

# Lecture 8a: Nutrient Uptake

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## 1 Lecture Transcript: Nutrient Uptake – Focus on Nitrogen

### 1.1 Introduction: The Centrality of Nitrogen

Today's lecture is centred on the topic of nutrient uptake. We are using nitrogen as our principal example, given its status as a ubiquitous nutrient, essential to all plants for successful growth. Additionally, we'll be considering the environmental consequences of there being excessive

nitrogen in the environment. This is tied directly to the planetary boundaries concept expounded by Johan Rockström, specifically the quadrant concerning the nitrogen and phosphorus cycles—two key global biogeochemical cycles involving the transportation and transformation of these elements between the biosphere, geosphere, atmosphere, and oceans.

Nitrogen is a particular concern, as it is one of the major thresholds humanity has already exceeded globally. This excess results in numerous environmental problems, especially where processes involve plants—primarily aquatic and marine plants, although to a lesser extent, it does impact certain terrestrial plants as well.

### **1.1.1 Nitrogen in the Environment**

Nitrogen's importance is clear when you consider its abundant presence. Approximately 79% of the air we breathe is composed of nitrogen, and it's found in soils, sand, and oceans, where it is accessed by plant roots or available in dissolved form for algae and marine plants. The most productive patches of green—on land and visible as blooms in the ocean—are areas of high nitrogen availability, where lush plant and algal growth is possible.

For this module, whilst terrestrial plants will feature in our discussions, our focus throughout the examples will be on aquatic environments, with particular attention to nitrogen dissolved in seawater and its role in triggering phytoplankton blooms. These can be so prolific that they're visible from space—swirls and green patches near the UK, Ireland, or east of the Falkland Islands, all testify to high concentrations of phytoplankton supported by nitrogen availability.

The twirling and swirling patterns you observe in satellite imagery arise from physical ocean mixing processes—currents, eddies—distributing dissolved nitrogen, which in turn supports phytoplankton blooms.

### **1.1.2 Environmental Consequences of Excess Nitrogen**

As I've mentioned, excess nitrogen in the environment, from pollution, sewage, or runoff from fertilisers, contributes to unsightly and sometimes malodorous nuisance algal blooms. These blooms are ecologically damaging, reduce water quality, and negatively affect ecosystems and human livelihoods. They're typically accompanied by visible pond scum, floating litter, and other environmental degradation.

For instance, in China, the large population density and the dispersal of untreated sewage directly into water bodies has led to massive blooms of phytoplankton. Later in the lecture, we'll discuss the process of eutrophication, which explains in detail how these blooms develop.

Additionally, certain bacteria, such as photosynthetic cyanobacteria ("blue-green algae"), are part of the problem. As blooms expand, they block light, darkening the water and, through their respiration (especially at night), use up oxygen. Upon death, bacteria decompose the overwhelming biomass, a process which consumes even more oxygen and releases large amounts of CO<sub>2</sub>. The result—known as a dystrophic or anoxic event—is hypoxia or complete anoxia, which leads to further die-offs, especially of aquatic animals requiring oxygen. The largest consumer of oxygen here is the decomposition of dead organic material by bacteria through respiratory processes.

## 1.2 Understanding Nutrients and Their Uptake

### 1.2.1 What Makes a Nutrient Essential?

Nutrients—alongside light, oxygen, and carbon dioxide—are indispensable for plants and algae to grow, reproduce, and persist. In aquatic environments, algae are fully immersed in nutrient-rich water, allowing them to absorb dissolved nutrients directly. In contrast, terrestrial plants can only access nutrients through roots that penetrate soil, extracting dissolved nutrients from soil water.

Algae, because of their immersion, do not require roots. Their entire body (the “thallus”) is bathed in nutrients. By contrast, plants depend on root systems both for nutrient uptake and for transport to other parts of the organism. You should recall from previous modules how the surface area to volume ratio becomes decisive for nutrient uptake efficiency, particularly in aquatic environments where mixing is driven by environmental processes.

#### 1.2.1.a Symbiotic Relationships

Terrestrial plants often benefit from symbiotic relationships with fungi and bacteria—mycorrhizae and root nodules—helping them acquire and process nutrients from the soil. Aquatic algae generally do not require such associations, although bacteria in the marine environment do help make nitrogen available for algal uptake.

Bacteria, in terms of both biomass and individual numbers, are among the planet’s most abundant organisms; without them, no form of life would exist.

### 1.2.2 Historical Perspective

Our current understanding of plant nutrient uptake is largely indebted to studies conducted between the 1930s and 1970s. Algae, because of their direct exposure to dissolved nutrients, provided a simple and convenient model to study the principles of nutrient uptake, eventually informing our understanding of the entire plant kingdom.

#### 1.2.2.a Categories of Nutrients

Through these studies, nutrients have been sorted in multiple ways, principal among which are:

- **Essential versus beneficial nutrients:** Essential nutrients are those without which a plant cannot survive or complete its life cycle. Even the absence of a single essential nutrient will halt growth, productivity, or reproduction. Beneficial nutrients enhance or facilitate physiological processes, but are not strictly required for survival or completion of the life cycle.
  - By Epstein’s (1972) definition, a nutrient is essential if the plant cannot complete a normal life cycle without it, and the element forms part of an essential plant constituent (e.g., magnesium in chlorophyll a).
  - Essential nutrients cannot be substituted by another element and must have a direct effect, not just act as a cofactor.
- **Macronutrients versus micronutrients:** This classification reflects the relative quantity needed by the plant. Macronutrients are present and required in much higher concentrations; their roles are often structural, contributing to the biomass of the plant (e.g., carbon, nitrogen, phosphorus, oxygen, potassium). Micronutrients, though required in far smaller amounts, function mainly as catalysts or regulators (e.g., iron in nitrate reductase).

