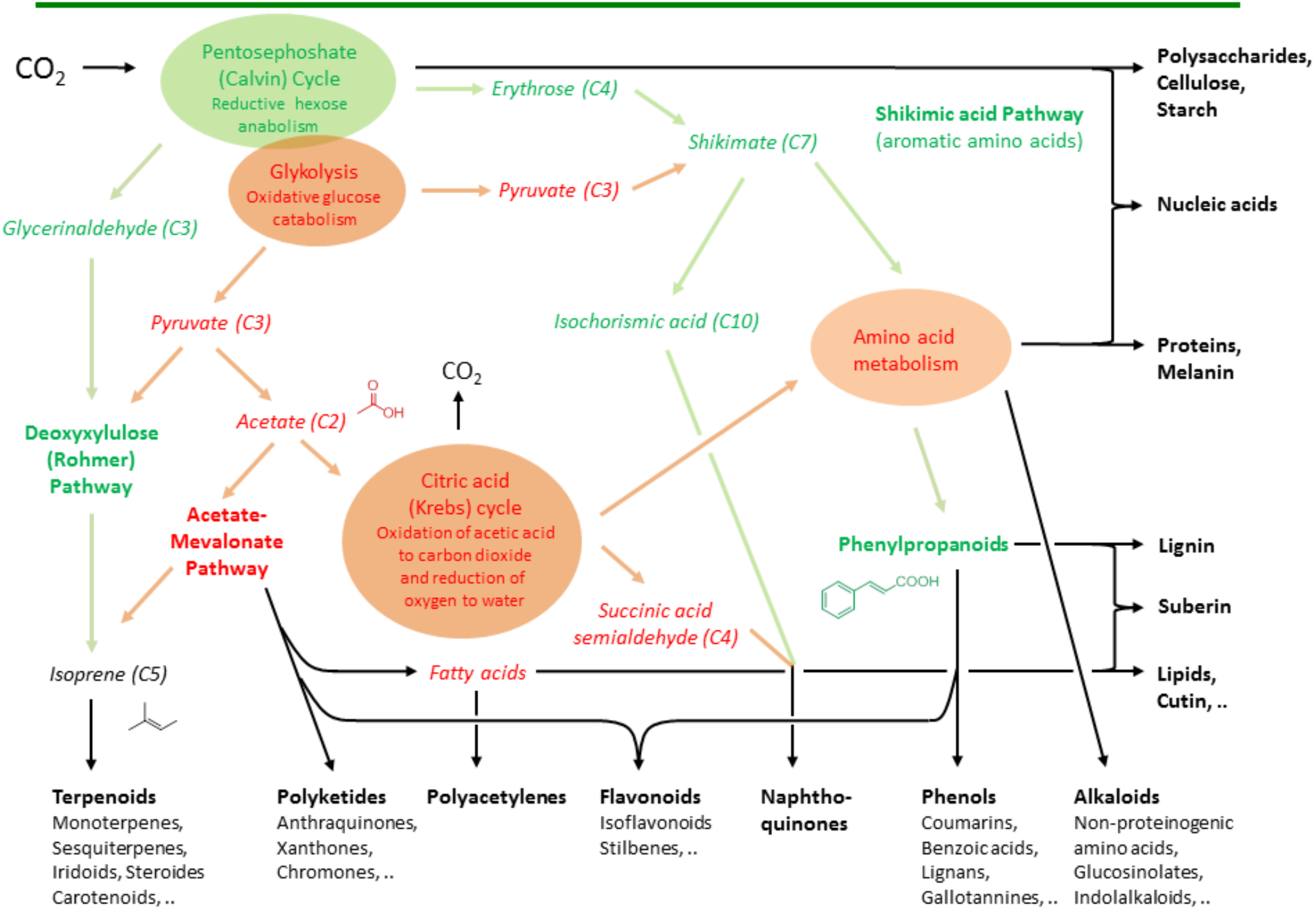
Organische Säuren



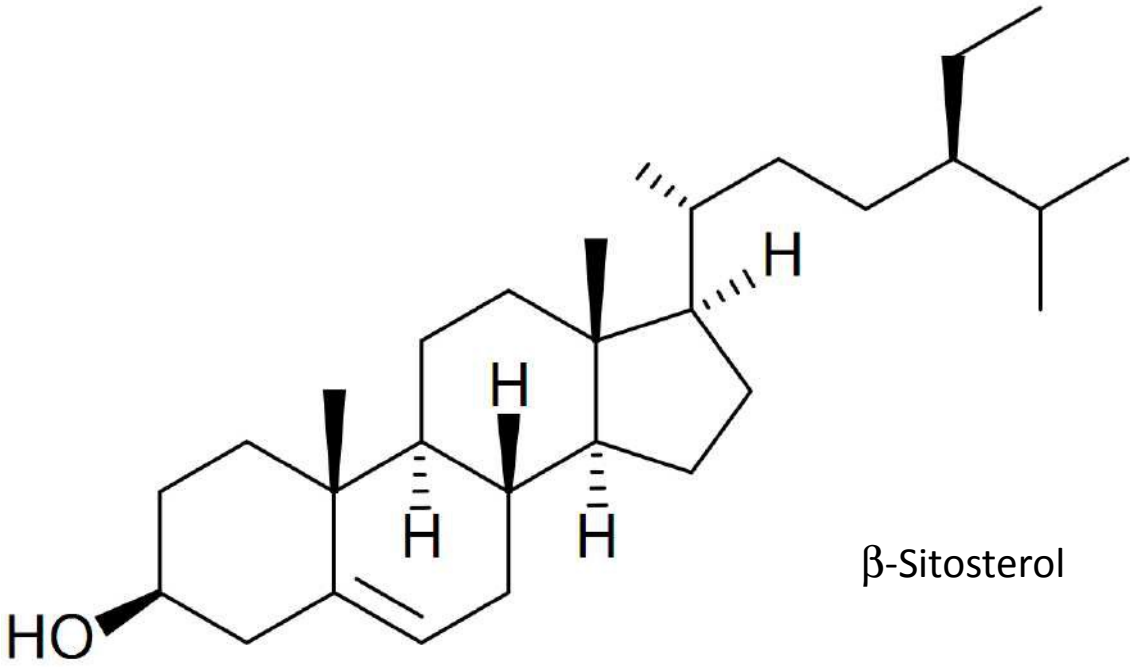
Fettsäuren


CH3—CH2—CH2—COOH
COOH
Buttersäure (C4)
CH3—(CH2)10—COOH
COOH
Laurinsäure (C12)
CH3—(CH2)14—COOH
COOH
Palmitinsäure (C16)
CH3—(CH2)16—COOH
COOH
Stearinsäure (C18)

