Processes determining limitation in aquatic systems

- a review

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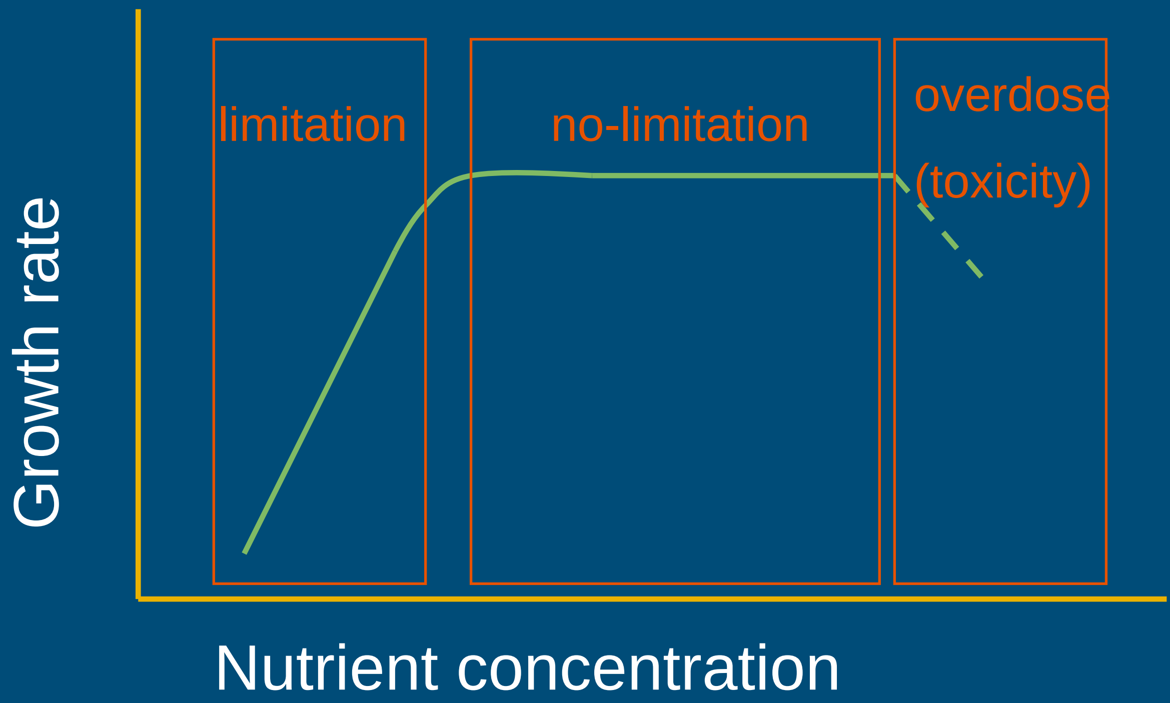
Outline

- Nutrient limitation in aquatic systems
- Measurement of nutrient limitation
- Nutrient concentrations, ratios, loads
- Different primary producers & nutrient cycling
- General patterns
- Landscape processes
- Discussion

Definition – monoculture level

- Von Liebig's Law of the Minimum (1878)



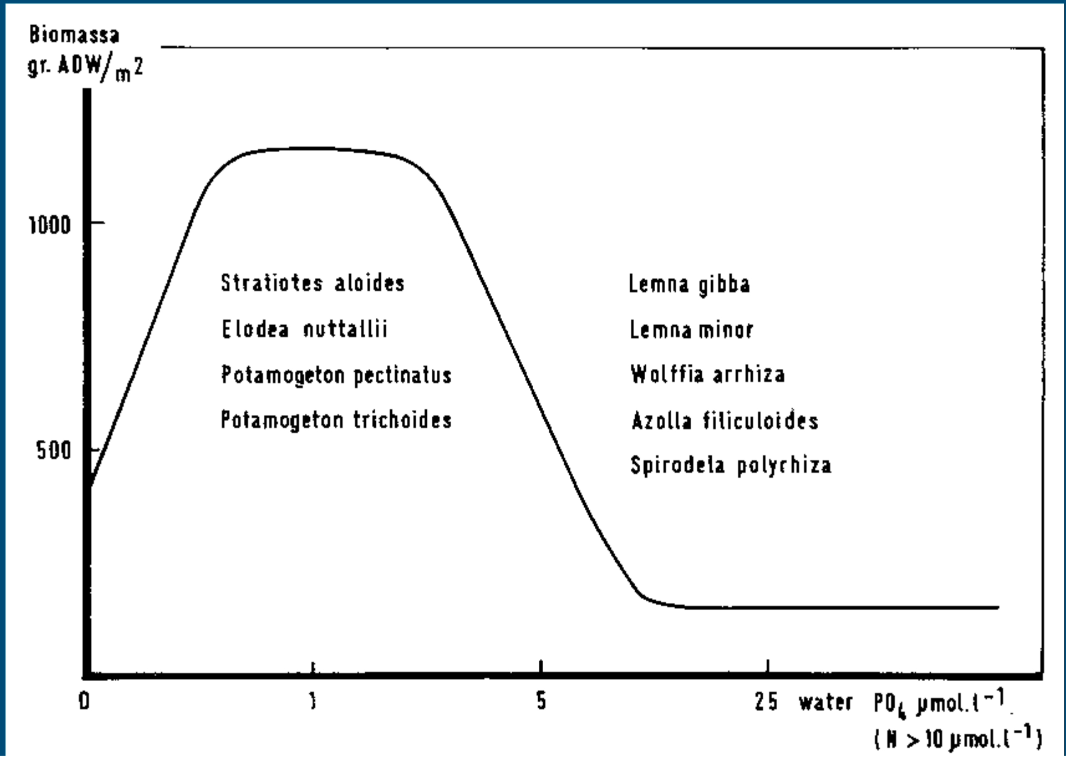
Definition- vegetation level

- Fast-growing species (prodigal) and slow growing species (economical) → competition
- (semi)-terrestrial vegetations: addition limiting nutrient → increase biomass + changes in vegetation composition
- Increase in biomass: easily measurable

Definition- vegetation level

- Aquatic environment: not necessarily biomass growth primary producers with addition of nutrients
  - Shift from vertical to horizontal growth strategy causes light limitation for other plants

Biomass (g DW/ m²)