### 1.2.2.b Tables and Quantitative Comparisons

Tables commonly show, per kg of dry plant material, that macronutrient concentrations are several orders of magnitude greater than those of micronutrients.

### 1.2.3 Structural and Regulatory Roles

To reiterate: macronutrients contribute to the structure and mass of the plant; micronutrients act as catalytic or regulatory substances. For example, if you removed all the iron from a large tree, you'd be left with only a handful, but that tiny amount is indispensable for the plant's metabolic processes.

### 1.2.4 Essential Elements in Seaweeds

Algae (seaweeds) require around 20 varieties of nutrients, including: - **Nitrogen** - **Phosphorus** - **Potassium** - **Calcium**, among others.

Nitrogen is crucial—found in amino acids, nucleic acids, proteins—because proteins require nitrogen for their formation. Phosphorus is critical for structural and metabolic functions such as nucleic acids, phospholipids in membranes, and ATP transfer. Potassium and others play similar roles.

While the precise list of essential nutrients varies modestly between algae and higher plants (the latter require 17 essential elements), the principle remains the same: the majority of biomass is composed of macronutrients.

#### 1.2.4.a Assessment Relevance

I will not set examination questions that require simple regurgitation of lists (such as “List five essential elements in seaweeds”). Focus, rather, is on understanding the processes and underlying principles.

## 1.3 Concentration Gradients and Uptake Mechanisms

A key physiological contradiction prompts interesting questions: inside the plant, the concentration of key nutrients is typically much higher than outside—in seawater or soil. Passive uptake via diffusion or osmosis cannot account for this, as both processes follow concentration gradients (from areas of high to low concentration).

Therefore, nutrient uptake often requires *active* transport—energy-dependent mechanisms that move nutrients against their concentration gradient into the plant, where they are assimilated into new biomass.

### 1.3.1 Empirical Data

If we compare concentrations (for example, micrograms per gram of seawater versus of seaweed dry mass), plants can have much higher internal nutrient concentrations. For iron, particularly scarce in seawater, seaweeds maintain relatively high tissue concentrations, which demands an energetic uptake strategy.

## **1.4 Nutrient Classes and Special Cases**

Besides inorganic nutrients (the “bare elements,” not bound in organic molecules), plants can, through mixotrophy, also absorb dissolved organic compounds, though this is much less common and less of a focus for today’s discussion.

### **1.4.1 Limiting Nutrients: The Concept and Experiments**

Beginning in the 1960s-70s, researchers recognised that at any time, a particular nutrient could be ‘limiting’. That is, if it is removed or absent, growth ceases. Professor Dugdale and colleagues demonstrated that in most seawaters, nitrogen is the major limiting nutrient. Experiments adding nitrogen to seawater samples resulted in rapid phytoplankton growth; adding other nutrients like phosphorus or potassium generally produced no such effect unless these were limiting.

Therefore, a nutrient is ‘limiting’ in a given context if its addition results in increased growth; if not, it isn’t currently limiting. In most marine environments, nitrogen is limiting; phosphorus sometimes is, but this is more common in freshwater environments.

## **1.5 The Redfield Ratio and Nutrient Limitation**

The “Redfield ratio” is a critical empirical observation: for every 106 atoms of carbon in microalgae, there must be 16 atoms of nitrogen and 1 atom of phosphorus for optimal growth. That is, the ideal C : N : P ratio is 106 : 16 : 1.

For macroalgae, a similar ratio exists: 550 : 30 : 1 (C:N:P), reflecting the greater carbon requirement for structural integrity in larger, multicellular algae.

This optimal ratio is essential. Any deviation means one of the nutrients becomes limiting, restricting growth. Microalgae, being unicellular and minute, need less structural carbon than macroalgae.

## **1.6 Liebig’s Law of the Minimum**

Liebig’s law, or “the law of the minimum,” was articulated in the 19th century. It states that the yield of a plant is determined by the single most limiting nutrient, regardless of the abundance of others. Thus, if any one nutrient is below its critical threshold, it will restrict growth, no matter how abundantly everything else is supplied.

This principle is vital for optimising fertilisation strategies in both agriculture and aquaculture: knowing which nutrient is limiting allows for targeted supplementation for maximal growth.

### **1.6.1 Practical Application**

For a red macroalga with an optimal N:P ratio of 30 : 1, suppose more nitrogen is present than phosphorus as required. Phosphorus becomes the limiting nutrient, constraining growth despite surplus nitrogen. Conversely, if nitrogen is below the required ratio, then it is the limiting nutrient.

This concept extends to all primary producers—seaweeds, microalgae, and terrestrial plants.

## **1.7 Luxury Consumption**

Luxury consumption describes the phenomenon where some plants — particularly certain seaweeds — can take up more of a nutrient than is immediately required for growth, storing the excess

for future use. When environmental levels of nitrogen or phosphorus later dip below optimal, the plant draws on these internal reserves to maintain growth.