Primary and Secondary Plant Metabolism

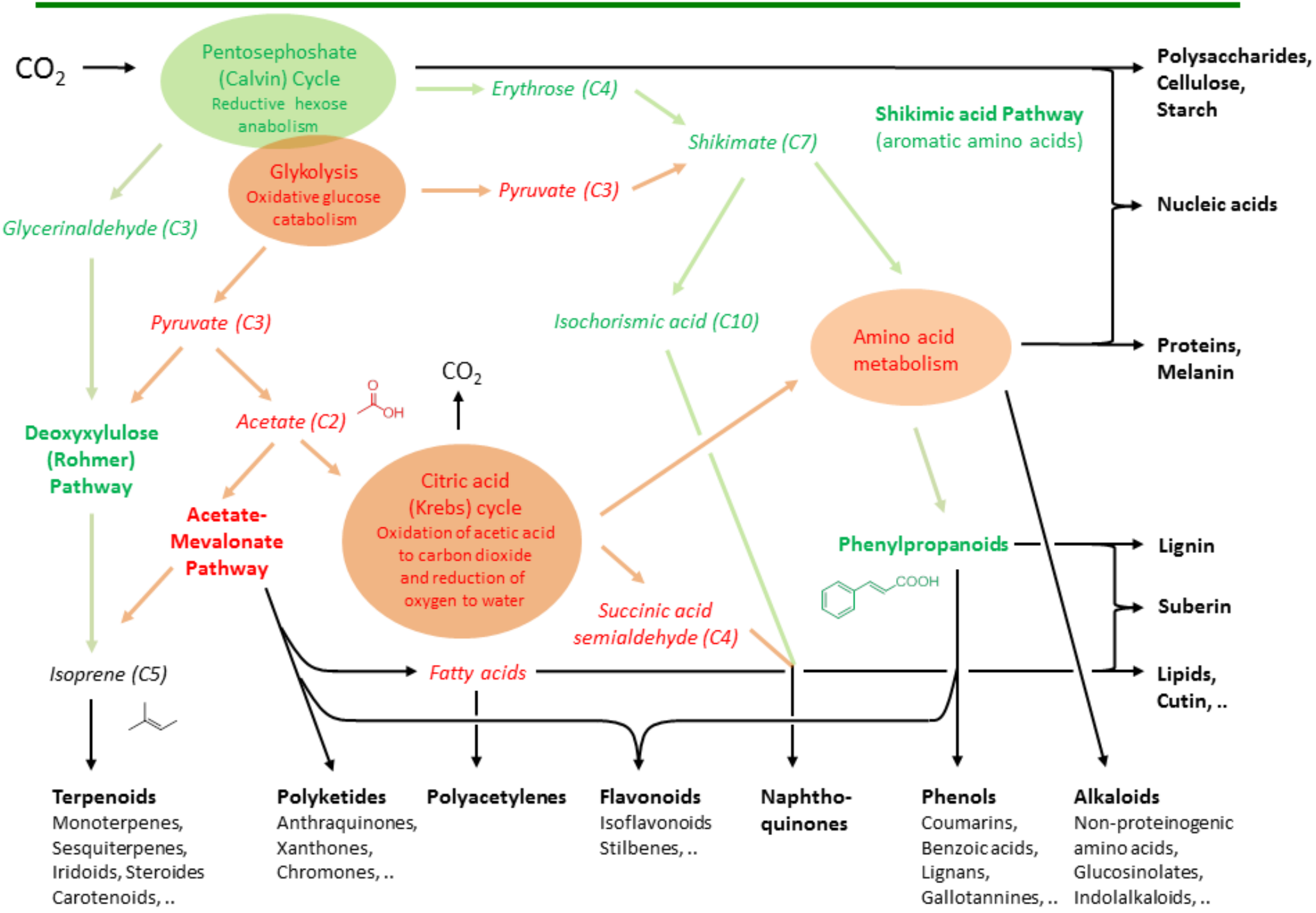


Steroide



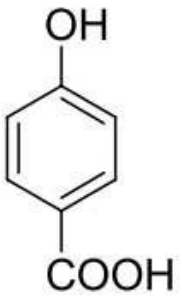
β-Sitosterol

Primary and Secondary Plant Metabolism

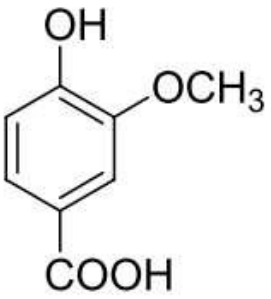


Phenolische Säuren

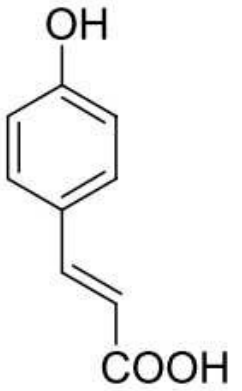
Benzoesäure



p-Hydroxybenzoesäure

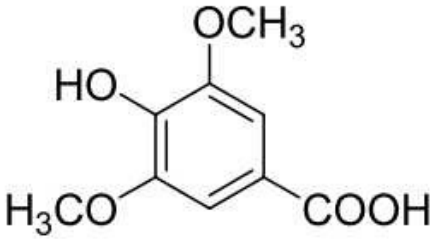


Vanillinsäure

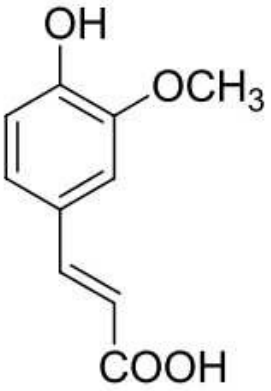


p-Cumarsäure

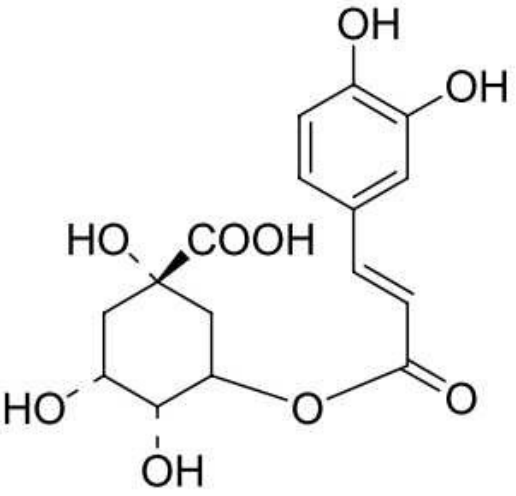
Phenylessigsäure



Syringasäure

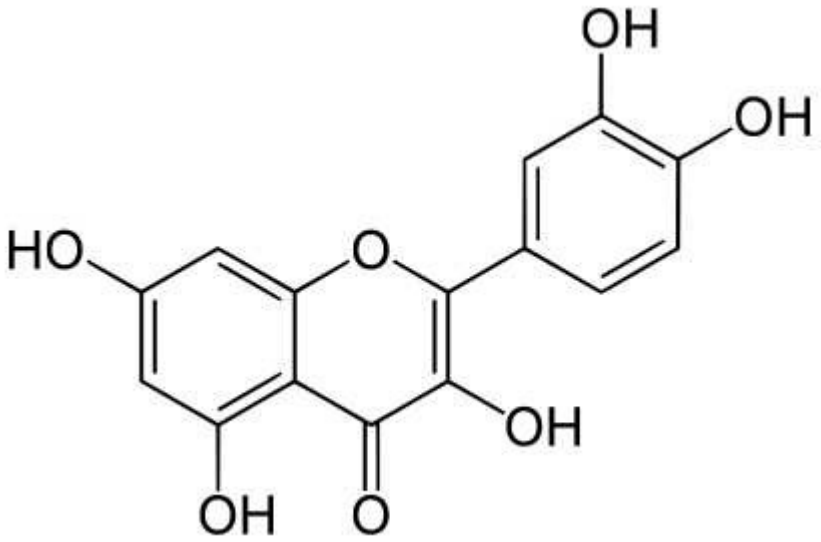


Ferulasäure

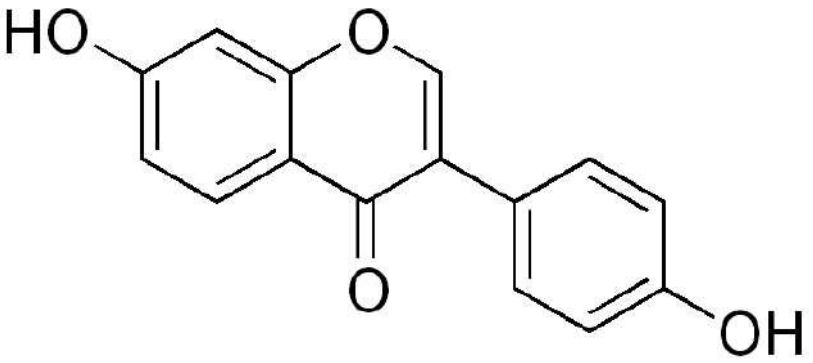


Chlorogensäure

Flavonoide

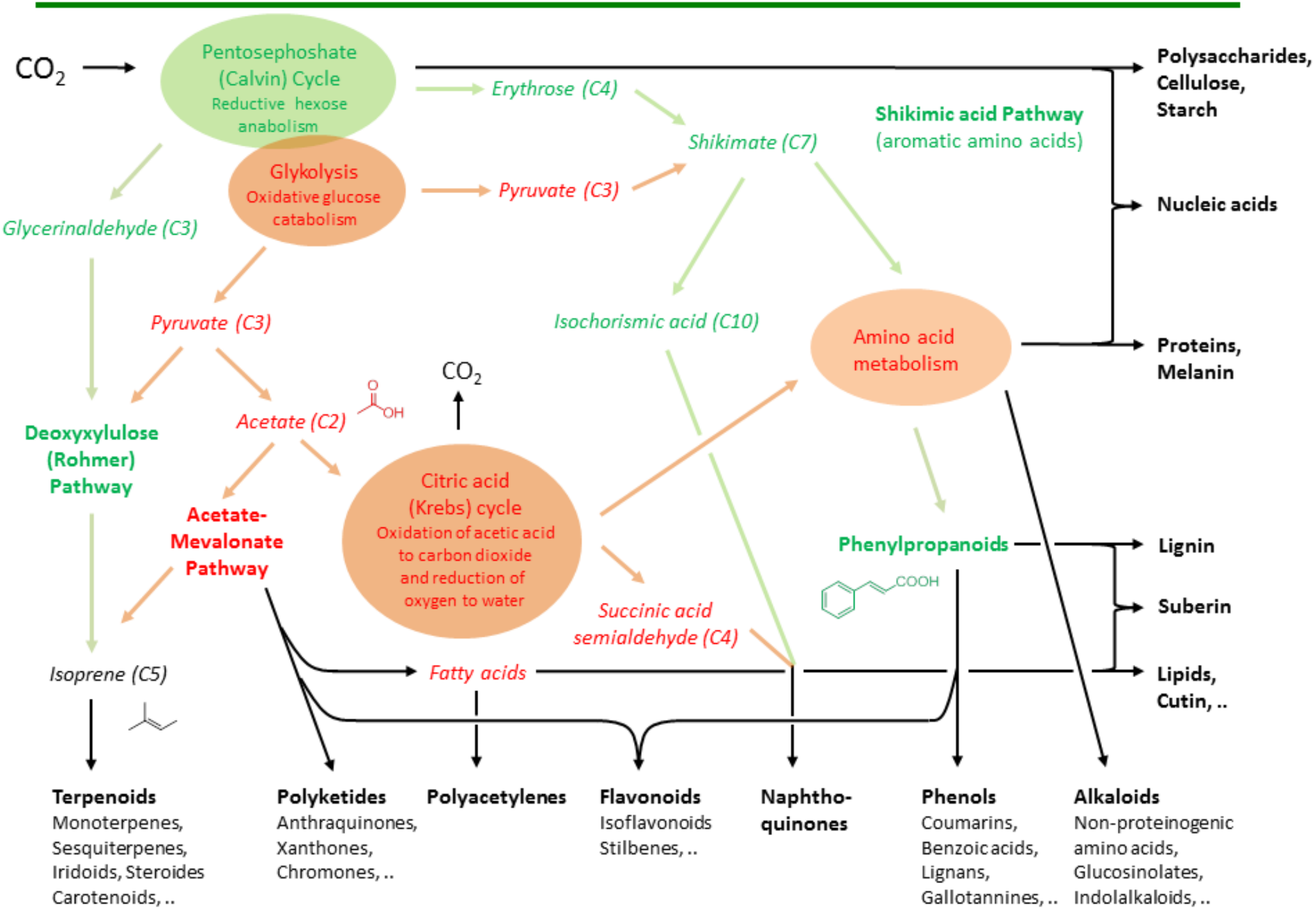


Quercetin

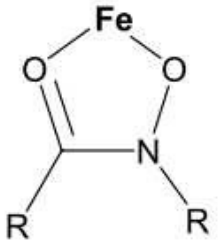


Daidzaidin

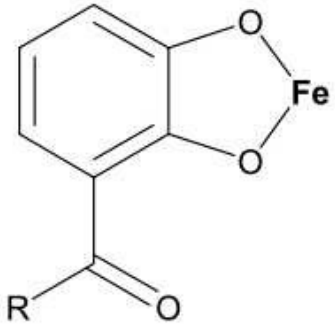
Primary and Secondary Plant Metabolism



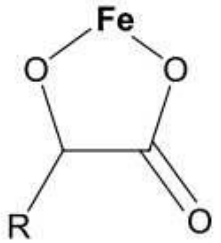
Siderophore



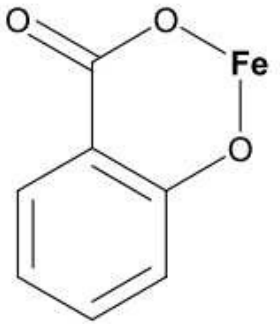
Hydroxamate



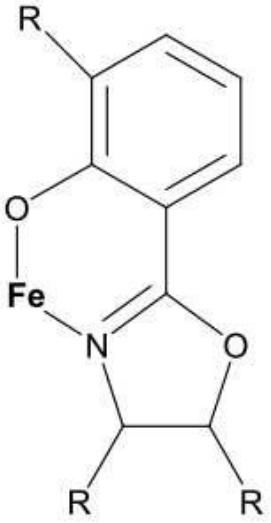
Catechol



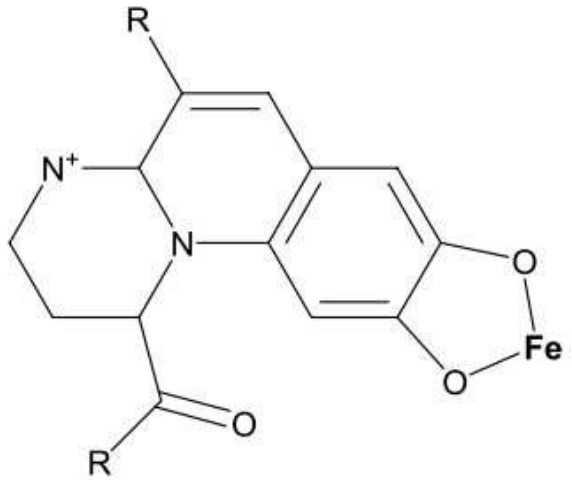
α-Hydroxysäure
(Zitronensäure)



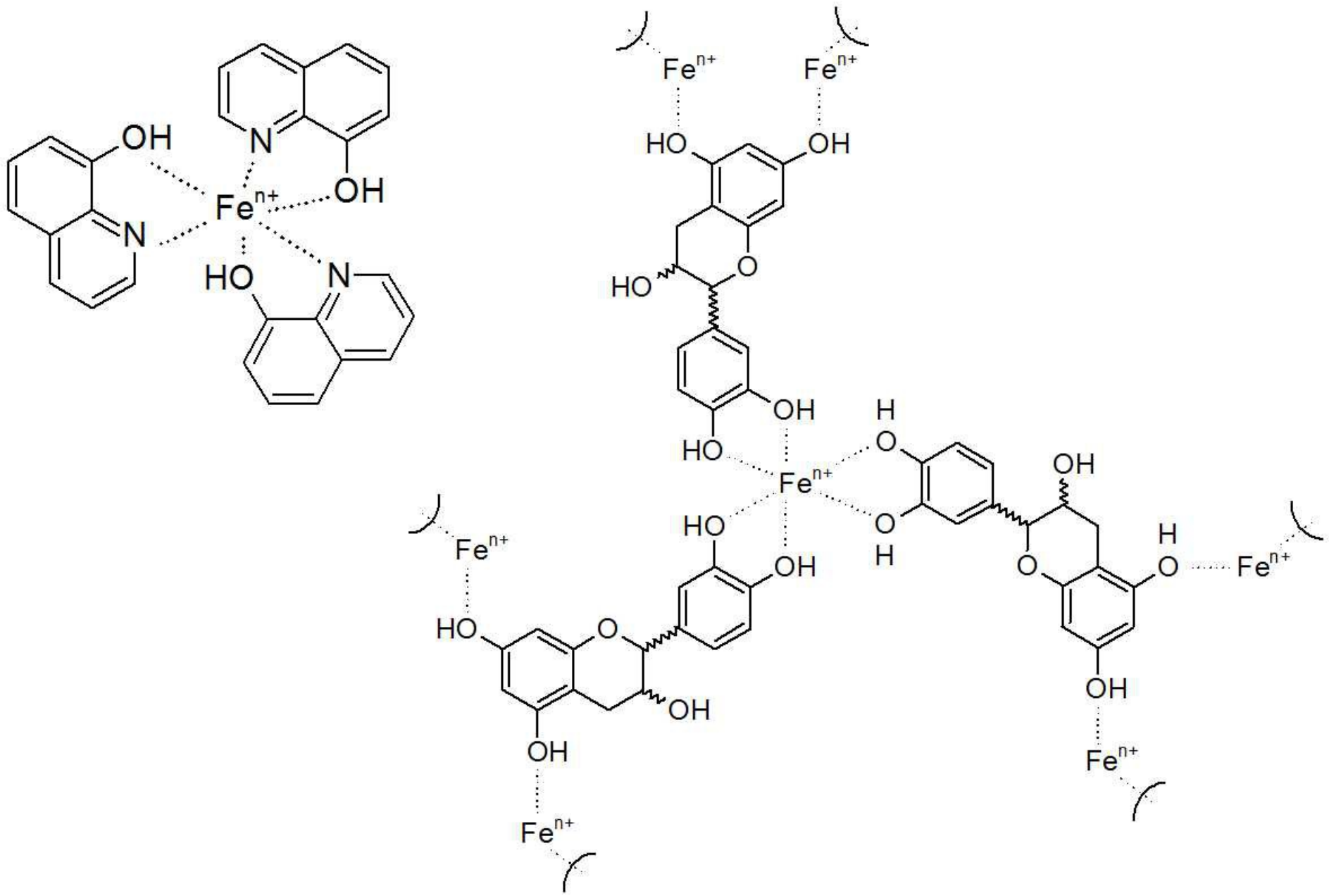
Salicylsäure



Mycobactine



Pseudobactine


OH
N
Fe n+
OH
N
HO
N
Fe n+
Fe n+
HO
OH
HO
O
HO
OH
H
O
Fe n+
HO
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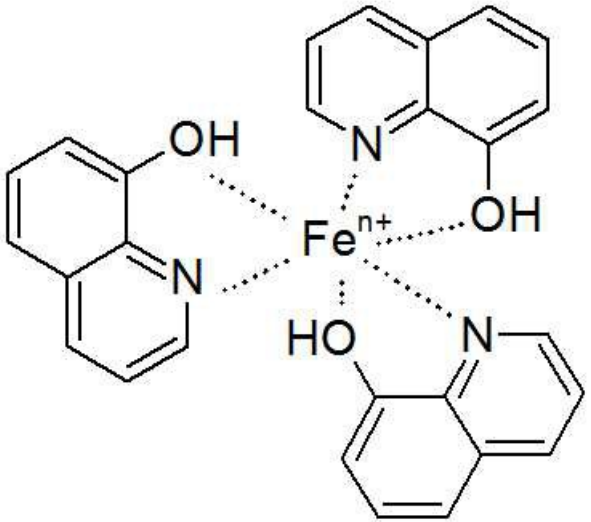
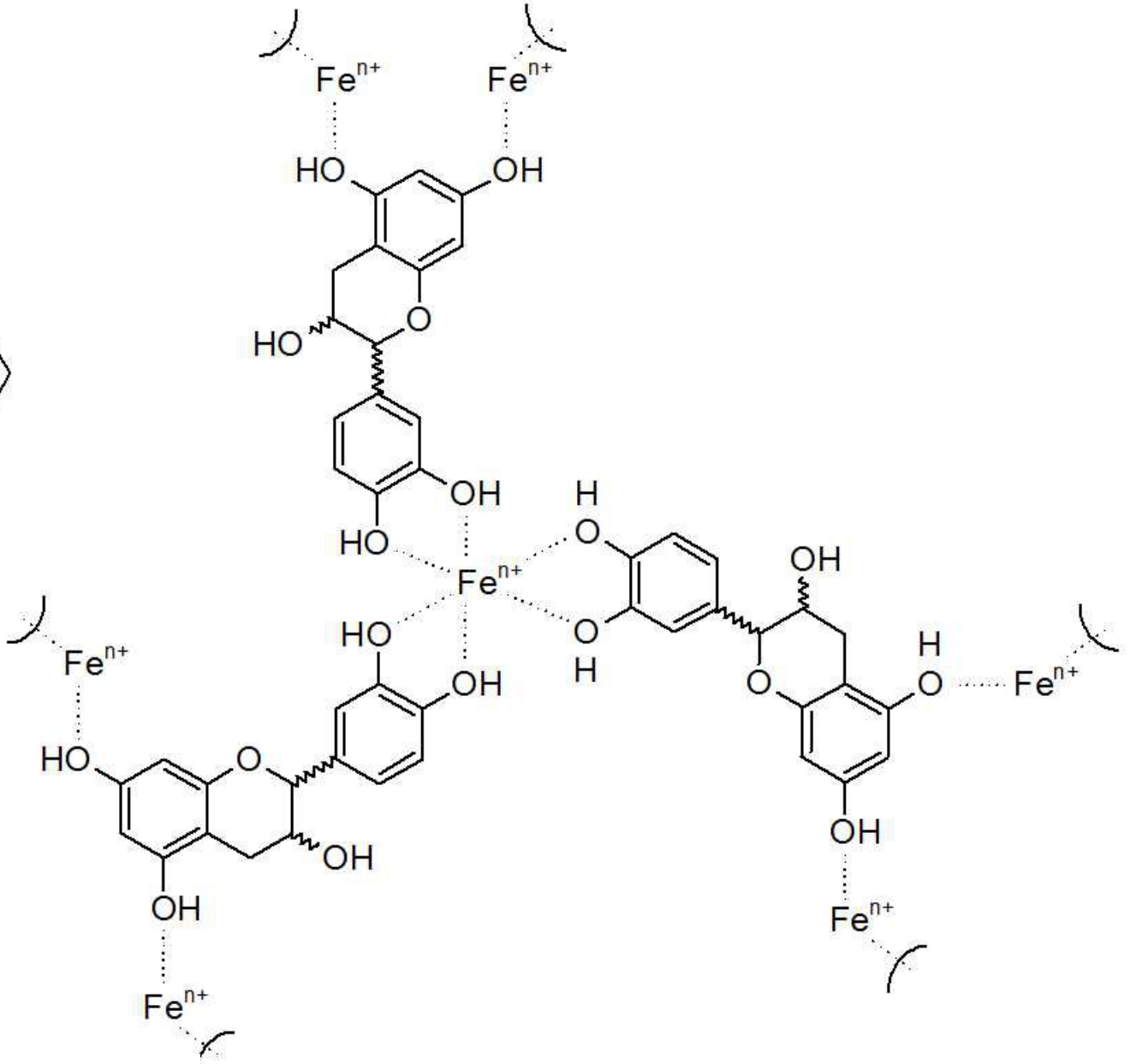
Fe n+





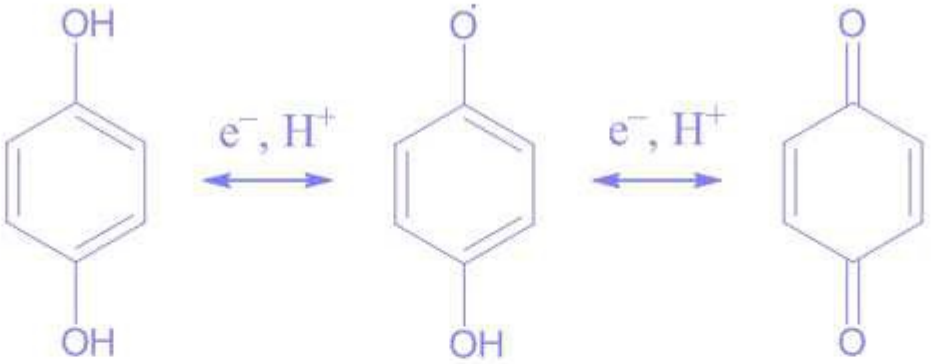
Haber-Weiss Reaktion (1+2)
Fenton Reaktion (2)

1.) $Fe^{3+} + \bullet O_2^- \longrightarrow Fe^{2+} + \bullet O_2$

2.) $Fe^{2+} + H_2O_2 \longrightarrow Fe^{3+} + \bullet OH + \bullet OH^-$

Redox chemistry

Q



hydroquinone semiquinone quinone

$$> Fe^{III}OH + QH_2 \longleftrightarrow > Fe^{II}OH^- + QH + H^+$$

$$> Fe^{III}OH + QH \longleftrightarrow > Fe^{II}OH^- + Q + H^+$$

$$> Fe^{II}OH^- \longleftrightarrow Fe(H_2O)_6^{2+}$$

Richter DD et al. (2007) In: The Rhizosphere: An Ecological Perspective, Cardon ZG, Whitbeck JL eds., Academic Press.