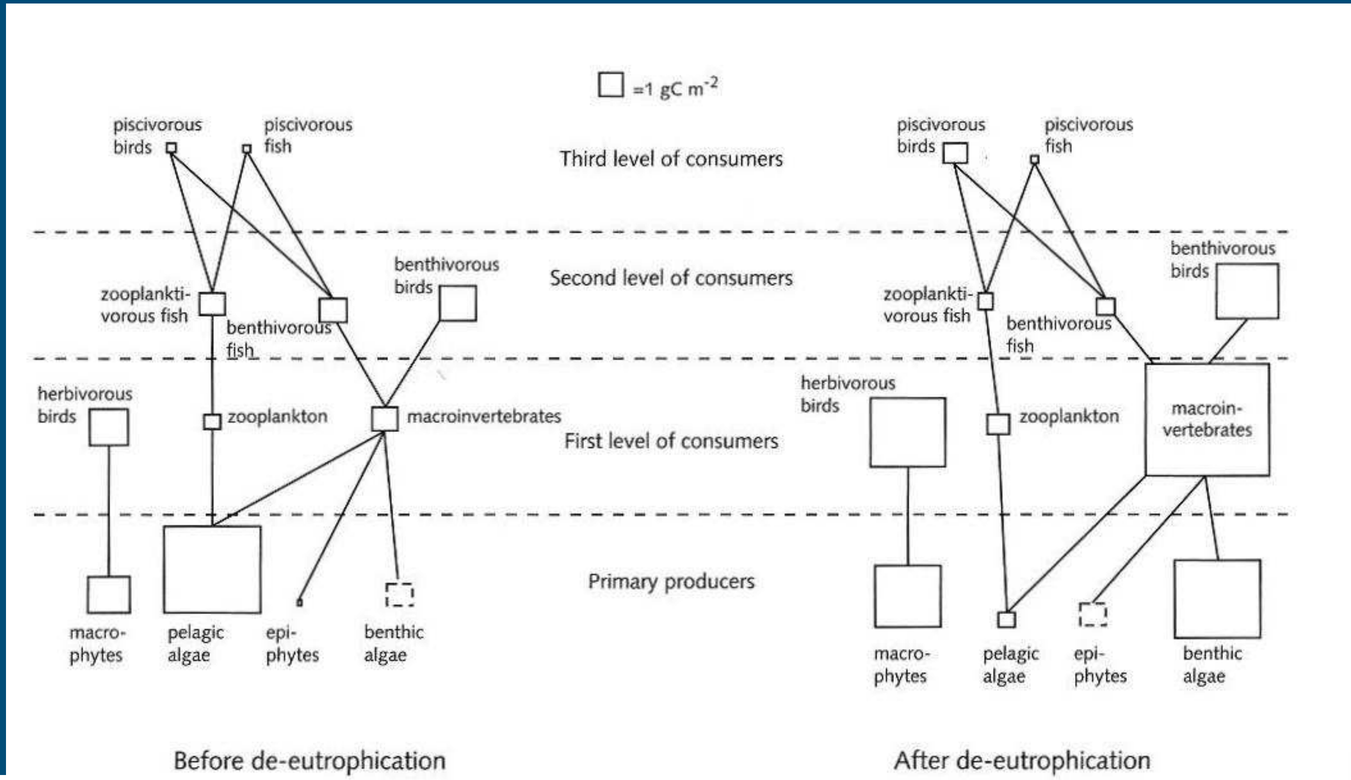


From: Roelofs & Bloemendaal, 1988

PO$_4$ concentration (µmol/l)

Definition- ecosystem level

- On ecosystem level:
  - effects on consumer levels
  - also negative feedback (e.g. algae – zooplankton) → effects nutrient addition less visible



From: Van den Berg, 1999 *

* See references on last slides

Definition

- If the effects of addition of the limiting nutrient are not defined, how can we assess the type of nutrient limitation?
  - Different methods use different proxys and gain different results

Measurement of nutrient limitation

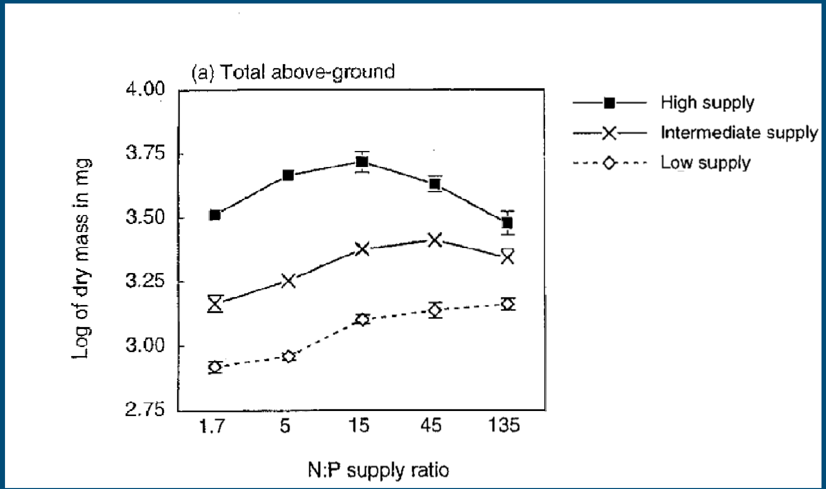
- Bio-assay: phytoplankton incubation with nutrient addition
  - + fast
  - - no supply of nutrients from sediment
- Mesoscom study
  - + interaction with sediment
  - - no foodweb interactions
- Enclosure study
  - + resembles field situation
  - - limited foodweb interaction
- Experiments with total water body
  - + real field situation
  - - high impact of experiment
- Correlation of field measurements
  - + general overview of different waterbodies
  - - intercorrelation of nutrients & exceptions do not stand out

Measurement of nutrient limitation

- Historical studies
  - + effects of certain measures visable
  - - lack of data
- Tissue nutrient ratios/concentrations
  - + fast
  - - does not indicate absence of nutrient limitation of other nutrient than N or P limitation
- Water nutrient ratios
  - + very easy measurement
  - - seasonality important (uptake by plants) & does not show nutrient supply from sediment
- Physiology (e.g. enzymes like nitrate reductase and alkaline phosphatase)
  - + visability the effects of nutrients on cell level
  - - only possible for phytoplankton
- Models
  - + fast & effects on ecosystems as a whole
  - - lack of knowledge