This adaptation is especially valuable in environments with fluctuating nutrient availability and features prominently in aquaculture. Here, seaweeds can be provided with nitrogen and phosphorus at optimal ratios, and their ability to undertake luxury consumption helps buffer against subsequent scarcity.

Luxury consumption is a survival strategy most evident among K-selected, climax species in the ocean, conferring resilience in the face of unpredictable nutrient supply, and ensuring continued survival and growth despite external variability.

## **2 Lecture Transcript: Environmental Consequences of Nutrients and Uptake by Seaweeds**

### **2.1 Introduction**

Yesterday we spoke about nutrients. I gave you a brief introduction to what nutrients are, and explained that they can be classified into macronutrients and micronutrients, as well as essential and beneficial nutrients. Today, we need to talk about the consequences—the environmental consequences—of nutrients. We'll also begin to explore the field of measuring the uptake of nutrients by seaweeds. That's our plan for today.

One of the things we're going to do is to use nitrogen as our example. Nitrogen is convenient and easy to work with. The uptake mechanisms seen in many other nutrients are similar to those for nitrogen, so we can use it as a nice case study. But, of course, nitrogen is also one of the most important nutrients, both in the ocean and on land. It's often a limiting nutrient in the ocean and is important in many environmental problems we face today, such as eutrophication.

In today's lecture, I'll provide some of the ecophysiological background for why some seaweeds respond particularly well under eutrophic conditions. You will understand the physiological basis for why some seaweeds become what we refer to as nuisance algae.

### **2.2 Case Study: The Beijing Olympics and Eutrophication**

As an example, I'll refer to what happened during the Beijing Olympics in around 2008. Just prior to the Olympics, vast parts of the Chinese shoreline were covered with nuisance green seaweeds. Authorities had to employ a whole group of people to clean up the shoreline. All those green bits—the seaweed blooms in China—were a direct result of nitrogen entering the ocean and polluting the waterways. It's unsightly, it's smelly, and it's dangerous, so it's a huge problem around the world.

### **2.3 Sources and Forms of Nitrogen**

So, where does nitrogen come from? Nitrogen is quite abundant in the atmosphere—actually, the bulk of the atmosphere is comprised of nitrogen, about 79% of it is gaseous nitrogen,  $N_2$ . Gaseous nitrogen itself cannot be used by plants, so certain processes are required to convert that nitrogen into a bioavailable form that plants can take up.

Nitrogen is brought into the oceans via rivers, mostly in the form of nitrate and ammonium. It can also be present in the atmosphere as nitrous oxides and, in water, as nitrous oxides, entering the ocean via river runoff or various atmospheric processes. Other sources include processes in the Earth's crust, like volcanic eruptions, as well as fossil fuel burning from industrial operations, which both put nitrous oxides into the atmosphere. In certain cases, that nitrogen becomes available as a very acidic form—nitric acid—which is a source of some acid rain.

But once the nitrogen enters the ocean, many interesting processes take place. It gets recycled, taken up by algae, released by algae, released by animals that feed upon the algae—so the whole big global biogeochemical process is seen in the ocean, as well as elsewhere on the planet.

We'll delve a bit more into the detail of the global biogeochemical cycles shortly.

## 2.4 Nitrogen Fixation and Cycling

As I said before, gaseous nitrogen in the atmosphere, which is the bulk of it, cannot be used directly by plants. It must somehow become available, and this is accomplished by the process of nitrogen fixation, carried out by organisms such as cyanobacteria. Cyanobacteria can take up atmospheric dinitrogen ( $N_2$ ), lock it internally in organic forms or as ammonia. When the cyanobacteria die and decompose or are eaten, that nitrogen is recycled in the form of ammonium or nitrate back into the ocean. Thus, cyanobacteria fix atmospheric nitrogen, making it available to the rest of the ecosystem to be taken up as ammonium or nitrate. This supports much of the planet's photoautotrophs, on both land and in the ocean.

If we look at the various sources of nitrogen: gaseous nitrogen is very abundant in the ocean and atmosphere. In the ocean, once it's dissolved, the total amount of all forms of nitrogen in the ocean is about 95% or so gaseous nitrogen—meaning dissolved  $N_2$  from the atmosphere. A much smaller fraction is available as nitrate— $NO_3^-$ —which comprises about 5% of the nitrogen in the ocean. An even smaller amount is present as nitrite  $NO_2^-$ ; it's almost immeasurable in many instances, because nitrite is only present in seawater for very short periods as an intermediary between ammonium and nitrate. Concentrations of nitrite are, therefore, very low.

Nitrogen is also present as ammonium ( $NH_4^+$ ); close to about 0.1% of the total nitrogen in the ocean is present as ammonium. So those three compounds— $NO_3^-$ ,  $NO_2^-$ , and  $NH_4^+$  (nitrate, nitrite, and ammonium)—are together known as DIN: dissolved inorganic nitrogen. This is the amount of nitrogen available for uptake by plants in the ocean.

“Dissolved” because it's in ionic form, within the water; “inorganic” because, while it's not bonded within an organic molecule, it does not contain carbon-hydrogen structures; and “nitrogen” because the major macronutrient atom in all these is nitrogen.

## 2.5 The Marine Nitrogen Cycle

Once nitrogen enters the ocean, it is cycled in various different ways. It's a complex set of reactions and processes, involving uptake by phytoplankton, their death, their consumption by zooplankton and fish, as well as decomposition—a whole host of processes.