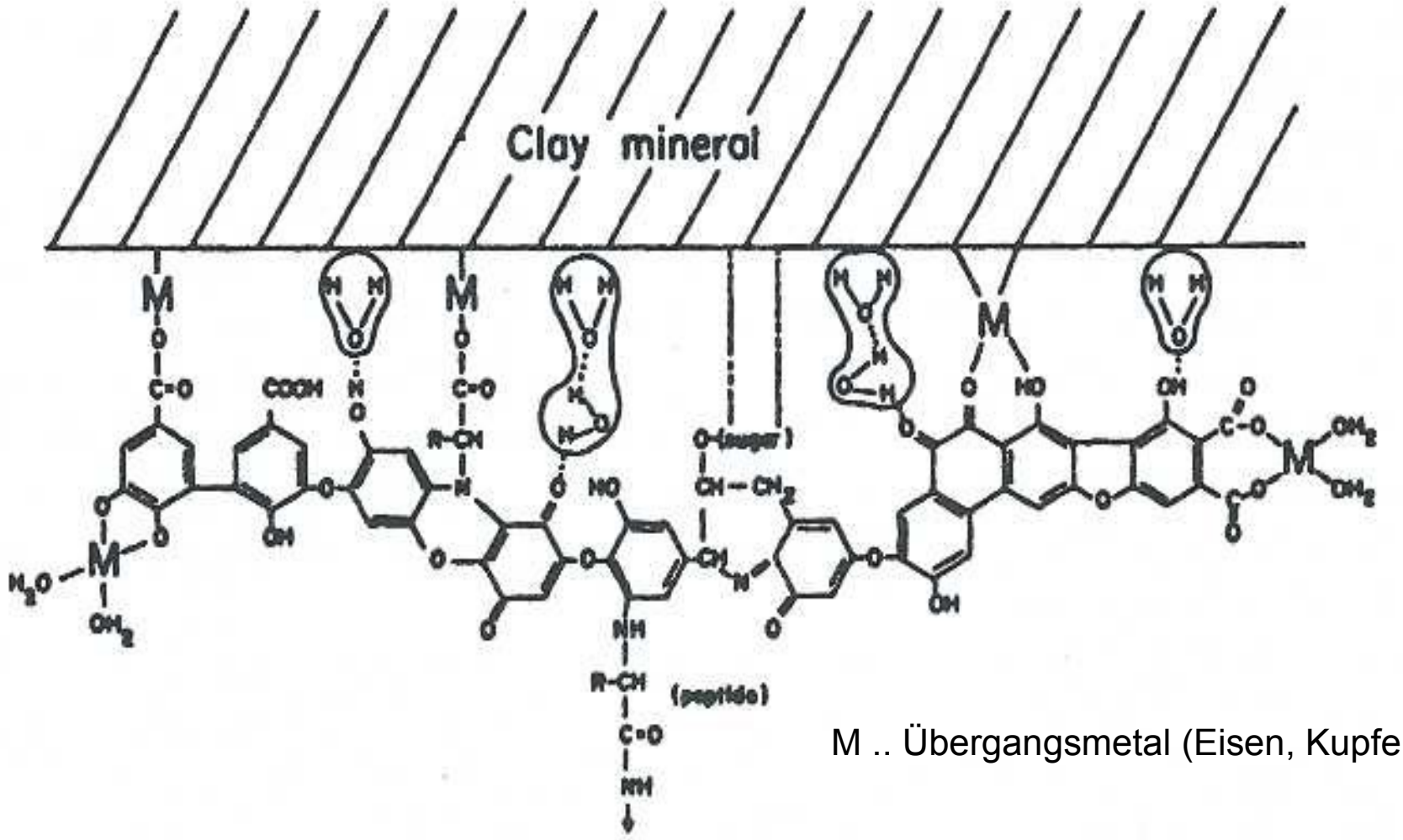


Fig. 18.3 Schematic diagram of clay–humate complex in soil. From Stevenson and Ardakani[20]

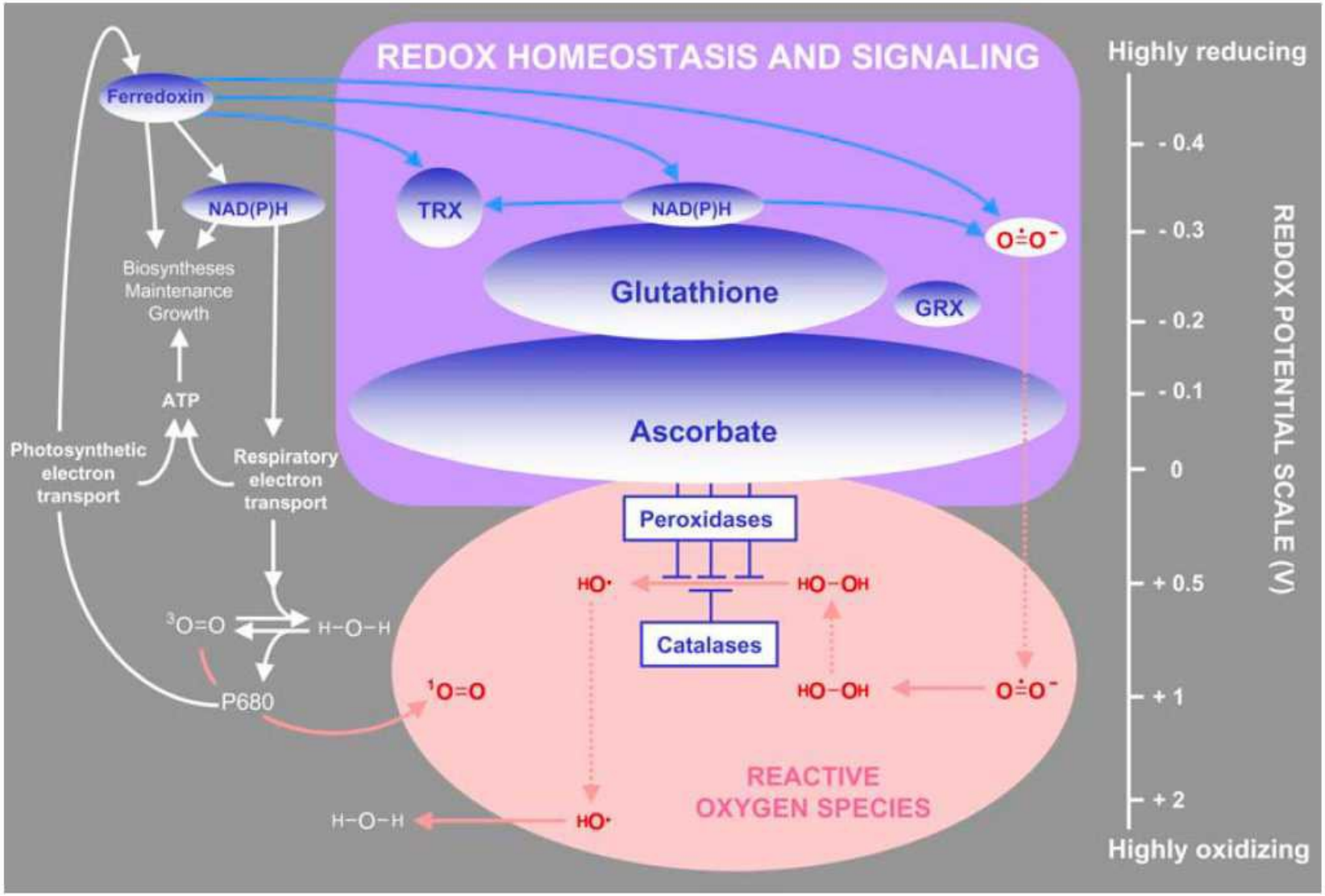


Figure 1. Reductant–Antioxidant–Oxidant Interactions in Redox Homeostasis and Signaling.

Nonenzymic components are positioned on a nonlinear scale (right) at their approximate electrochemical potential in volts. In nonquiescent cells under optimal conditions, large pools of glutathione and ascorbate are maintained in a highly reduced state, and buffer ROS that are continuously produced by oxidases or by electron transport components, such as FeS centers, semiquinones, or (as depicted) ferredoxin. Other key redox signaling components are thioredoxins (TRX) and glutaredoxins (GRX), which are reduced by ferredoxin, NADPH, or glutathione. Production of the superoxide anion ($OO^{\cdot -}$) and H_2O_2 (HOOH) can be induced or promoted under certain conditions, leading to increased oxidative charge on the reductant-antioxidant system. Reductive cleavage of H_2O_2 produces the hydroxyl radical ($OH^{\cdot}$), an extremely reactive electron and hydrogen acceptor whose reduction potentially involves indiscriminate oxidation of cellular components. Excessive production of $OH^{\cdot}$ is avoided by enzymatic processing of H_2O_2 to water by peroxidases or to water and O_2 by catalases. Signaling linked to increased availability of ROS may be caused, limited, or mediated by changes in antioxidant capacity (see text).

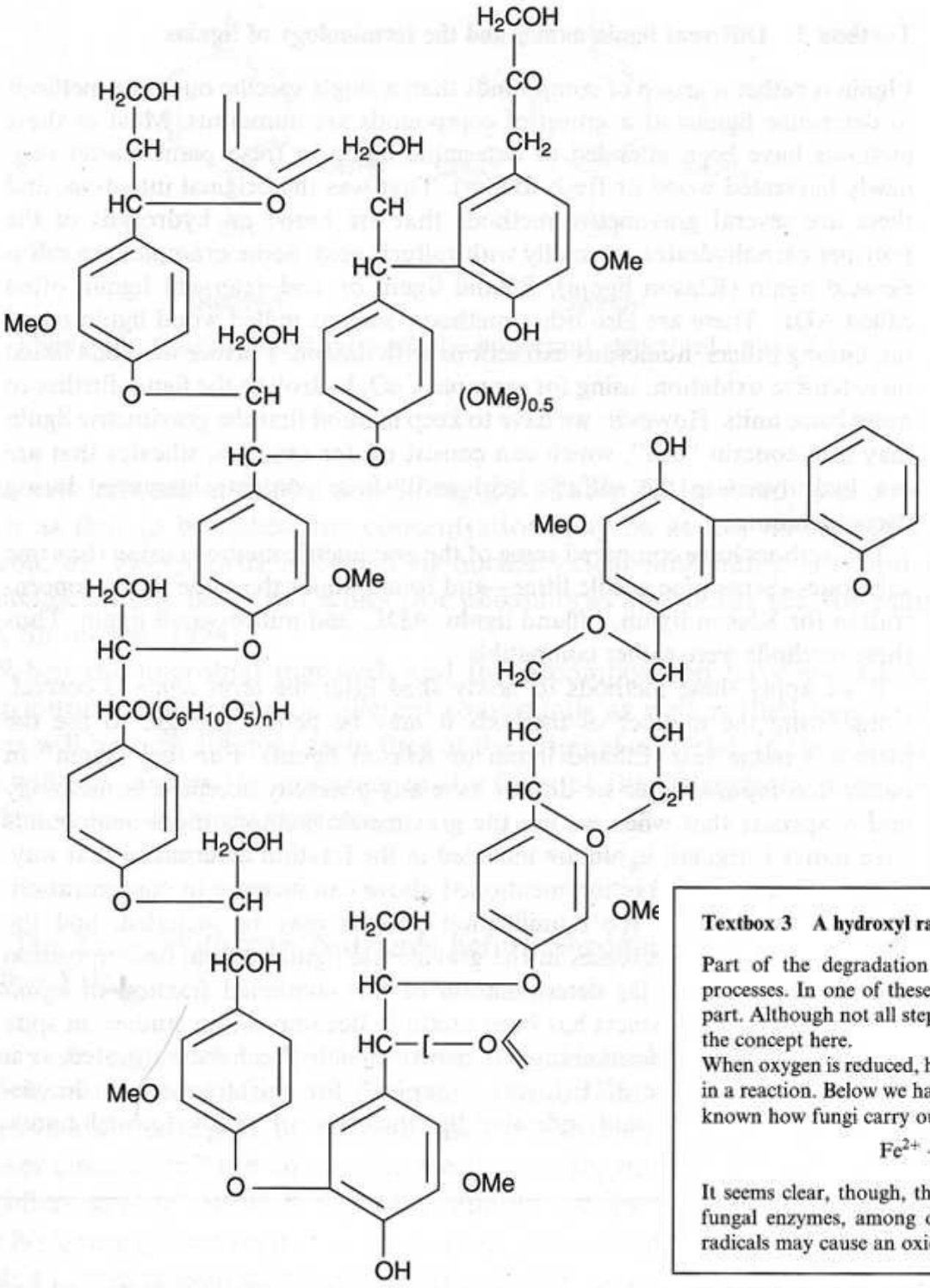
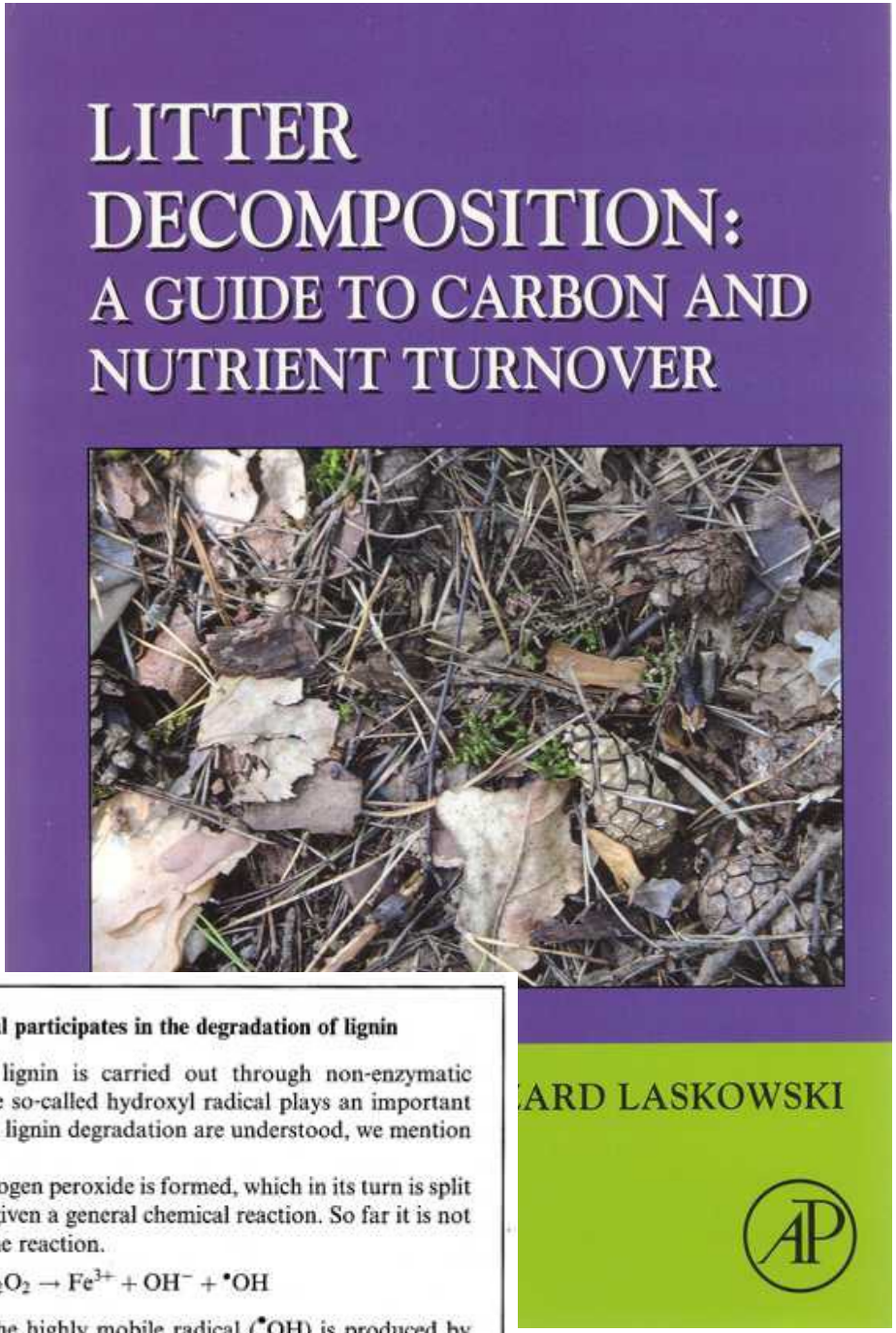