Concentrations, ratios or loads

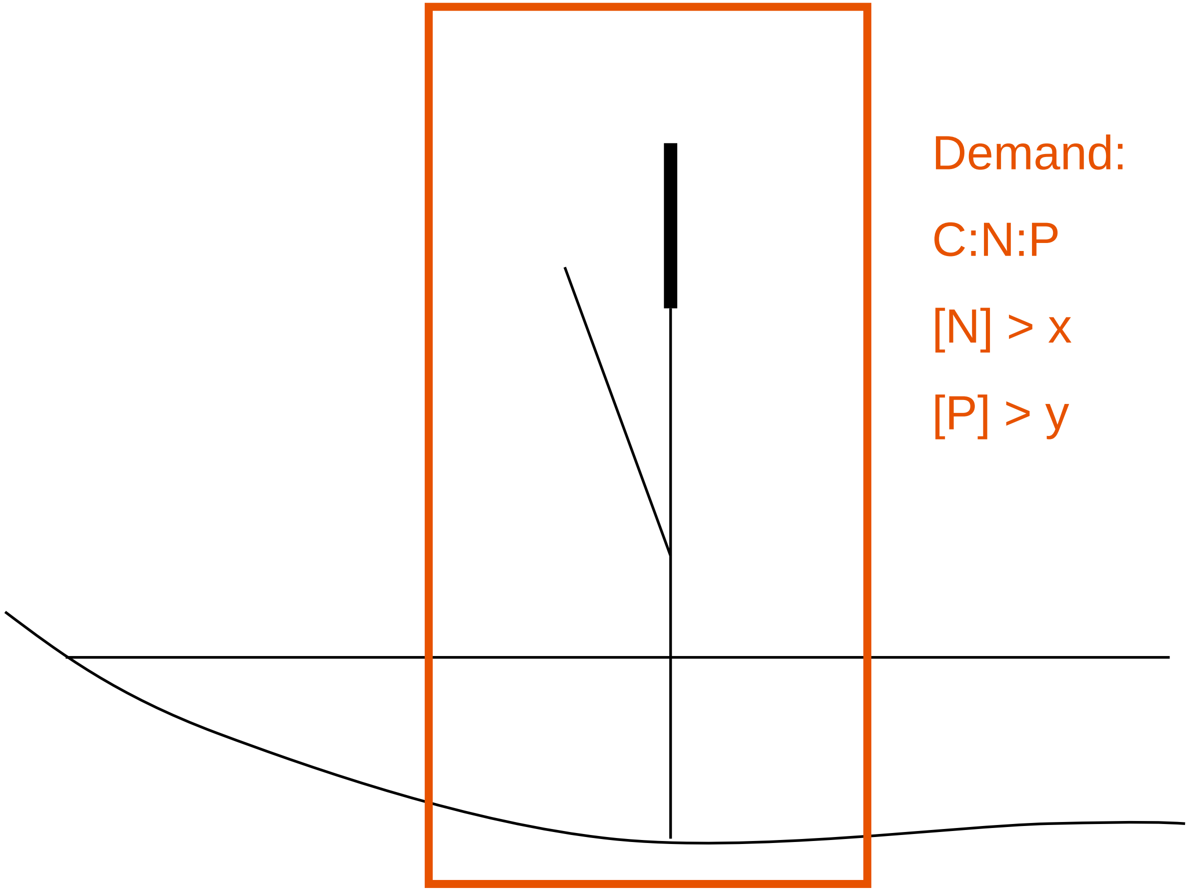
- Concentrations determine eutrophication and dominance of types of primary producers (isoetid species, vertical growth strategists (e.g. *Ceratophyllum*, *Elodea*), algae
- Ratios determine type of limitation
  - Also interactions between concentrations & ratios



From: Güsewell & Bollens, 2003

- Load often better predictor for eutrophication than actual concentration, because of uptake and adsorption

different primairy producers & nutrient cycling



Demand:

C:N:P

[N] > x

[P] > y

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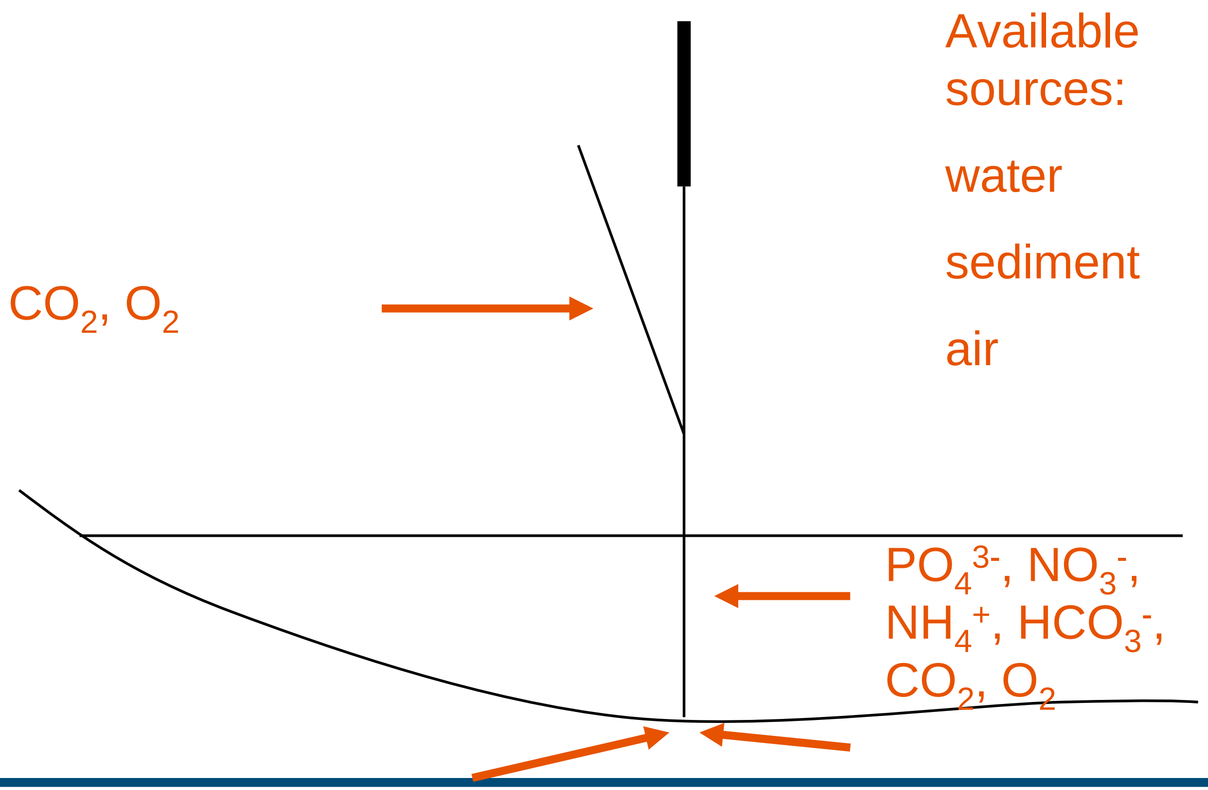
- Demand
  - Algae: Redfield ratio C:N:P 106:16:1
  - Wetland plants/macrophytes C:N:P 550:30:1