The science that studies the transformation of various forms of nutrients between abiotic and biotic pools within the Earth system is called biogeochemistry. Biogeochemistry is concerned with the movement and the rates of transformation of nutrients between, for example, phytoplankton and zooplankton (organic or biotic components), the ocean (the hydrosphere), the atmosphere, and the geosphere.

Here is a basic, simplified representation of the nitrogen cycle in the ocean: At the top, you have the atmosphere, at the bottom the ocean floor, and in between is the water column. In and out of the atmosphere, gases such as  $O_2$ ,  $CO_2$ , and  $N_2$  move into the ocean, so we end up with DIN (ammonium, nitrate, nitrite) dissolved in the water. Algae then take up this DIN to produce algal biomass via photosynthesis. Animals consume phytoplankton, relying on them for biomass production, and in turn carry out respiration, taking up oxygen produced by the algae.

As animals eat algae, they excrete waste products, releasing  $CO_2$ , more DIN, and dissolved organic forms of nitrogen into the water. In feeding on algae, animals might only consume parts, allowing algal cell contents to leak out, making dissolved organic nitrogen (DON) available to the environment. Algae can then take up this DON.

Here, you see a cycling: nitrogen comes from the atmosphere, dissolves in seawater, is taken up by algae, consumed by animals, and released again. But not all nitrogen is continually cycled—some is lost. Particulate forms of nitrogen, called POM (particulate organic matter), settle down through the water column as “marine snow.” As it falls, marine snow is decomposed by bacteria, which release more DIN and  $CO_2$  in the process. Thus, concentrations of DIN generally increase deeper into the ocean, as marine snow decomposes and releases more nutrients.

## 2.6 Remineralisation and Upwelling

Animals on the seafloor can consume marine snow, releasing DIN, DON, and  $CO_2$  into the water column, with bacteria contributing to remineralisation. Remineralisation is the process that converts organic forms of nitrogen back into inorganic forms like ammonium and nitrate.

Over time, DIN accumulates in the deeper ocean, but physical ocean processes, such as ocean currents (upwelling), transport some of this deep, nutrient-rich water back to the surface, injecting remineralised nitrogen into sunlit upper layers, where algae can again take it up.

So, these cycles are coupled by biological processes—linking algae to animals through heterotrophy (predation, grazing), decomposition, excretion, faecal pellet production, as well as by physical processes like upwelling. Photosynthesis is a surface process, so nitrogen uptake by algae occurs mainly in surface waters, not in the deep ocean where there is no light.

Also, don't forget the role of nitrogen-fixing bacteria like cyanobacteria, which fix atmospheric nitrogen and make it bioavailable for oceanic and other organisms. This is how atmospheric nitrogen becomes available in the surface ocean.

## 2.7 Definitions: Some Key Terms

Some important definitions:

- **DIN:** Dissolved Inorganic Nitrogen; includes ammonium, nitrate, nitrite.

- **DIP:** Dissolved Inorganic Phosphorus; phosphorus equivalents to DIN.
- **DON:** Dissolved Organic Nitrogen.
- **POM:** Particulate Organic Matter; also includes particulate forms of both nitrogen and phosphorus.

The biogeochemical cycle operates similarly on land, but most of the transformations happen within the soil, particularly around plant roots, as well as via aboveground decomposition processes—for example, as leaves fall, decompose, and transfer nitrogen back into the soil.

## 2.8 Units, Concentrations, and Oceanographic Patterns

When reading literature about nitrogen as a macronutrient, you'll encounter various units: micromolar ( $\mu\text{M}$ ), microgram atom per litre, and so on. These all describe the concentration of nitrogen in water or solid solution. You should recall from first-year chemistry how to convert between micromolar and microgram atom per litre ( $\mu\text{M}$  to  $\mu\text{g atom L}^{-1}$ ), and vice versa. Be familiar with these conversions, as you will encounter them in tests.

You must also know the SI prefixes and the number of zeros associated with each—grammes, milligrammes, microgrammes, nanogrammes, picogrammes, et cetera. In plant physiology, a basic grasp of chemistry and SI unit prefixes is assumed.

### 2.8.1 Typical Oceanic Nitrogen Concentrations

Here's a range of concentrations that nitrogen is available in the ocean:

- **Tropical regions (ca. 10°S to 10°N):** Very low nitrogen; concentrations may be in the nano- to picogramme range ( $\text{ng L}^{-1}$  –  $\text{pg L}^{-1}$ ).
- **Most of the ocean:** Microgramme to milligramme range.
- **Freshwater systems:** Often reach the milligramme range.
- **Upwelling regions (e.g., the Benguela upwelling off South Africa, Canary Current off North Africa, Humboldt off South America, California Current off North America):** Highest oceanic nutrient levels. Here, total inorganic nitrogen can reach up to  $40 \mu\text{mol L}^{-1}$ , while inorganic phosphorus typically reaches  $2 \mu\text{mol L}^{-1}$ .

Note the ratio here, approximately 10:1, closely corresponding to the Redfield ratio.

During active upwelling, nutrient concentrations rise to  $20\text{--}40 \mu\text{mol L}^{-1}$  nitrogen,  $2 \mu\text{mol L}^{-1}$  inorganic phosphorus. When upwelling subsides, these values drop below  $4 \mu\text{mol L}^{-1}$  for nitrate and  $0.2 \mu\text{mol L}^{-1}$  for inorganic phosphorus.