Figure 9 Lignin molecule from Norway spruce.



Textbox 3 A hydroxyl radical participates in the degradation of lignin

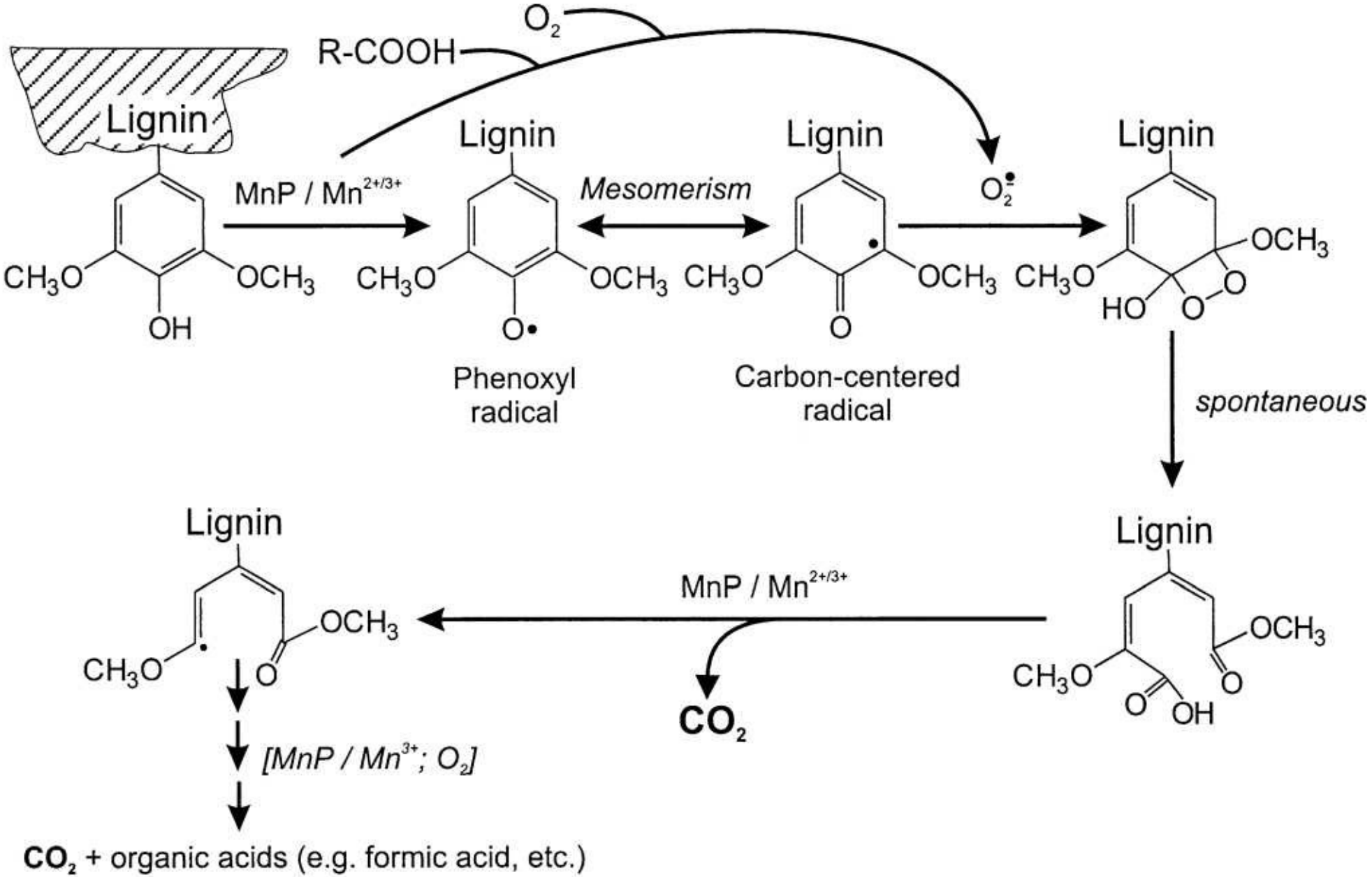
Part of the degradation of lignin is carried out through non-enzymatic processes. In one of these, the so-called hydroxyl radical plays an important part. Although not all steps in lignin degradation are understood, we mention the concept here.

When oxygen is reduced, hydrogen peroxide is formed, which in its turn is split in a reaction. Below we have given a general chemical reaction. So far it is not known how fungi carry out the reaction.

$$Fe^{2+} + H_2O_2 \rightarrow Fe^{3+} + OH^- + {}^{\bullet}OH$$

It seems clear, though, that the highly mobile radical ($^{\bullet}OH$) is produced by fungal enzymes, among others, a cellobiase oxidase and laccase. Hydroxyl radicals may cause an oxidation of lignin to quinines.

Mangan Peroxidase (MnP)



pH = 5-6

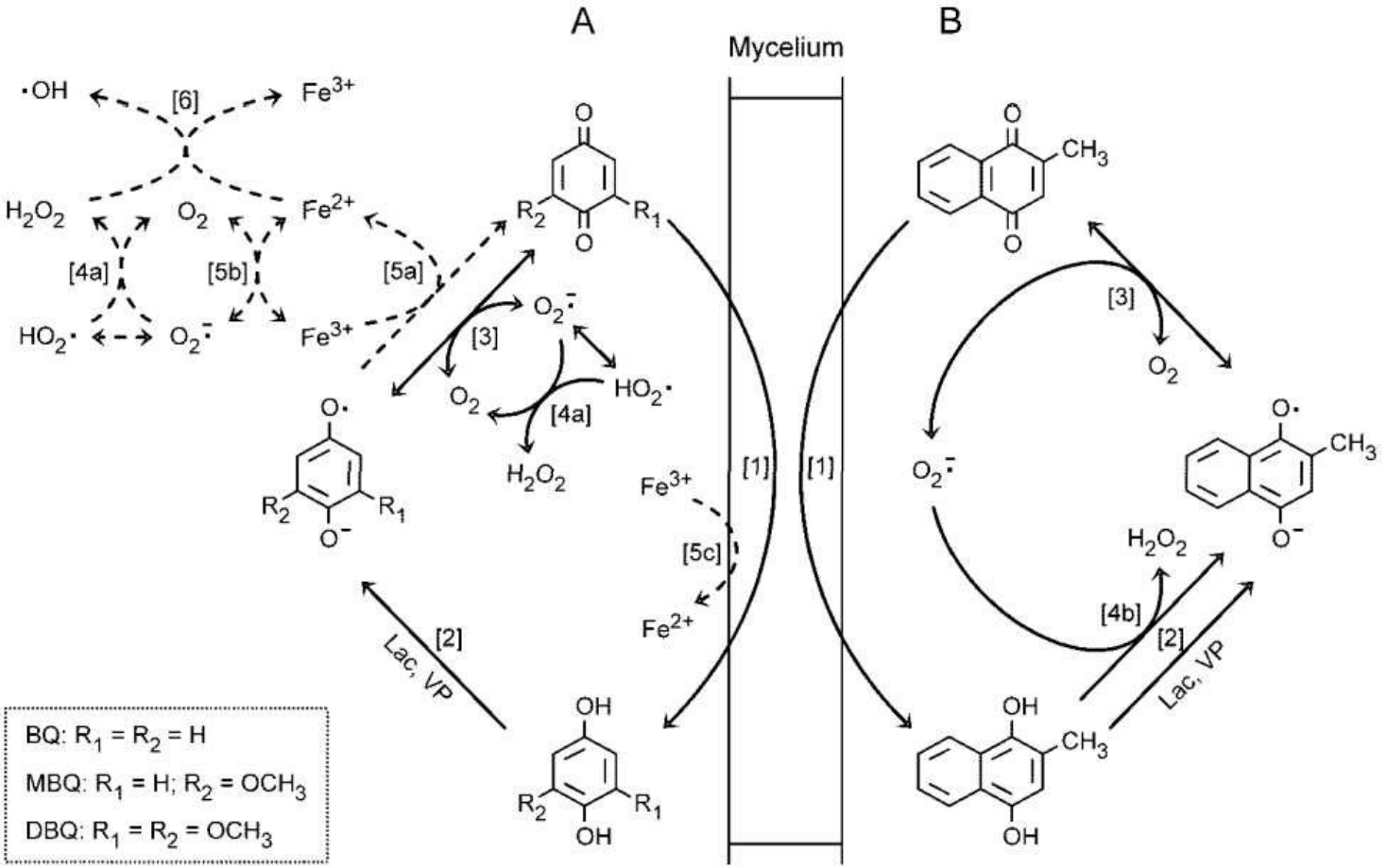


FIG. 8. Scheme of the quinone redox cycling process in *P. eryngii* (see Discussion for an explanation). (A) Main reactions involved in ROS production through BQ, MBQ, and DBQ redox cycling in the absence and presence of Fe^{3+}-EDTA (solid and dashed arrows, respectively). (B) MD redox cycling, showing hydroquinone propagation by $O_2^{\cdot -}$. Reversible reactions are indicated by double arrows.

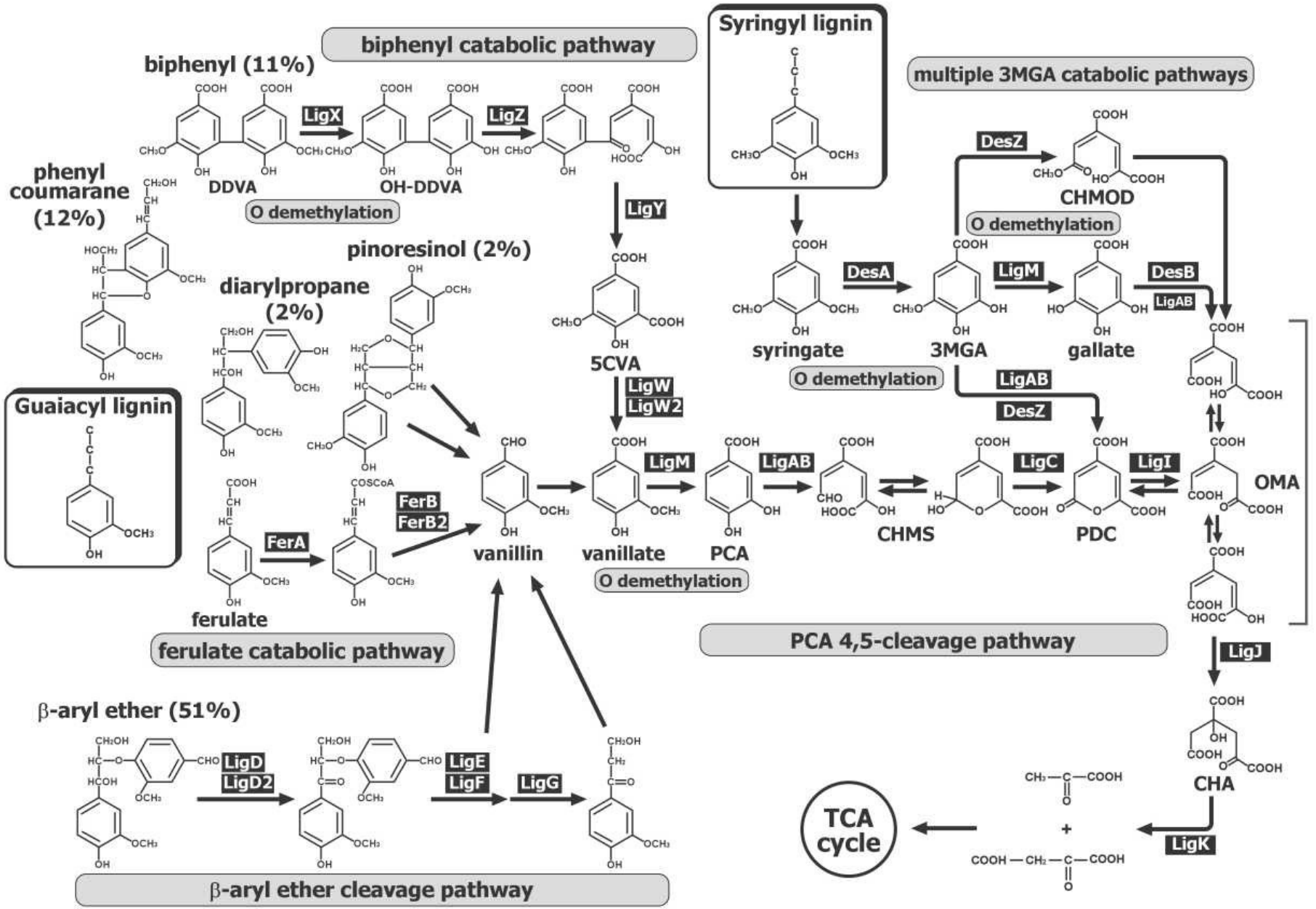


Fig. 1. Catabolic Pathways for the Degradation of Lignin-Derived Aromatic Compounds by *S. paucimobilis* SYK-6.