    (Atkinson & Smith, 1983; Duarte, 1992; Verhoeven et al., 1996; Koerselman & Meuleman, 1996)

    Also higher light demand (Sandjensen & Borum, 1991)
  - Diatoms: high Si demand for silica skeleton

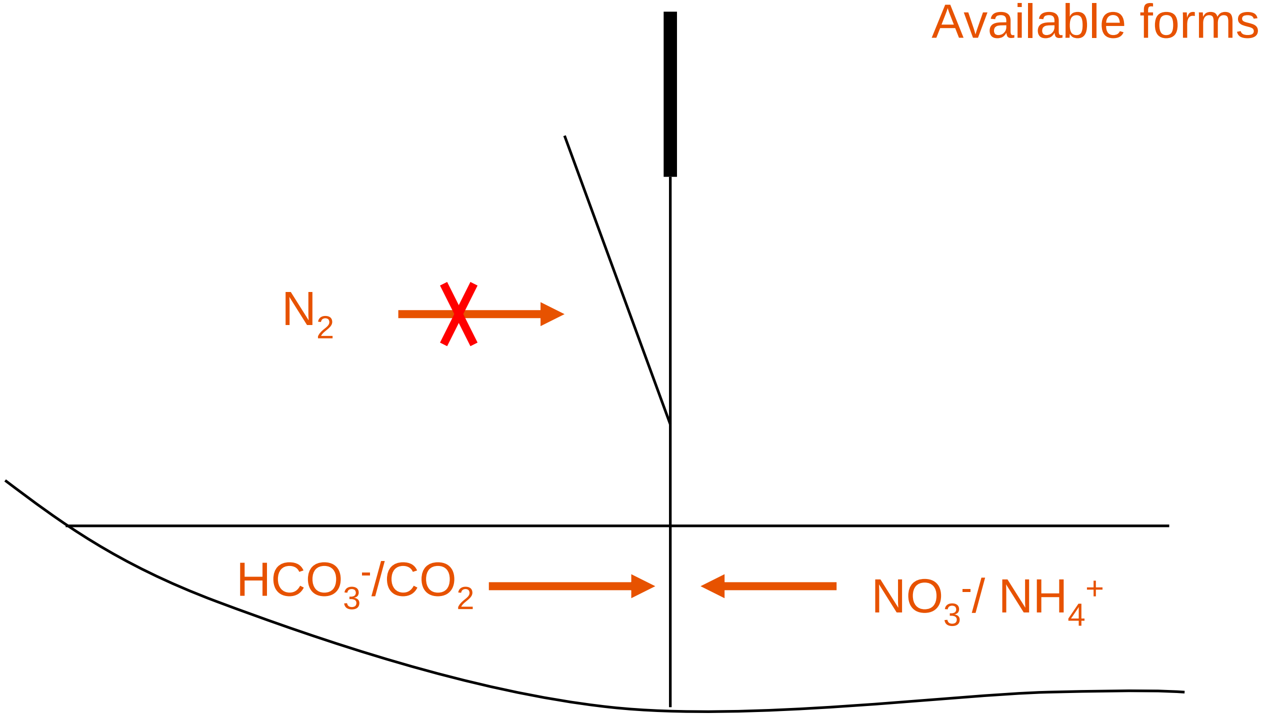
different primairy producers & nutrient cycling



different primairy producers & nutrient cycling

- Available sources
  - Non-rooting plants/algae: only water
  - Rooting plants: also sediment
  - Emerging plants/floating plants: also air

different primairy producers & nutrient cycling



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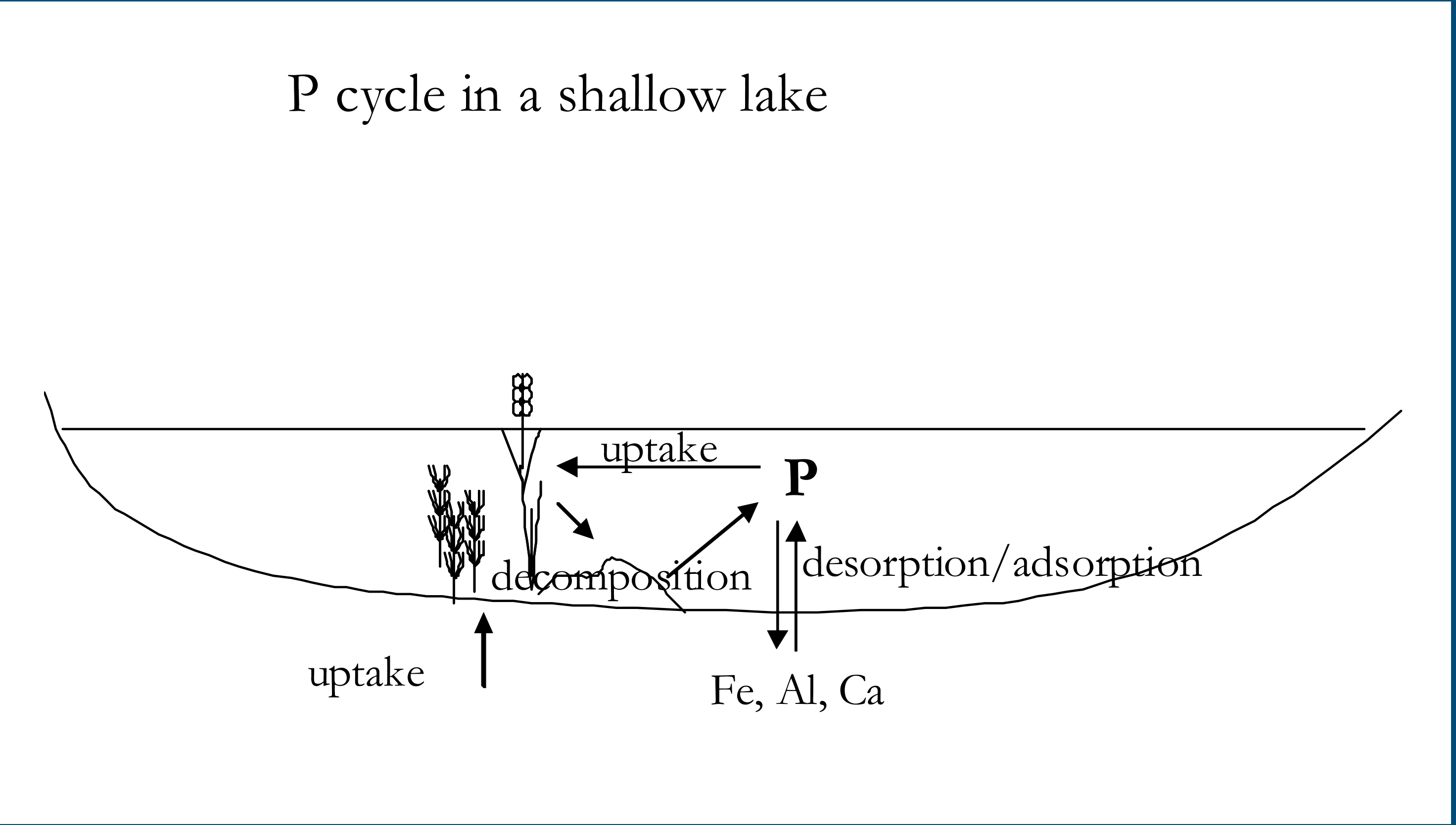
- Available forms
  - Fixation of N_2 by part of cyanobacteria and *Azolla* species
  - Some plants only CO_2, some also HCO_3^-
  - Preference for NO_3^- or NH_4^+