Thus, in the ocean, background nitrogen levels are not fixed but fluctuate, sometimes very rapidly (over tens of minutes) due to oceanographic processes such as upwelling. Algae have evolved various adaptations to cope with the intermittent and transient nature of nitrogen availability in the ocean—a stark contrast to terrestrial systems, where changes are usually slower.

## 2.9 Classification of Oceanic Systems Based on Nutrient Levels

The ocean can be classified into:

- **Oligotrophic:** Low nutrient, e.g., tropical regions, almost no nitrogen.

- **Mesotrophic:** Intermediate, e.g., upwelling zones, fluctuates temporally.
- **Eutrophic:** High nutrients, often due to human influence—unnaturally high nitrogen.

In the ocean, nitrogen is typically limiting. However, excessive input causes problems—most notably, eutrophication.

## 2.10 The Nitrogen Bomb: Human Impact

For your self-study: read the article “The Nitrogen Bomb” (available on Ecoma). The Haber-Bosch process has resulted in a huge problem worldwide in both terrestrial and aquatic systems. “Nitrogen bomb” is a metaphor for the disastrous potential of excessive and unwisely applied nitrogen, most sharply observed in eutrophication. This is examinable content.

## 2.11 What is Eutrophication?

Eutrophication usually occurs when too much nitrogen is added to a body of water that would naturally be nitrogen limited. In these systems, certain algae or seaweeds respond rapidly to the enrichment. For instance, the three illustrated species all possess high surface area to volume ratios, meaning nearly every cell is exposed directly to the environment and can immediately take up available nutrients. This capacity allows rapid growth and biomass accumulation.

More complex seaweeds with lower surface area to volume ratios respond more slowly, if at all, to such nutrient pulses; the response is more distributed and structurally limited. In contrast, these high surface area opportunistic algae (sometimes called R-selected species) bloom excessively when nutrients are introduced, becoming nuisance species and disrupting the ecological balance.

In a natural system, there is a high diversity of plants and animals. After eutrophication, one species becomes dominant, reducing community composition, species richness, and causing the biomass of that one species to increase exponentially.

In severe cases, the system can become anoxic. Imagine a dense bloom of photosynthesising algae; at night, without photosynthesis, respiration consumes all the oxygen in the water. Species that require oxygen die off, and their decomposition consumes even more oxygen, eventually producing low-oxygen, or dystrophic, conditions.

Bacteria are key to these processes, as they drive decomposition and thus increase total ecosystem respiration and oxygen consumption.

## 2.12 Mitigating Eutrophication

As for what can be done: removing the blooming nuisance algae is not addressing the underlying issue. We must ensure that sources of nitrogen entering the water are addressed—by improving sewage treatment, reducing fertiliser runoff from agriculture, and proper waste management. Rivers seen as convenient dumping grounds simply transfer the problem downstream; the consequences are borne by someone else or by the ecosystem.

## 2.13 Linking Form and Function: Surface Area to Volume Ratio

I’ve mentioned that response to eutrophication is connected to both the morphology and physiology of algae. Those species with high surface area to volume ratios can absorb nutrients rapidly

and outcompete others. This is where Littler and Littler's "functional form model" comes into play, explaining why morphology is crucial to ecological dynamics under eutrophic conditions.

## 2.14 Summary and Integration

In summary, you should now connect previously disconnected ideas—such as surface area to volume ratio and nutrient uptake. Understanding this enables a more comprehensive view of how eutrophication alters ecosystems.

If you have questions or do not grasp a particular aspect, you're welcome to ask on WhatsApp. Please ensure you read the assigned articles and refresh your knowledge of unit conversions and SI prefixes, as you will be expected to use this knowledge fluently.

Read further on eutrophication. Much more can be said, but the core is straightforward biology playing out in an ecosystem that simplifies under stress—one species dominates as nutrients increase, reducing diversity and altering physiological and ecological processes within the system.

## 3 Lecture Transcript: Nutrient Uptake

### 3.1 Introduction

Right, so today we will continue to talk about nutrient uptake. Last week, we spoke about nutrient uptake experiments, and I showed you how to derive information from the depletion curve—the relationship that shows uptake rate versus substrate concentration. When we plotted that relationship, the graph appeared as a hyperbolic tangent curve. At low concentrations, the uptake rate increases rapidly, and then at high nutrient concentrations, it reaches a plateau. This type of relationship is known as the Michaelis–Menten uptake relationship, and it serves as an example of one of three different uptake mechanisms called active uptake.

On Thursday, we will discuss passive transport and facilitated diffusion, which are two additional uptake mechanisms. Generally speaking, algae and most other plants can display one of these three mechanisms—active transport, passive transport, and facilitated diffusion. Today, our focus will remain on active uptake.

### 3.2 Review of Active Uptake Parameters (Refer to slide text if available)

Last week, after we explored the uptake curve—the  $V$  versus  $S$  relationship—of active uptake as determined for nitrate, I explained the various parameters:  $V_{max}$ ,  $K_s$ , and  $\alpha$ . On this slide, you will find text discussing the ecological significance of these parameters. We have covered this before, so I will not repeat it in detail. Instead, let us delve a bit further into what active uptake involves.