SYK-6 is able to grow on various lignin-derived biaryls and monoaryls *via* the PCA 4,5-cleavage pathway and the multiple 3MGA catabolic pathways. The percentages are the ratios of the intermonomer linkages in native lignin.[101] *Abbreviations*: DDVA, 5,5′-dehydrodivanillate; OH-DDVA, 2,2′,3-trihydroxy-3′-methoxy-5,5′-dicarboxybiphenyl; 5CVA, 5-carboxyvanillate; PCA, protocatechuate; CHMS, 4-carboxy-2-hydroxymuconate-6-semialdehyde; PDC, 2-pyrone-4,6-dicarboxylate; OMA, 4-oxalomesaconate; CHA, 4-carboxy-4-hydroxy-2-oxoadipate; 3MGA, 3-*O*-methylgallate; CHMOD, 4-carboxy-2-hydroxy-6-methoxy-6-oxohexa-2,4-dienoate; TCA, tricarboxylic acid.

Exudationsmechanismen

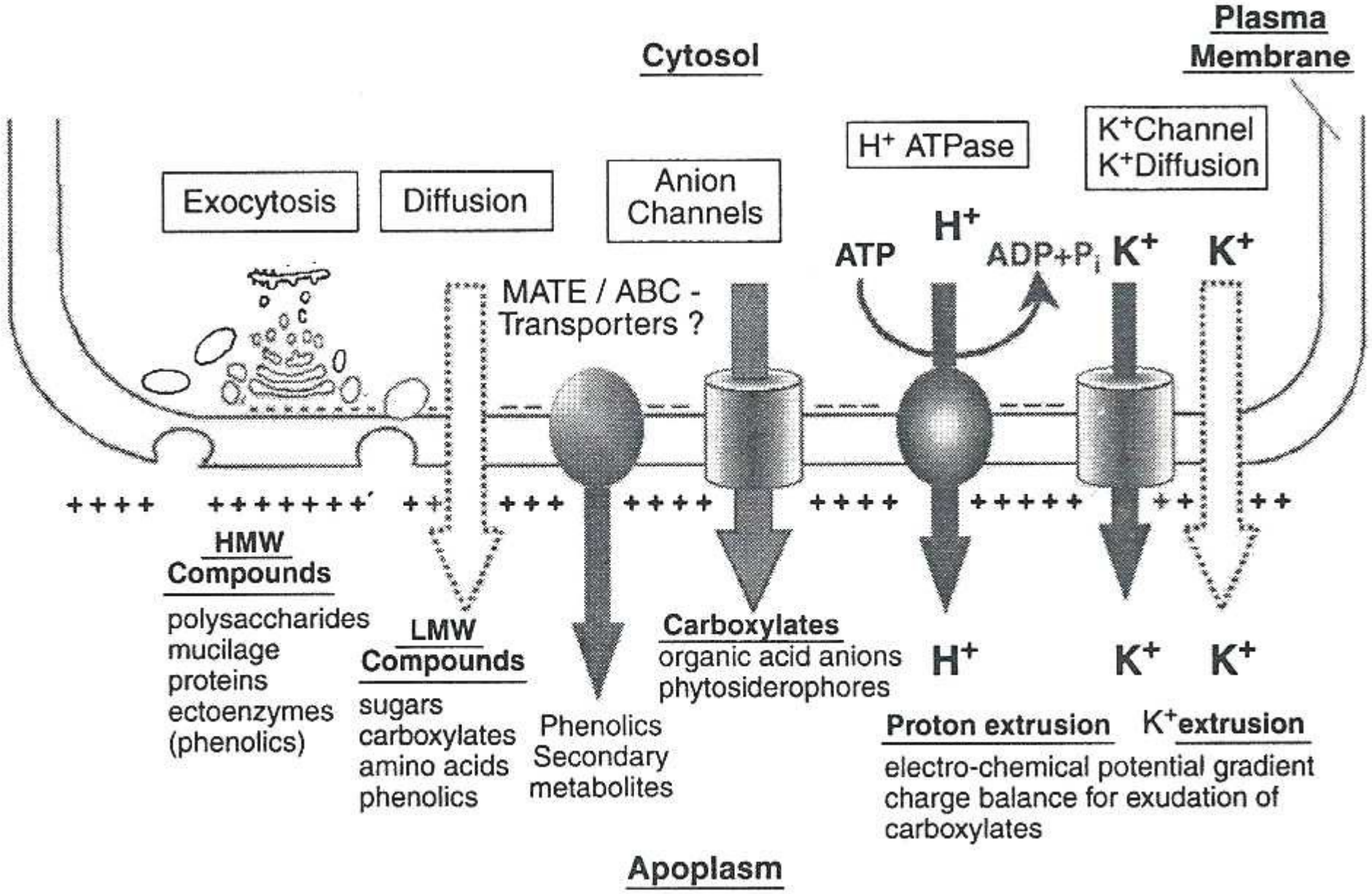
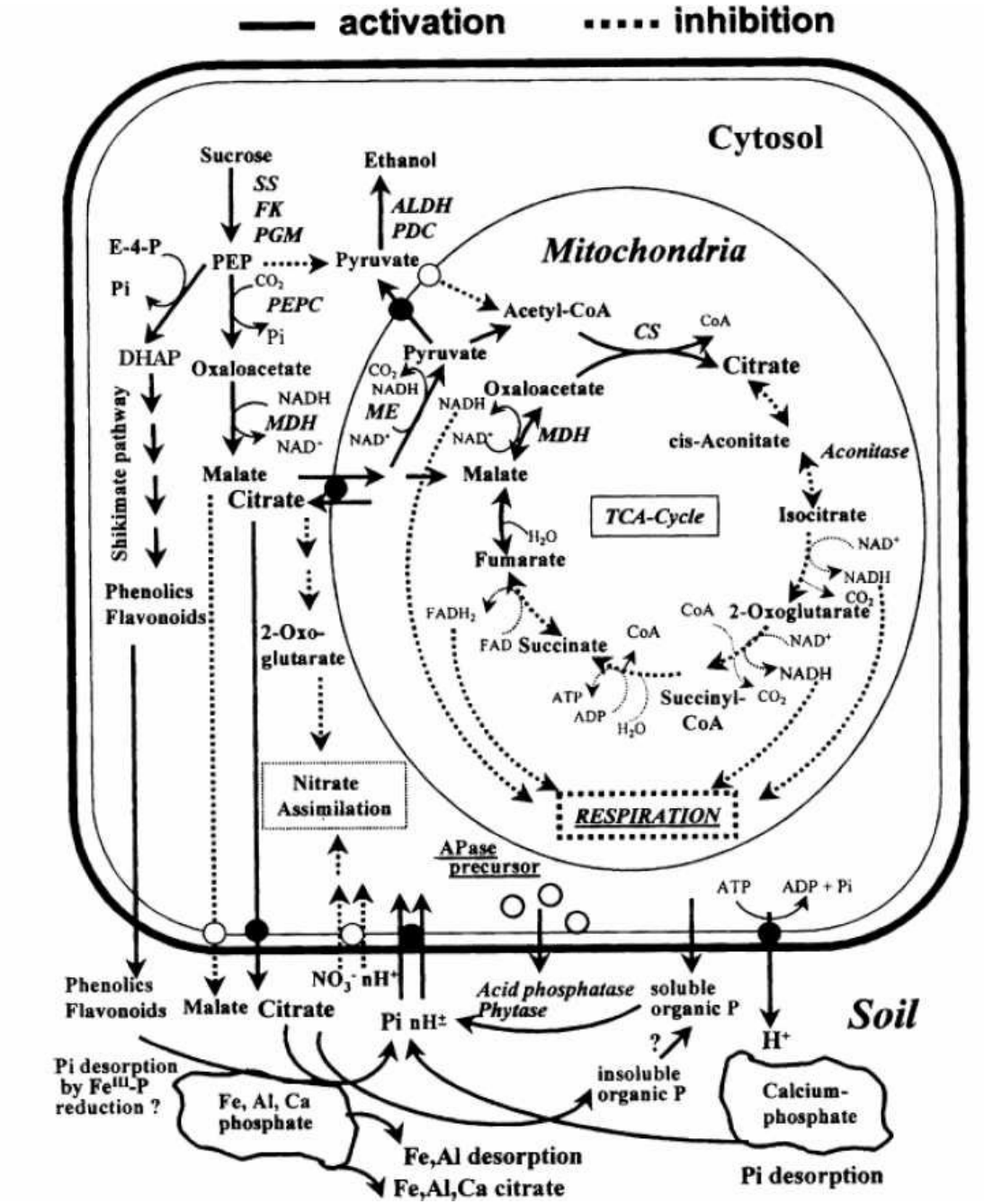


FIGURE 2.2 Model for mechanisms involved in the release of root exudates.

Exsudation organische Säuren bei Phosphormangel

ALDH	*Alkoholdehydrogenase*
CS	*Citratsynthase*
DHAP	*Dihydroxyacetonphosphat*
E-4-P	*Erythrose-4-phosphat*
FK	*Fruktokinase*
PGM	*Phosphoglukomutase*
MDH	*Malatdehydrogenase*
ME	*Malic Enzyme*
PDC	*Pyruvatdecarboxylase*
PEP	*Phosphoenolpyruvat*
PGM	*Phosphoglucomutase*
SS	*Saccharose Synthase*