different primairy producers & nutrient cycling



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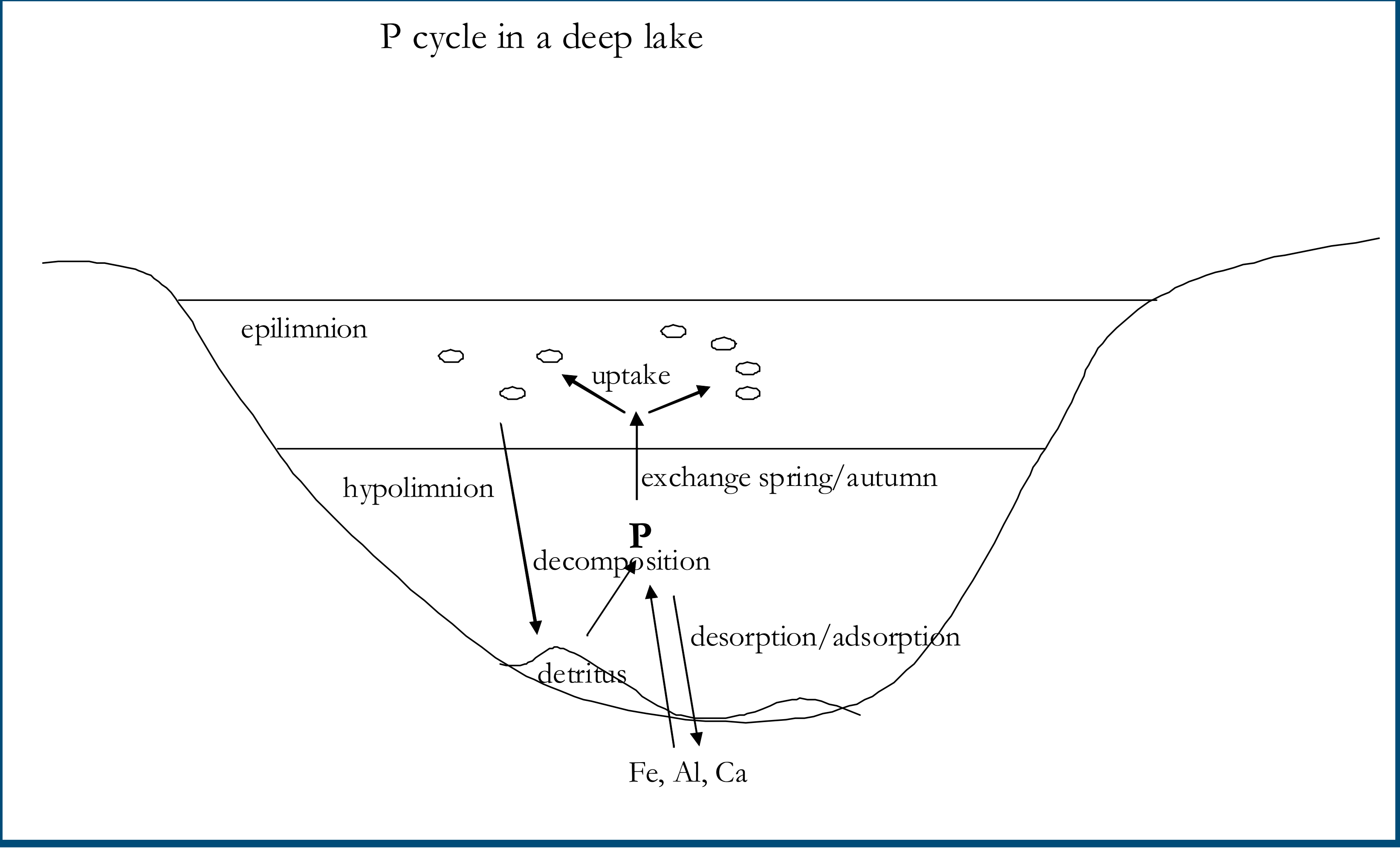