### 3.3 What is Active Uptake?

Active uptake allows most plants to maintain nutrient concentrations inside their cells that are much greater than those found in the external environment. This process enables nutrients to be transported from an area where there is a lower concentration to an area inside the plant where there is a higher concentration—essentially moving against the concentration gradient. More formally, this occurs against the electrochemical potential gradient.

For most cases, external concentrations are in the micromolar range ( $\mu\text{mol}$ ), while internal concentrations inside the cell are in the millimolar range ( $\text{mmol}$ ). This situation implies that passive diffusion alone cannot account for the movement of nutrients into the cell, because diffusion typically moves substances from high to low concentration—not the other way around.

Passive diffusion is – at most – responsible for the movement of nutrients from the environment across the boundary layer. This specific process is determined by passive diffusion. However, the major uptake of nutrients into the cell is described by active uptake. For this to occur—from a region of low concentration to one of high concentration—cells must expend energy, namely metabolic energy.

The energy expended is generally light-dependent, with ATP being the most likely source. This is achieved by a system that involves proton-pumping ATPases, setting up a gradient between the external and internal environment in terms of pH. The proton gradient, or the pH gradient, establishes the electrochemical potential gradient, which then drives secondary ion transport. The secondary ion in question is the nutrient—such as nitrate, in our previous example.

This coupling between the pH gradient and the nutrient gradient facilitates the active uptake of nutrients. Coupled transport may arise from differing movements of ions at different sites, either in opposite or the same direction. When hydrogen ions are pumped out of the cell and nutrients are pumped in, this form of counter-transport is known as anti-port, or anti-porter transport. Conversely, some nutrients move in the same direction as the protons—this is called symport or co-transport.

In algae, the proton pump is linked to the co-transport of substances like sugars and thiourea, and there are also mechanisms involving the pumping of sodium ions, which can be responsible for the co-transport of other nutrients from the environment into the cell.

### 3.3.1 Key Points of Active Uptake

You must remember that cellular energy, primarily derived from ATP, is required to drive active uptake. ATP drives the proton pump, which establishes the primary gradient, and then nutrients are brought into the cell by coupling to this gradient.

This is the mechanism by which an energetic, active process brings nutrients into the cell—by coupling with a proton pump generated by ATP and ATPases. While this is a complex physiological process, knowing this overview will suffice; we will not explore all the fine physiological details.

## 3.4 Characteristics that Define Active Uptake

Beyond its energy requirement, active uptake is defined by several additional characteristics:

1. **Selectivity for Particular Ions:** Only specific ions are taken up via active transport, not all. For example, nitrate, phosphorus, and sulphates can be taken up in this way. One of the components of dissolved inorganic nitrogen (DIN), ammonium, is typically not taken up via active transport and is excluded here.

2. **Saturation of the Carrier System:** There is a stage in the uptake process where the carrier system becomes saturated. At high nutrient concentrations, there is a portion of the curve where  $V_{max}$  is reached—meaning uptake rate will not increase, despite increasing external nutrient concentration. This is because the enzymatic systems responsible for transport become saturated and cannot operate any faster.
3. **Movement Against the Concentration Gradient:** As previously discussed, active uptake involves the movement of ions against their concentration gradient.

These features—selectivity, saturation, and movement against the gradient—define active uptake. Note that some of these factors also apply to facilitated uptake, which we shall discuss later.

### 3.5 Graphical Representation: $V$ vs $S$ Curves

When a graph of uptake rate ( $V$ ) versus substrate concentration ( $S$ ) displays a hyperbolic tangent curve—a steep rise at low concentrations and a plateau at high concentrations—this signifies active or facilitated uptake. The maximum rate of uptake ( $V_{max}$ ) is primarily set by factors intrinsic to the algae, such as the enzymatic processes involved.

Consequently, environmental factors that influence enzyme activity—like light intensity or temperature—will impact how high  $V_{max}$  can be. Thus, active uptake is largely determined and influenced by environmental conditions that promote growth, photosynthesis, and metabolic activity—for example, high temperatures and abundant light.

### 3.6 Surface Area to Volume Ratio and Uptake Parameters

Suppose we gather several seaweeds, spanning all six or seven different functional form categories outlined by Littler and Littler, and conduct uptake experiments. We would discover that  $V_{max}$  and  $K_s$  vary as a function of the surface area to volume ratio.

Plants with flat, membranous, or highly filamentous forms tend to grow rapidly and thus have a much higher  $V_{max}$ —thanks to their high surface area to volume ratio, which allows every cell direct exposure to the nutrient-rich environment. They are also typically able to acquire nutrients effectively even in environments where nutrient levels are low, implying they often have a low  $K_s$  (and thus a high affinity for nutrients).

On the other end of the spectrum, algae with a low surface area to volume ratio—where the bulk of the cells are internal—grow more slowly, with reduced access to light and slower diffusion rates. Consequently, they possess a low  $V_{max}$  and often a higher  $K_s$ , making them less able to acquire nutrients when these are scarce.

If these low  $V_{max}$  species are placed in a nutrient-rich (eutrophic) environment, it makes little difference, because their limitation is set by internal cellular processes, not external nutrient supply. In contrast, fast-growing, high-surface-area species with high  $V_{max}$  and low  $K_s$  will respond rapidly to eutrophic conditions. This helps explain why some algae become nuisance or problematic under excessive nutrient conditions—their physiological traits make them well-suited to exploit high nutrient environments.