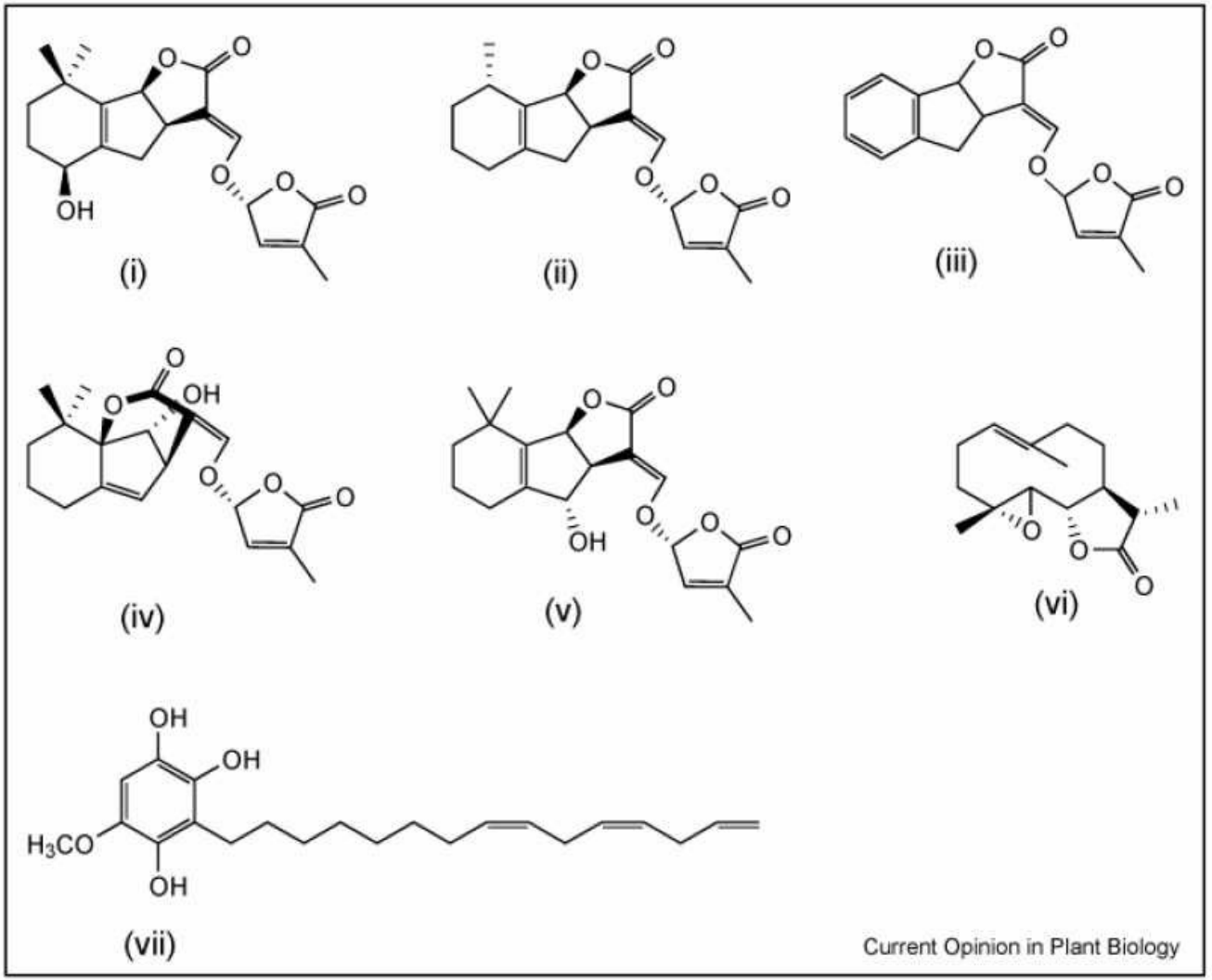


Parasitische Pflanzen

Striga

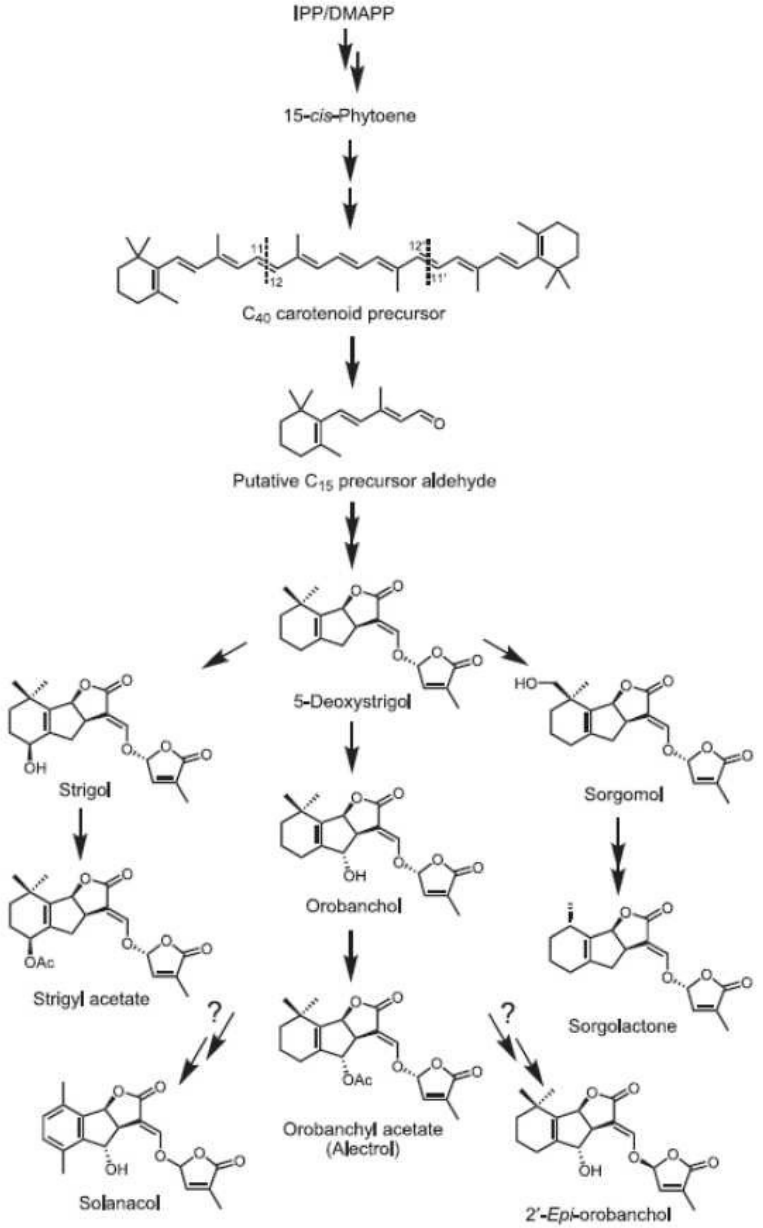
Orobanche

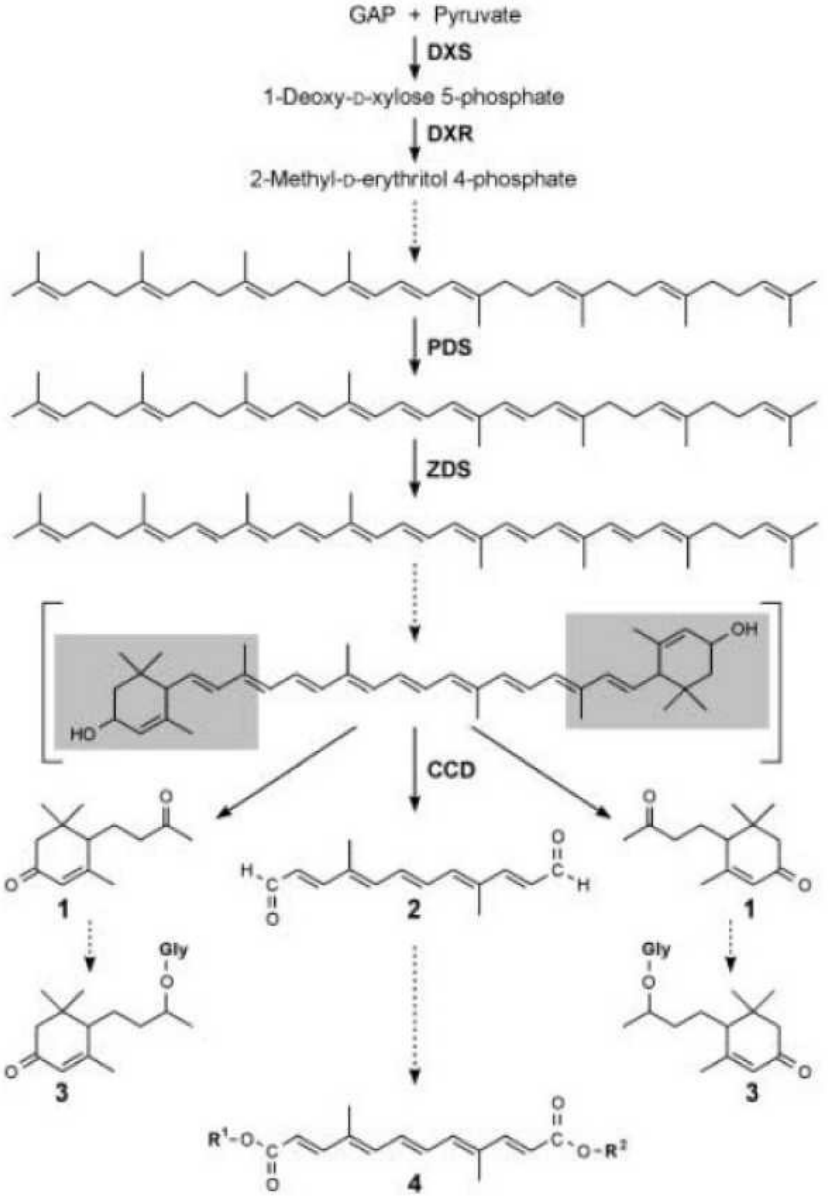
Strigole



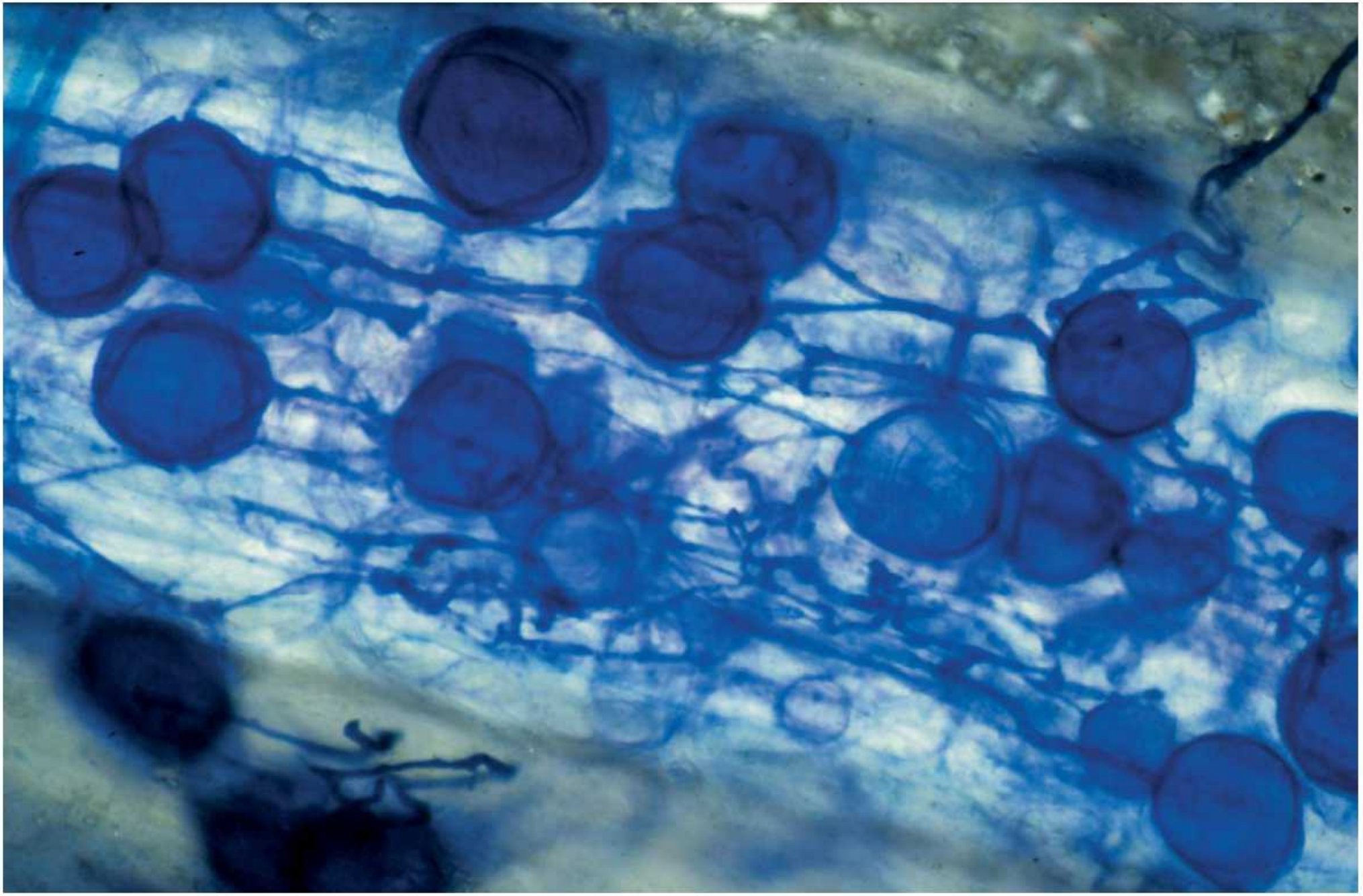
Germination stimulants of parasitic weed seeds. (i) (+)–Strigol, a germination stimulant for *Striga* spp., has been isolated from root exudates of the false host cotton, from the true hosts sorghum and maize, and from *in-vitro*-cultured *Menispermum dauricum* and *Stephania cepharantha*. (ii) Sorgolactone, a germination stimulant for *Striga* spp., has been isolated from the root exudate of the host plant sorghum. (iii) The synthetic germination stimulant GR24. (iv) Alectrol, a germination stimulant for *Striga* and *Orobanche* spp., has been isolated from the root exudates of the hosts cowpea and red clover. (v) Orobanchol, a germination stimulant for *Orobanche* spp., has been isolated from root exudate of host red clover. (vi) Dihydroparthenolide, sesquiterpene lactone that induces the germination of *Striga* and *Orobanche* spp. (vii) Dihydrosorgoleone, a germination stimulant of *Striga* spp., has been isolated from the root exudate of the host sorghum [9,13,21,23•]. The structure of (iv) is still under debate [13].

Apocarotenoide

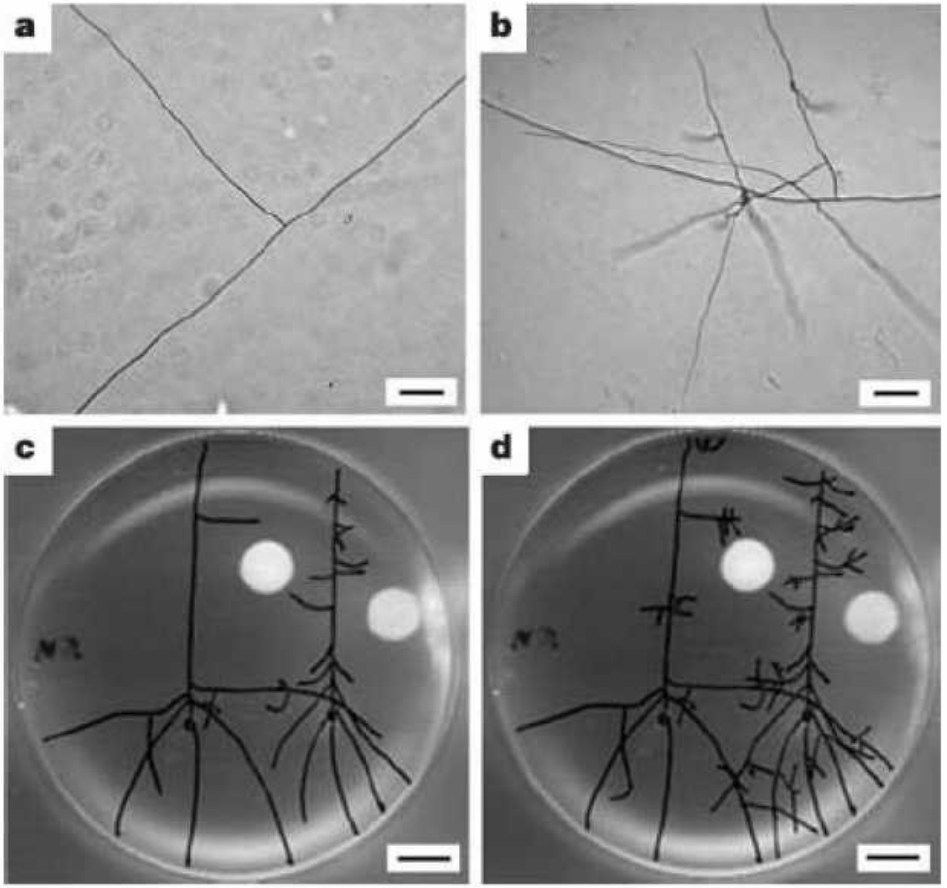




Arbuskuläre Mykorrhiza (Glomeromycota)



Signal für Mykorrhizapilze



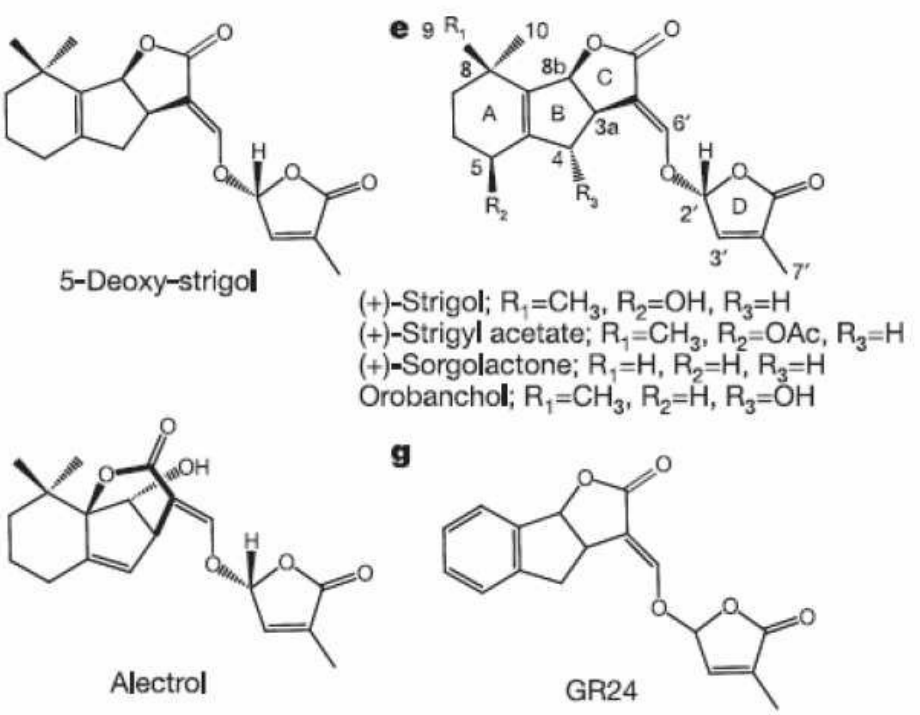


Figure 1 | Hyphal branching of *G. margarita* induced by lipophilic fractions from root exudates of *L. japonicus* using the paper disk diffusion method. **a**, Control hypha (70% ethanol in water). **b**, Hyphal branching from a secondary hypha upon treatment with the ethyl acetate extracts (15 μg per disk). Scale bars, 300 μm. **c**, **d**, Tracings of hyphal branches directly traced on a Petri dish at 0 h (**c**) and 24 h (**d**) after treatment with the ethyl acetate soluble-neutral fraction (15 μg per disk). Extensive formation of hyphal branches from secondary and primary hyphae was induced. Scale bars, 6 mm.

Signal für Mykorrhizapilze

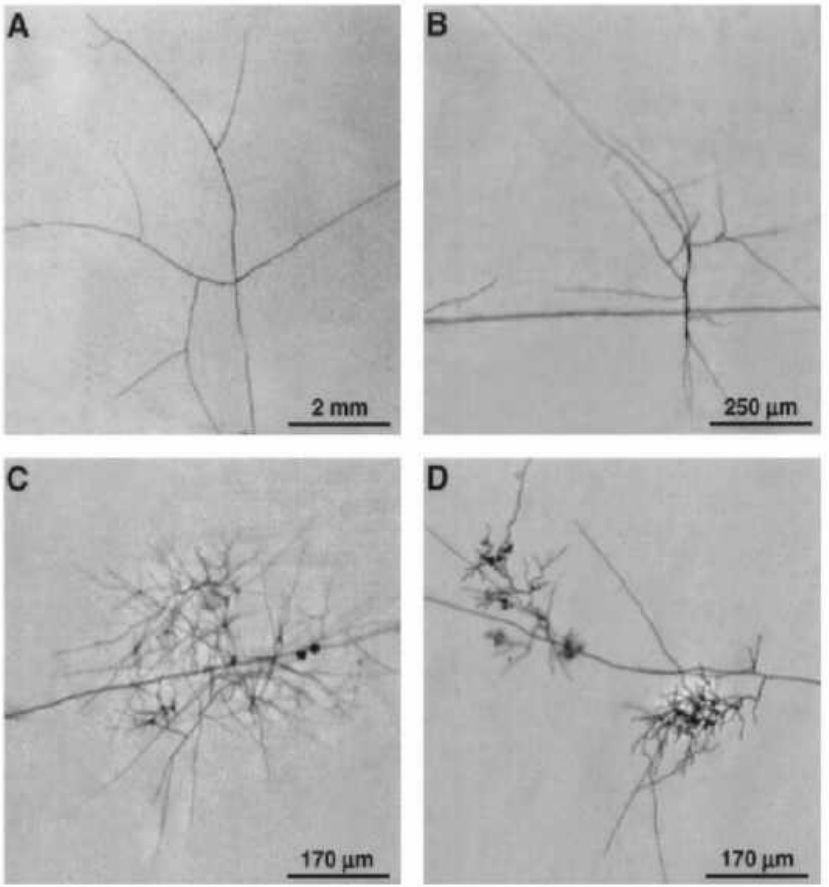
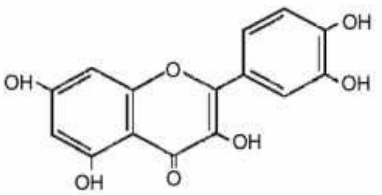
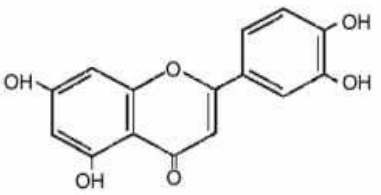


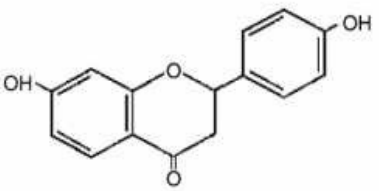
Fig. 4. Actual micrographs of magnified portions of the branching patterns depicted in Fig. 3. Individual branching clusters are shown so that the three dimensional spread of hyphae can be observed. (A) +1 branching (1:1000 dilution). (B) +2 branching (1:100 dilution). (C) +3 branching (1:10 dilution). (D) +4 branching (concentrated exudate fraction).