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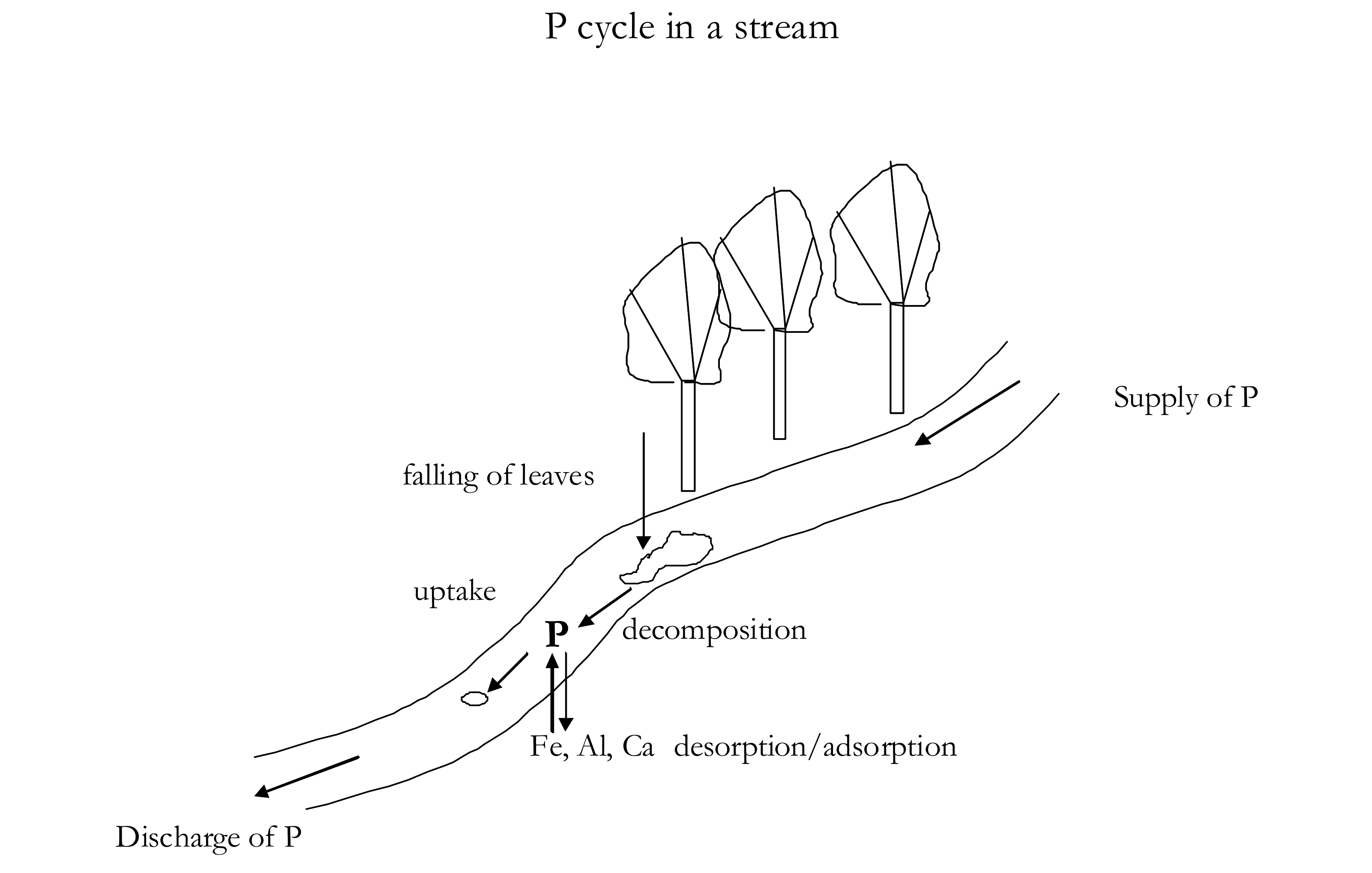

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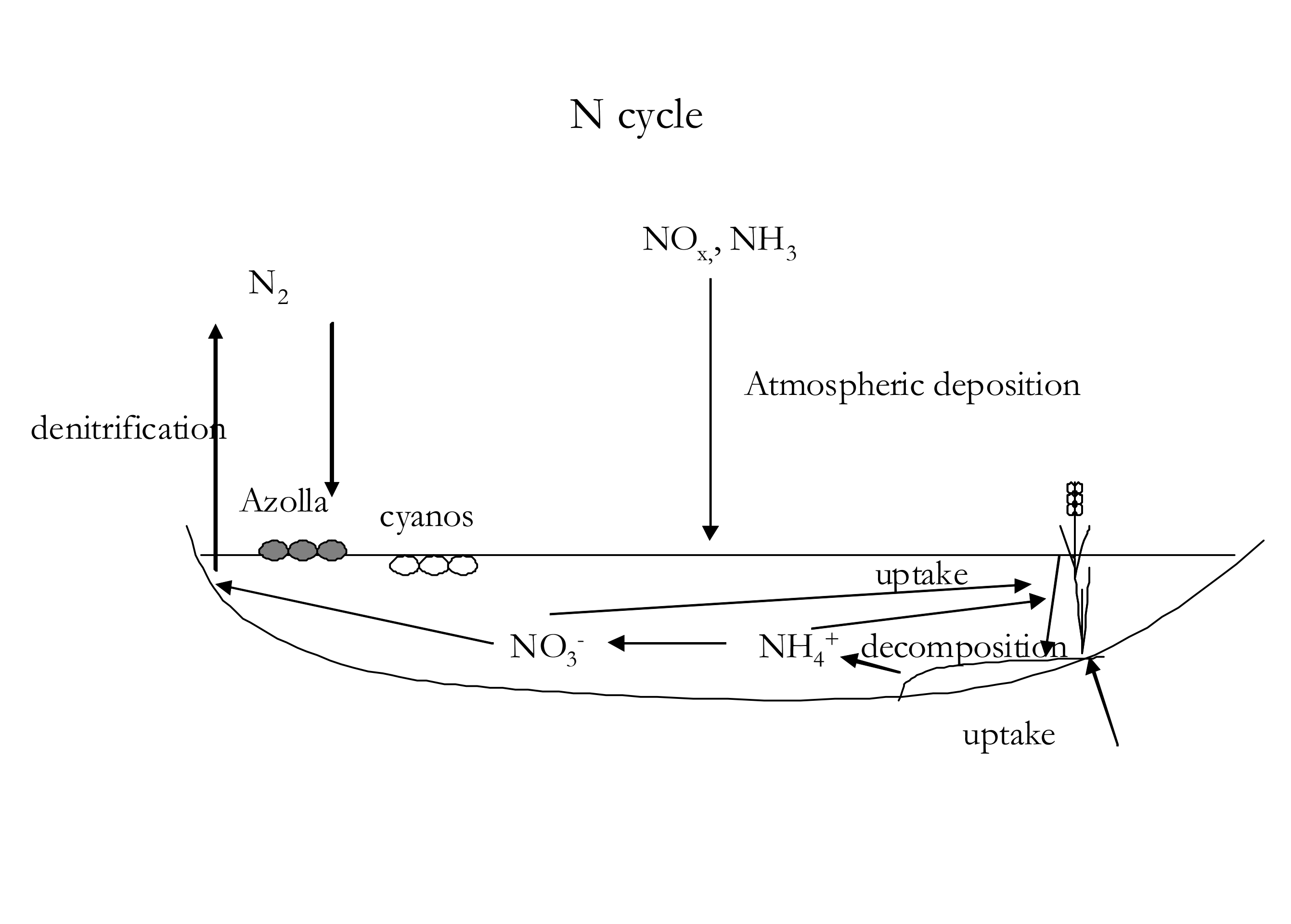