Understanding the ecological significance of high or low  $V_{max}$  and  $K_s$  is crucial; it explains the circumstances under which species will thrive and proliferate based on the environmental nutrient regime.

### 3.7 The Three Phases of Active Uptake

Active uptake can be described as having three phases:

1. **The Surge Phase**
2. **The Internally Controlled Phase**
3. **The Externally Controlled Phase**

Let's discuss each in detail.

#### 3.7.1 The Surge Phase

The surge phase is observed at the very beginning of nutrient uptake. Imagine taking a seaweed that had not previously been exposed to nutrients and placing it into fresh seawater or a beaker with abundant nutrients. At the start, the environment is nutrient-rich, but the internal pools within the seaweed cells are nutrient-poor.

Immediately after exposure, there is a rapid influx of nutrients—nutrients rush into the cellular pools (like vacuoles) which had been depleted. Once the concentrations equalise, the surge phase ends. This rapid initial movement is the surge phase, driven by a steep concentration gradient.

The surge phase only occurs at the beginning of exposure to high nutrient concentrations. Once the internal pools are filled, the diffusive flux equalises, and the rapid uptake stops.

#### 3.7.2 The Internally Controlled Phase

After the surge phase, once the internal pools are filled, the rate of nutrient conversion—transforming inorganic nutrients already inside the cell into organic compounds (such as amino acids or other macromolecules)—becomes the limiting step. This is the internally controlled phase.

Here, the rate of nutrient uptake is governed by enzyme activity, and this phase sets the plateau seen in the uptake curve ( $V_{max}$ ). The maximum rate is determined by how quickly the enzymes can process nutrients.

#### 3.7.3 The Externally Controlled Phase

If the plant remains in the closed environment and continues to take up nutrients, eventually the external nutrient concentration will drop. At some point, the uptake rate is determined by the diffusion of nutrients from the environment to the cell—this is the externally controlled phase.

At very low ambient nutrient concentrations, the uptake rate also becomes low, because diffusion is limited. As nutrient concentrations increase, the concentration gradient increases, and so does the diffusive flux. In this region, the rate of nutrient uptake is determined by the difference in concentration across the boundary layer surrounding the organism.

Two main factors influence the movement of nutrients across the boundary layer:

1. The concentration gradient between the external environment and the cell.

2. The thickness of the boundary layer, which is influenced by water movement; high water movement results in a thin boundary layer and hence faster diffusion, while low water movement causes a thicker boundary layer which slows diffusion.

All these external physical factors combine to influence the maximum rate of diffusion across the boundary layer.

### 3.8 Surface Area to Volume Ratio and Growth Dynamics

In seaweeds with high surface area to volume ratios—flat, membranous, or highly branched filamentous forms—cells are optimised for maximum exchange with the environment, efficient light harvesting, and rapid gas exchange. When these are placed into a nutrient medium, their uptake is extremely rapid because their enzymatic machinery can sustain a high  $V_{max}$ . Biomass can, under certain conditions, double in just a day or two. For instance, if you have 1 gram of seaweed today, after a day or two you might have 2 grams—achievable because of the high  $V_{max}$  and the ample nutrient supply.

Other seaweeds, at the opposite end of the functional form spectrum with a low surface area to volume ratio, do not respond instantaneously. There is often a lag. Some of these can engage in luxury consumption—taking up more nutrients than needed at that moment, storing them internally (in either organic or inorganic forms) for later use when growth conditions (e.g., light, other nutrients) are optimal. These plants respond more slowly, remobilising stored nutrients once other environmental factors are favourable.

This links back to our earlier discussions on surface area to volume ratio and the ecological and physiological implications for nuisance algae under eutrophic conditions.

### 3.9 Factors Influencing Nitrogen Uptake

Nitrogen (and other macronutrient) uptake is influenced by many factors:

- **External Conditions:** The thickness of the boundary layer and the actual concentration of nutrients in the water are crucial. These are influenced by physical conditions outside the plant.
- **Form of Nutrient:** Ammonium is taken up much faster than nitrate; nitrate requires active uptake, while ammonium is acquired via passive diffusion.
- **Nutrient Starvation History:** Plants recently starved of nutrients will uptake rapidly when exposed to fresh supply; non-starved plants may not show a significant response.
- **Environmental Conditions:** High light intensity and high temperatures both enhance metabolism and, consequently, increase  $V_{max}$ , speeding up uptake rates.
- **Surface Area to Volume Ratio:** As discussed, this has a substantial effect on uptake dynamics.
- **Mechanisms of Uptake:** The presence of additional mechanisms (such as facilitated diffusion) can also influence overall nutrient uptake.

All of these together influence the rate at which macronutrients such as nitrogen and phosphorus are taken up from the environment.



## 4 Lecture Transcript: Nutrient Uptake Mechanisms in Algae

### 4.1 Introduction

Right, so today we shall continue our discussion of nutrient uptake. Last week, we considered nutrient uptake experiments, and I demonstrated how to derive uptake rates from depletion curves—those curves that plot uptake rate versus substrate concentration. When we plotted that relationship, we observed a graph resembling a hyperbolic tangent curve. At low substrate concentrations, the uptake rate increases rapidly, and as concentration rises, this levels off to a plateau. This type of relationship is known as the Michaelis-Menten uptake relationship, and is representative of one of three main uptake mechanisms, namely active uptake.