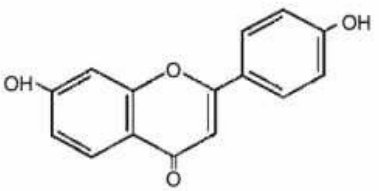
A. *Quercetin*



B. *Luteolin*



C. 4′,7-dihydroxyflavanone



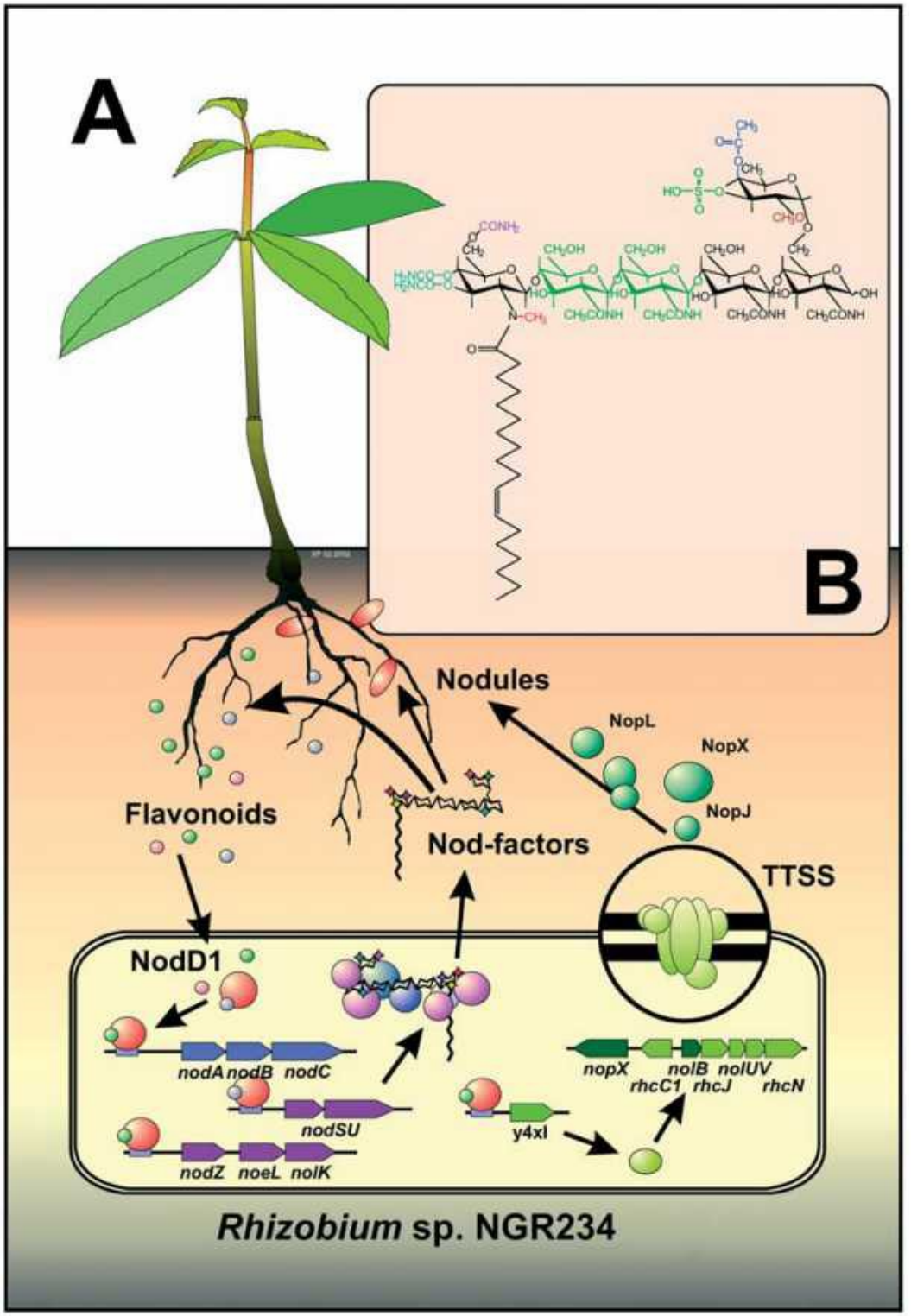
D. 4′,7-dihydroxyflavone

Fig. 1 Flavonoid molecules that promote germination of arbuscular mycorrhizal fungal spores/hyphal growth (A,C,D), induce nod genes in rhizobia (B,C,D) or stimulate growth of rhizobia (A).

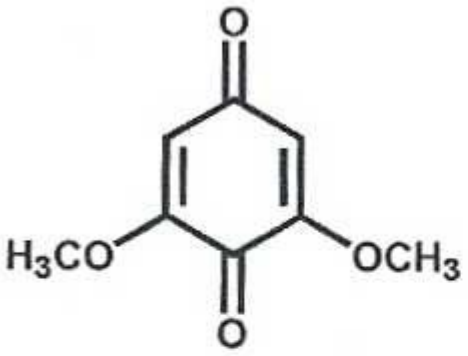
Signal für *Rhizobium* (Knöllchenbakterien)

MAMP
Microbe-associated molecular patterns

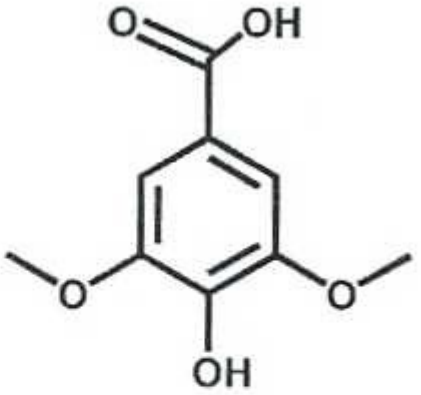
PAMP
Pathogen-associated molecular patterns



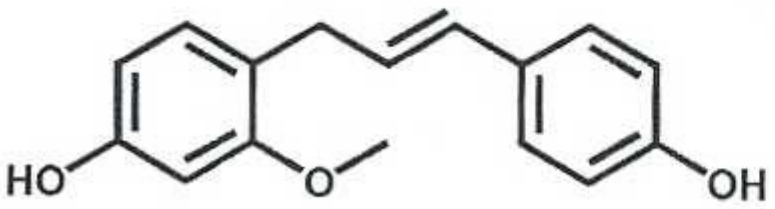
Haustorium inducing factors



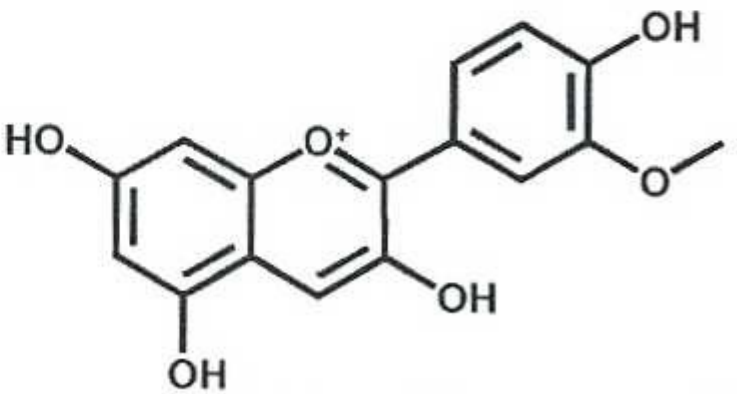
2,6-dimethoxy-p-benzoquinone



syringic acid

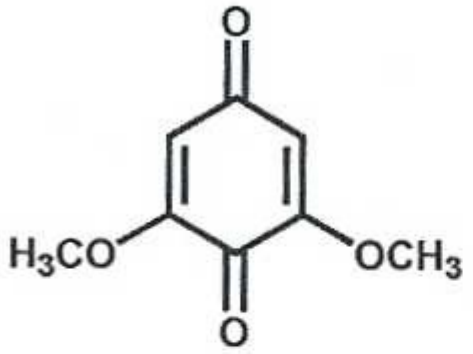


xenognosin A

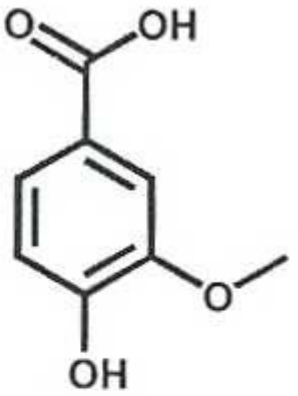


peonidin

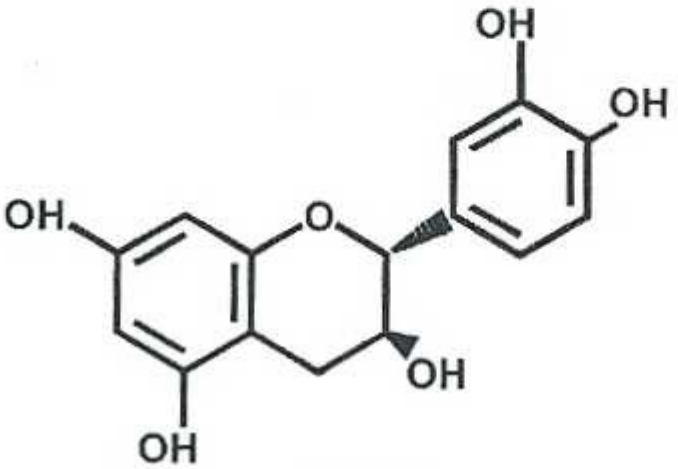
Phytotoxic allelochemicals



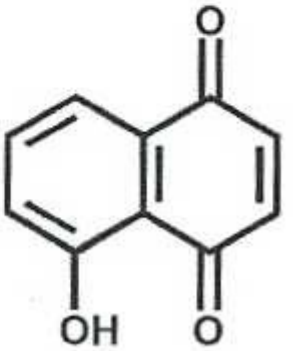
2,6-dimethoxy-p-benzoquinone



vanillic acid



catechin



juglone

Hormesis

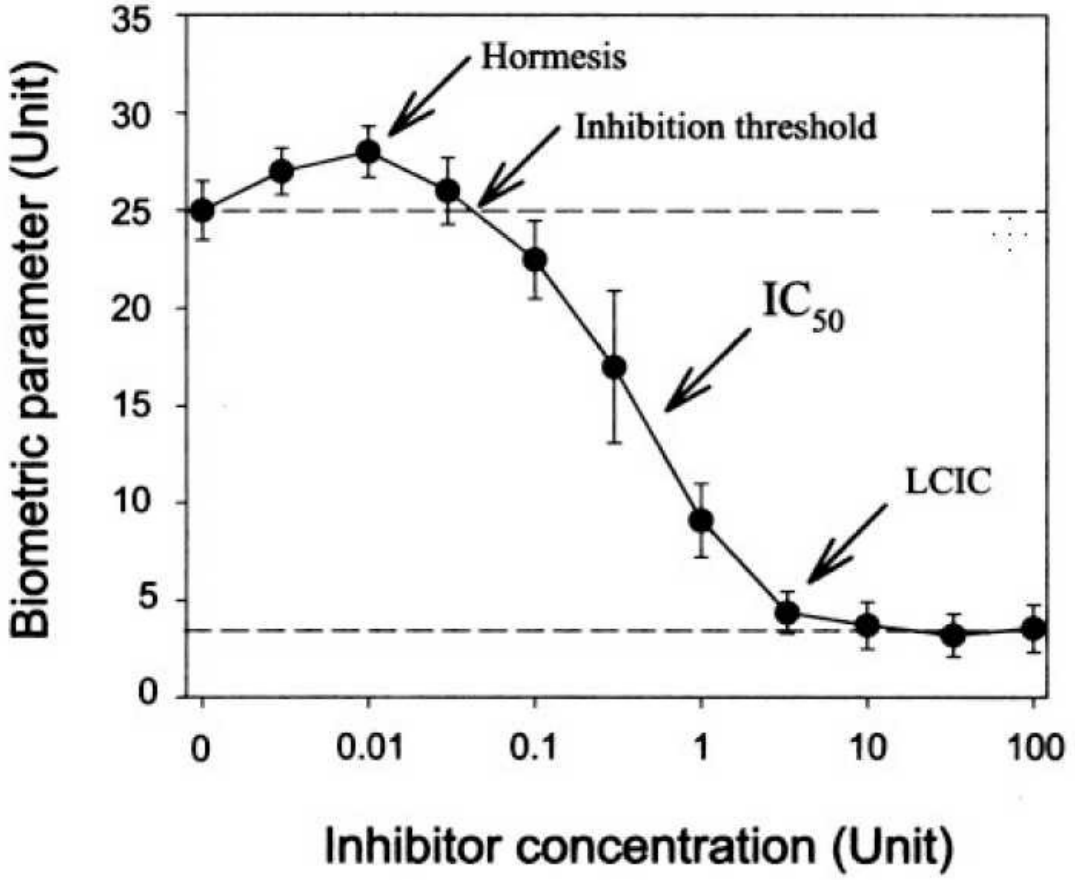
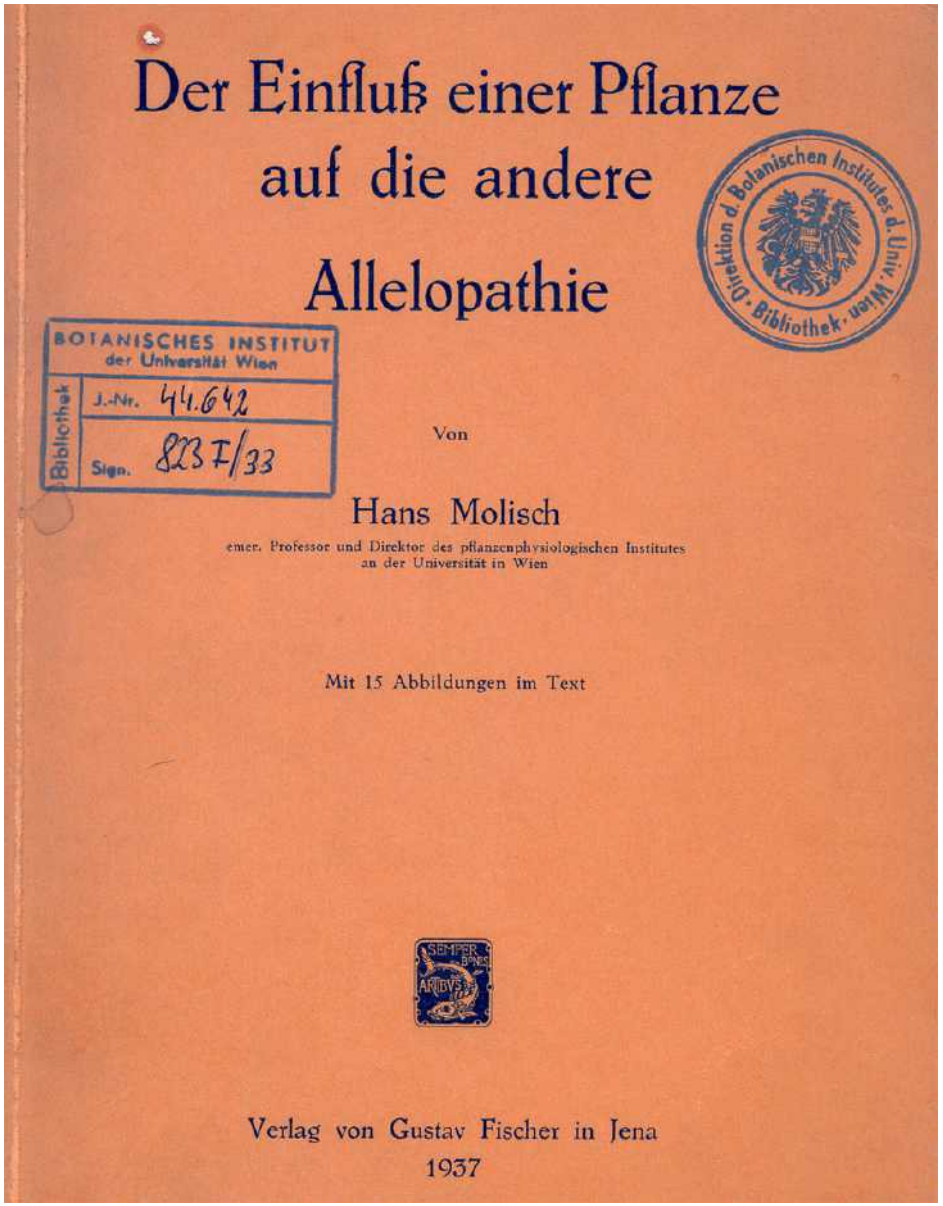