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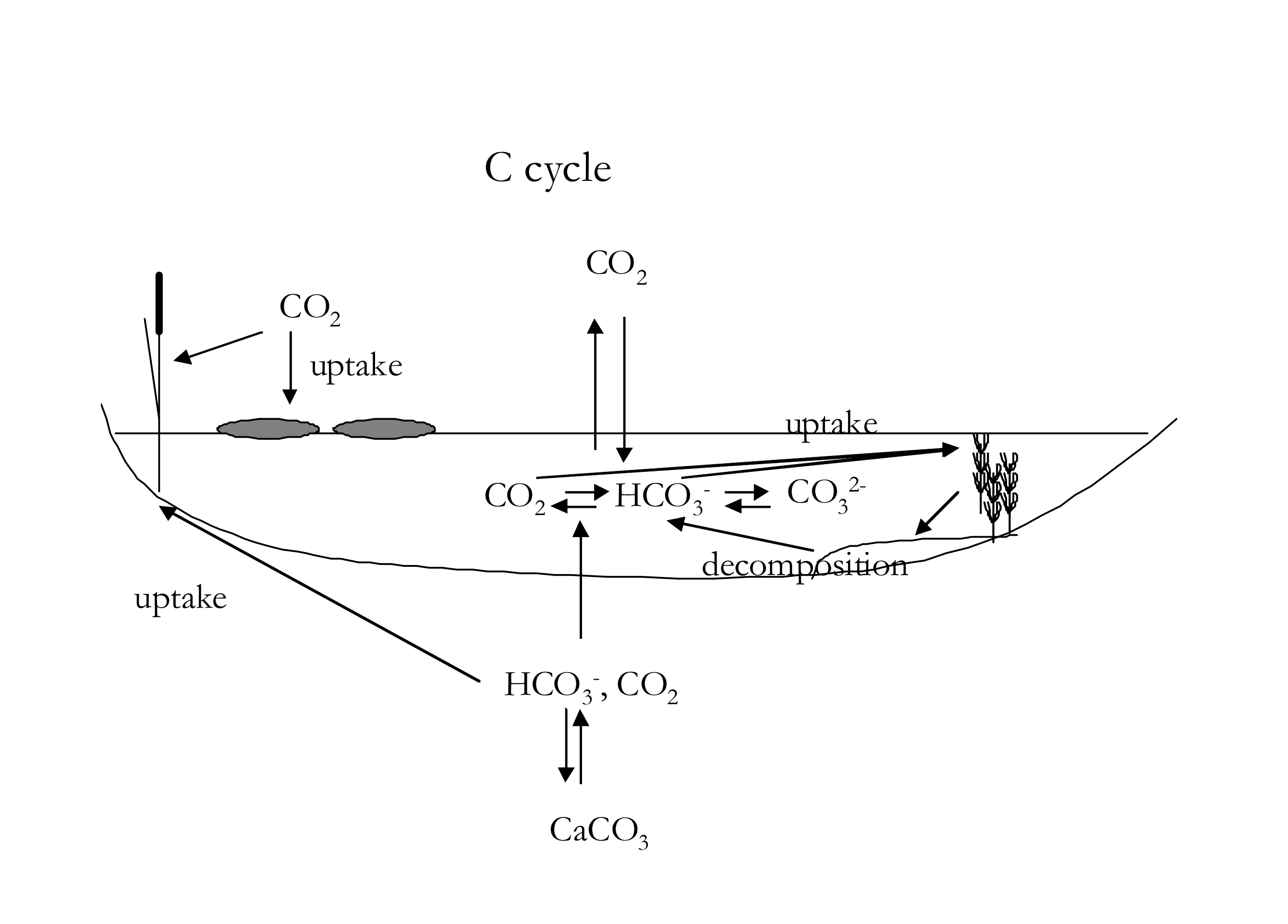


different primairy producers & nutrient cycling

- Phosphorus
  - Higher availability in soil
  - Rooting species: advantage in uptake
- Nitrogen
  - Ammonium slightly higher availability in soil
  - N-fixing cyanobacteria and Azolla: advantage
- Carbon
  - Easily available from air
  - Emerging/floating plants: advantage
  - Often higher availability in soil
  - Rooting plant species: advantage

General patterns in nutrient limitation

- General patterns phytoplankton lakes
  - P most often limiting (temperate zones+ tropics)
  - N limiting
    - in areas with little N deposition (Bergstrom et al, 2005)
    - in lakes with high P concentration (Moss et al., 1997; James et al., 2003)
  - C can become limiting in soft water lakes (Hein, 1997; Fairchild & Sherman, 1992; Roelofs et al., 2002); also temporarely in hard water lakes (Hein, 1997)
  - High P concentrations enhance temporary N and Si limitation (Sommer, 1993)

General patterns in nutrient limitation

- Cyanobacteria in lakes
  - N-fixing cyanobacteria (e.g. *Anabaena*) perform well under low N:P ratos; they stay limited by P, while green algae are limited by N (Schindler, 1977; Vitousek & Howarth, 1991)
  - Concentrations of P and N more important than N:P ratio (Gonzalez Sagrario et al., 2005; Jeppesen et al., 2005)
  - Not all cyanos can fixate N_2 (e.g. *Microcystus*)! In Dutch lakes no *Microcystes* blooms if concentration N < 1.35 mg N/l (Van der Molen et al., 1998)
  - N-fixing cyanos not always correlated with low N:P. N-fixing cyanos obtained < 2-9% of uptake N from air (Ferber et al., 2004)

General patterns in nutrient limitation

- Macrophytes in lakes
  - Macrophytes limited by light, not by nutrients (Sandjensen & Borum, 1991)
  - *Myriophyllum spicatum* limited by N in lake in Canada (Andersen & Kalff, 1986)
  - Only with high nutrient addition effect of light (> 2m) (Chambers and Kalff 1985)
  - *Elodea nutalli* (Best et al., 1996), *Hydrilla verticillata* (Barko et al., 1988) limited by N
  - *Litorella uniflora* limited by P (Christiansen et al., 1985)
  - Recent studies show negative correlation N and macrophytes:
    - In lakes Denmark no dominance of macrophytes > 2 mg N/l, irrespectively of P (Gonzalez Sagrario et al., 2005)
    - In lakes UK and Poland diversity of macrophytes much smaller if NO_3 > 1-2 mg N/l in winter (James et al, 2005)
    - Macrophyte community composition correletad with NH_4 in Lake Botshol (NL) (Rip, 2007)
  - Often effect of P on macrophyte dominance because of shading by algae (e.g. rare fen species in NL, IRL, PL correlated with P (Geurts et al, 2008))