Figure 1. Typical dose-response curve. Hormesis consists of a stimulation of the dependent parameter at low concentration of a phytotoxin. Inhibition threshold is the highest concentration at which no inhibition is observed. IC_{50} is the concentration at which 50% inhibition is observed. This part of the curve often has the most variations in the replicates. LCIC is the lowest-complete inhibition concentration.

Southam und Ehrlich (1932)

Hans Molisch



Einfluss von Apfelluft auf Erbsenkeimlinge

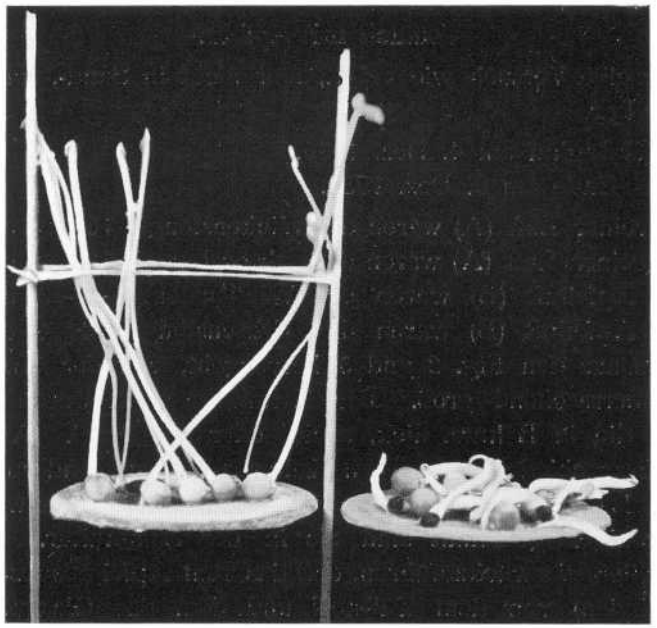


Fig. 3. Keimlinge der Erbse in reiner Luft, links. Keimlinge der Erbse in Apfelluft, rechts. Wasserkultur.

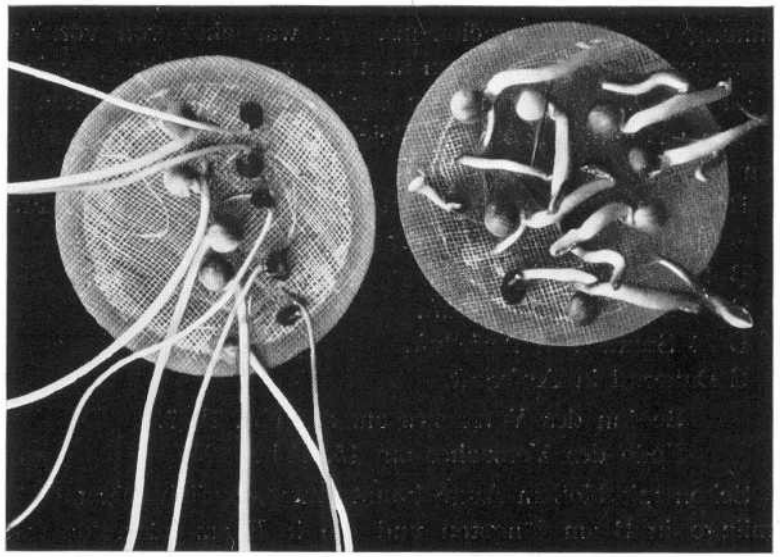


Fig. 4. Derselbe Versuch wie bei Fig. 3, aber von oben photographiert.

ELSEVIER

How plants communicate using the underground information superhighway

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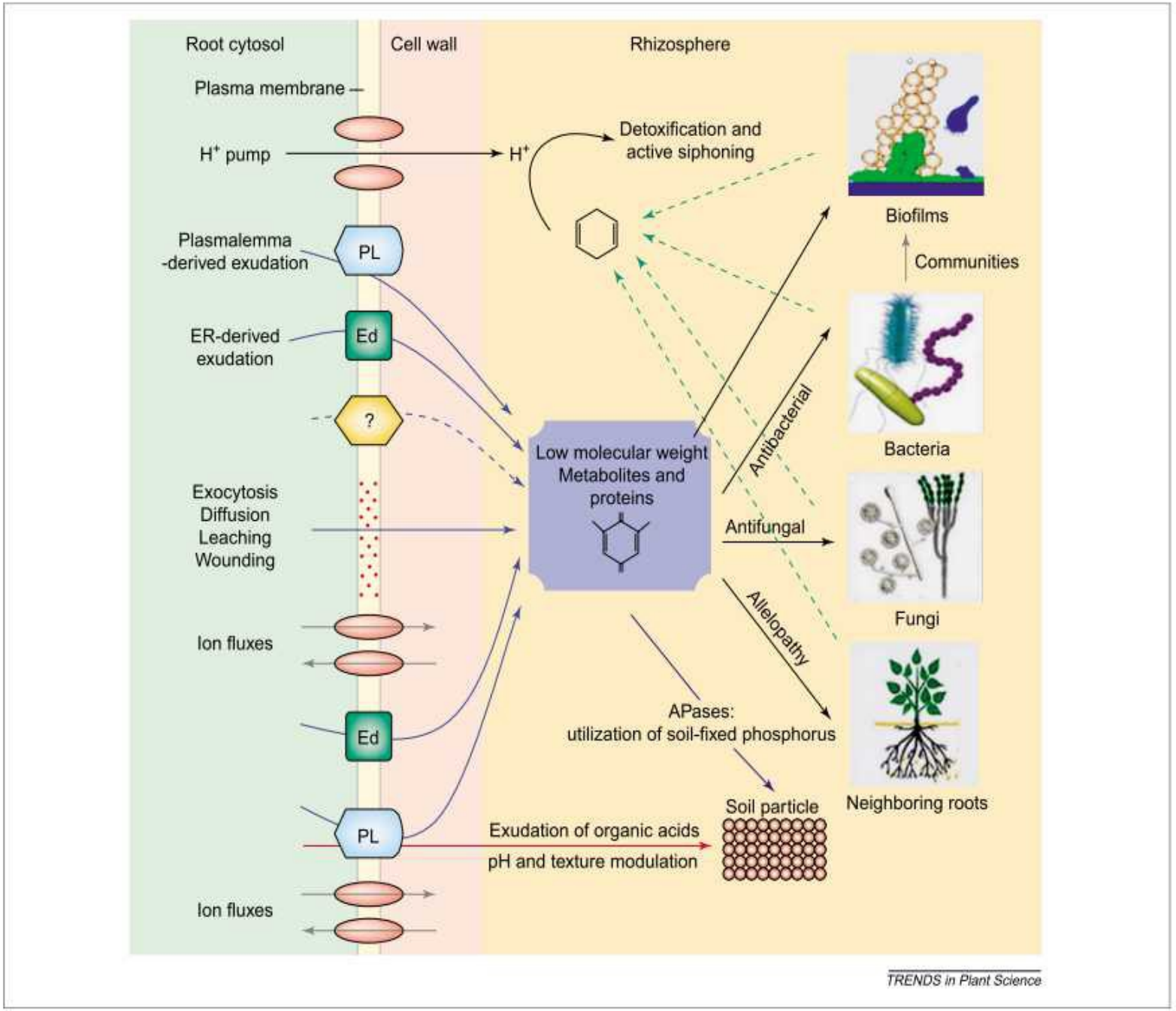
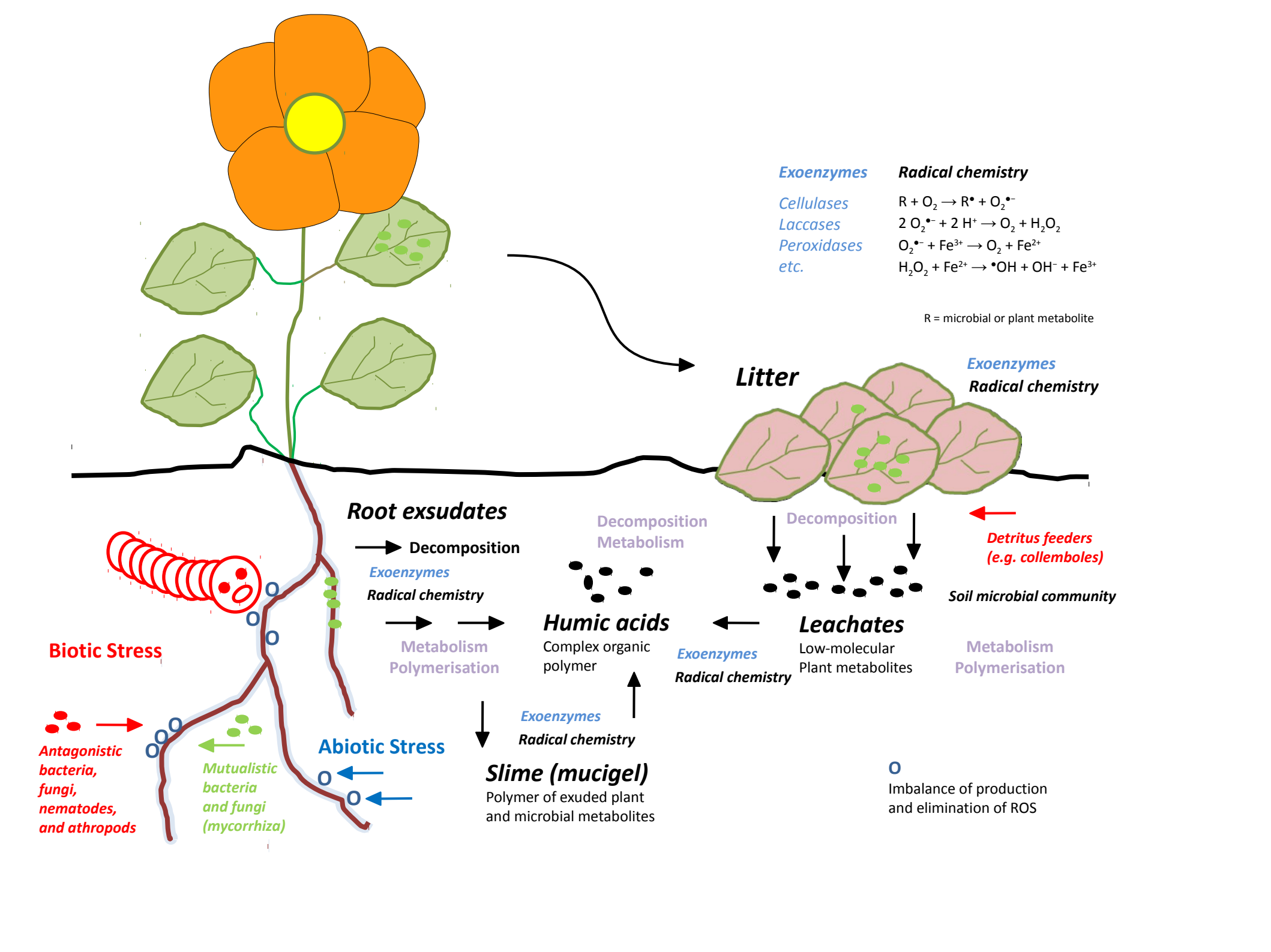


Figure 1. Model showing plausible mechanisms of root exudation and active rhizospheric interactions. The hexagon component in the detoxification process depicts the low molecular weight toxins produced by bacteria and fungi during the pathogen attack. Plant roots adopt a proton (H^+)-pumping mechanism to exclude the phytotoxins produced by bacteria and fungi. The green, broken arrows depict pathogen attacks against the plant. The blue, black and red arrows show the response of the host plant root to a pathogen attack. The blue, broken arrow represents an unknown mode of root exudation and host response against pathogen attack. On the right, the biofilm panel depicts bacterial communities that are much more resistant to plant-derived antimicrobials than planktonic bacteria are. Abbreviations: PL, plasmalemma-derived exudation; Ed, endoplasmic-derived exudation.


Exoenzymes
Radical chemistry
Cellulases
Laccases
Peroxidases
etc.
$R + O_2 \rightarrow R^\bullet + O_2^{\bullet-}$
$2\ O_2^{\bullet-} + 2\ H^+ \rightarrow O_2 + H_2O_2$
$O_2^{\bullet-} + Fe^{3+} \rightarrow O_2 + Fe^{2+}$
$H_2O_2 + Fe^{2+} \rightarrow {}^\bullet OH + OH^- + Fe^{3+}$
R = microbial or plant metabolite
Litter
Exoenzymes
Radical chemistry
Root exsudates
Decomposition
Exoenzymes
Radical chemistry
Decomposition
Metabolism
Decomposition
Detritus feeders
(e.g. collemboles)
Soil microbial community
Biotic Stress
Humic acids
Complex organic
polymer
Metabolism
Polymerisation
Exoenzymes
Radical chemistry
Leachates
Low-molecular
Plant metabolites
Metabolism
Polymerisation
Exoenzymes
Radical chemistry
Antagonistic
bacteria,
fungi,
nematodes,
and athropods
Mutualistic
bacteria
and fungi
(mycorrhiza)
Abiotic Stress
Slime (mucigel)
Polymer of exuded plant
and microbial metabolites
O
Imbalance of production
and elimination of ROS