General patterns in nutrient limitation

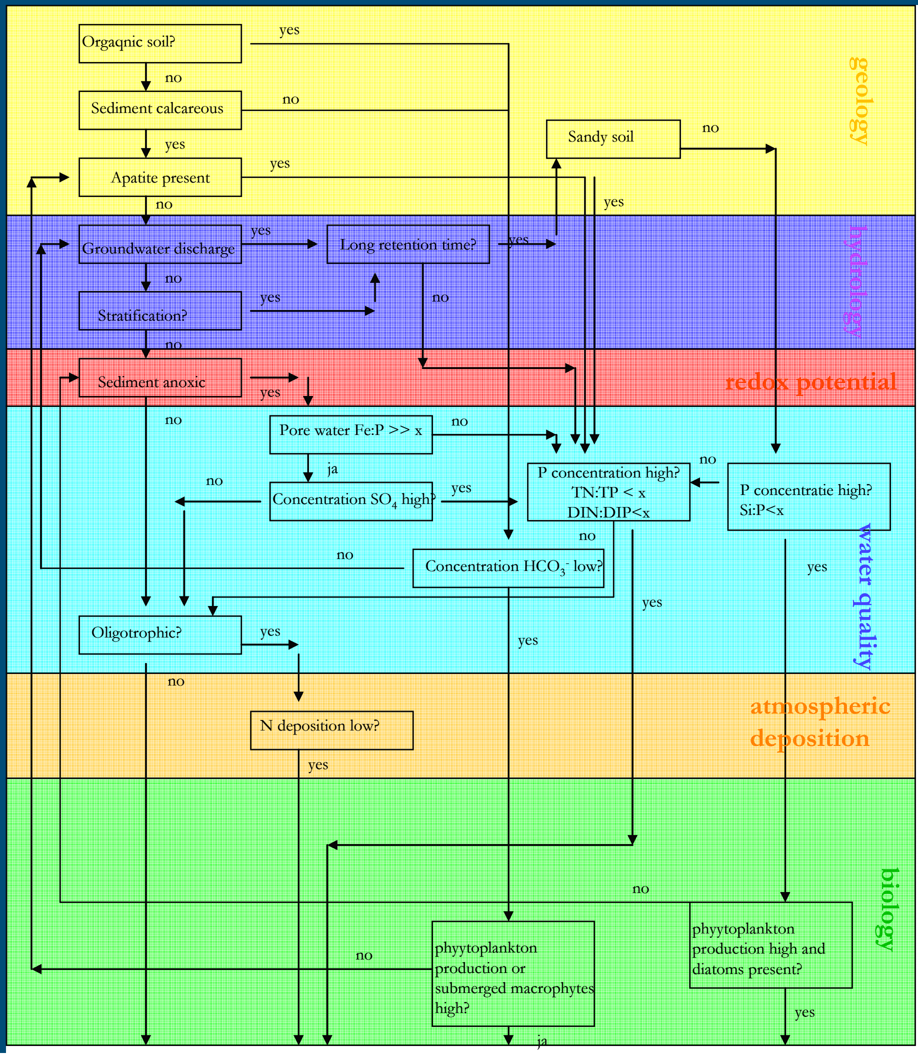
- Streams
  - More light limitation
    - Turbidity high due to sediment
    - Shading by trees
  - less susceptible for algal blooms because of hydraulic flushing
  - Hydraulic drag influences macrophyte growth (Hilton et al., 2006); drag force←→horizontal growth strategy/light limitation
  - Both P and N often found to be limiting for periphyton and phytobenthos
  - Macrophyte diversity in 2 streams in France determined by nutrient concentration (Thiebaut & Muller, 1998)
  - Eutrophication can cause changes in diatom composition, bigger diatoms → no food for grazers (Tall et al, 2006)

General patterns in nutrient limitation

- Floodplains, benches & wetlands
  - Important role in WFD
  - Limited by N, sometimes by P or K (Olde Venterink et al., 2003; Beltman et al. 2007; Loeb et al, accepted)
  - Very eutrophic systems: no nutrient limitation (Spink et al., 1998; Antheunisse et al., 2006)

→ even if a certain nutrient in an aquatic system itself does not affect plant growth, it still can matter in floodplains and benches

Landscape processes & type of limitation



P limitation N limitation C limitation Si limitation

Conceptual model of limitation types

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Landscape processes & type of limitation

- Geology
  - Organic soils: more N available, more often P-limited
  - Mineral soils: more retention of P, helophytes more often limited by N (Bedford et al., 1999)
  - Calcareous soils: lower availability of P, more often P limited (Noe et al, 2001; Ross et al., 2006)
  - Apatite in subsoil: more P available, limitation by N (Moss et al., 1997)

Landscape processes & type of limitation

- Hydrology
  - Groundwater discharge:
    - if groundwater rich in nitrate, supply of nitrate possible
    - If groundwater anoxic, supply of P and Fe possible
    - Groundwater discharge influences soil redox potential
  - Long retention time lake: increases chance on Si limitation
  - Thermal stratification of lakes
    - Silica skeletons sink to bottom, Si limitation in epilimnion
    - P desorbed from sediment can not reach epilimnion → possible P limitation

Landscape processes & type of limitation

- Redox potential
  - Low redox potential causes desorption of P from Fe
  - Reduction of sulphate → sulphide → binding to iron → more P desorbed
  - Nitrate acts as a redox buffer → less P available (NB nitrate can also stimulate decomposition and increase P availability)

- Water quality
  - N:P ratio
  - Si:P ratio and P concentration
  - Nitrate concentration
  - Sulphate concentration, in combination with Fe:P pore water
  - Concentration HCO_3^- (and CO_2)

Landscape processes & type of limitation

- Atmospheric deposition: if low, N limitation in oligotrophic lakes

- Biology:
  - High biomass production (algae or macrophytes) → C limitation if HCO_3^- concentration is low
  - High biomass production and low Si:P → Si limitation of diatoms

Discussion

- Due to differences in demand and availability, different groups of primary producers can be limited by different nutrients at the same time (algae by P, diatoms by Si, macrophytes by N)
- Phytoplankton is limited by P in most lakes
- The quantity of correlative lake studies (P vs Chl-a) may have obscured the presence of other limiting nutrients
- Limitation by N, C and Si is often seasonal and happens after depletion of P due to algae blooms
- In lakes with permanent N limitation, either P is very high (eutrophic lakes), or N is very low (oligotrophic lakes)
- Optimal N:P ratio for macrophyte species needs more empirical evidence

Discussion

- Under which circumstances did you find other nutrients than P limiting?
- Does nutrient limitation play an important role for macrophytes in streams?
- Does decreasing N load cause cyanobacteria blooms?
- Which other processes influencing the type of nutrient limitation did you find?

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