On Thursday, we shall discuss passive transport and facilitated diffusion, which are the two other primary uptake mechanisms. Overall, algae and most other plants exhibit active uptake, passive transport, and facilitated diffusion. For today's lecture, we are going to focus further on active uptake.

### 4.2 Recap: Active Uptake and Michaelis-Menten Kinetics

Previously, after introducing the uptake curve, or the  $V$  (uptake rate) versus  $S$  (substrate concentration) relationship for active uptake as determined for nitrate, I explained various parameters:  $V_{max}$ ,  $K_s$ , and  $\alpha$ . On this slide, you will find text detailing the ecological significance of  $V_{max}$ ,  $K_s$ , and  $\alpha$ . Since we've already discussed this, I'll not repeat myself here, but let's delve a bit deeper into active uptake.

### 4.3 Mechanism of Active Uptake

Active uptake is the process that accounts for why, in most plants, the internal concentration of a nutrient is much higher than the external concentration. This occurs because there is a cellular mechanism allowing the movement of nutrients from regions of low concentration (outside the cell) to regions of high concentration (inside the plant or cell), i.e., against the concentration gradient—or more properly, against the electrochemical potential gradient.

To quantify, external nutrient concentrations are usually in the micromolar range, while internal concentrations inside the cell are generally in the millimolar range—that is, from  $\mu\text{mol L}^{-1}$  externally to  $\text{mmol L}^{-1}$  internally. This large difference suggests that passive diffusion alone is insufficient, as diffusion would only allow movement from high to low concentration. Passive diffusion is mainly responsible for moving nutrients across the boundary layer, but the main uptake into the cell interior is accounted for by active uptake.

Therefore, moving nutrients from areas of low concentration to high concentration requires expenditure of cellular energy, typically metabolic energy. This process is generally light-dependent, and the primary energy source is ATP. The mechanism involves proton-pumping ATPases which establish a pH gradient between the exterior and interior of the cell. It is this proton (pH) gradient that sets up the electrochemical potential gradient necessary for secondary ion transport—the 'secondary ion' in this context is the nutrient being absorbed, for example nitrate in our previous examples.

This coupled transport can involve different ions moving in different directions. For instance, hydrogen ions are pumped out of the cell while nutrients are moved in; this is termed anti-porter or counter-transport. Alternatively, if nutrients are transported in the same direction as protons, this is termed symport or co-transport. In algae, the proton pump can be linked to the co-transport of molecules such as sugars and thiourea. There are also processes involving sodium ion pumping, which can similarly facilitate nutrient uptake from the environment into the cell.

The essential point to remember from this slide is that cellular energy is crucial for active uptake. ATP drives the proton pump, and the resultant proton gradient (established by ATPases) couples to nutrient uptake, allowing transport into the cell against the gradient.

We will not delve deeply into all physiological details here; it is sufficient, for now, to understand the concept as outlined above.

#### 4.4 Characteristics of Active Uptake

Apart from being energetically demanding, active uptake is also characterised by selectivity for particular ions—not all ions are absorbed via active transport, only some. In our prior example, nitrate is absorbed by active transport, but other ions, such as ammonium, are not.

Another key characteristic is saturation of the carrier system: as nutrient concentration increases, there is a stage where the system becomes saturated. This is observed at the plateau— $V_{max}$ —where the uptake rate no longer increases with greater nutrient concentration, as the enzyme-catalysed process is working at maximal capacity.

The three primary characteristics of active uptake, therefore, are: - Movement against an electrochemical gradient, - Selectivity for particular ions, - Saturation of the carrier system at high substrate concentrations.

These considerations also apply, to some extent, to facilitated uptake—but we shall cover that separately.

#### 4.5 Distinguishing Uptake Mechanisms by Kinetics

When uptake rate ( $V$ ) is plotted against substrate concentration ( $S$ ) and the curve shows a steep initial rise followed by a plateau—i.e., a hyperbolic tangent shape—we can infer the process is mediated by either active or facilitated uptake. The maximum uptake rate,  $V_{max}$ , is controlled by intrinsic factors within the algae, specifically those that govern enzyme function. Thus, environmental factors that influence enzyme activity, such as light intensity and temperature, will affect  $V_{max}$ .

Put simply, environments promoting rapid growth—higher temperature, more light—will increase enzyme activities, resulting in a higher  $V_{max}$ .

#### 4.6 Surface Area:Volume Ratio and Functional Morphology

Suppose we conduct uptake experiments across the six or seven different functional form categories established by Littler and Littler. We would find that  $V_{max}$  and  $K_s$  vary with surface area:volume ratio. Fast-growing forms—flat membranous or highly filamentous algae—display high  $V_{max}$  and tend to have lower  $K_s$  values, indicating high affinity for nutrients. These forms,

with large surface areas relative to their volume, excel at acquiring nutrients even in low-nutrient settings.

Conversely, algae with compact morphologies and low surface area:volume ratios (e.g., thick or bulky thalli), do not access light or diffuse nutrients as efficiently. They grow slowly and exhibit both low  $V_{max}$  and higher  $K_s$  values, so their affinity for nutrients is lower. In eutrophic conditions—where nutrients are abundant—such forms do not benefit as much as the high-surface area forms, since their  $V_{max}$  is constrained by internal physiological processes, not nutrient availability.

Therefore, algae with high surface area:volume ratios and high  $V_{max}$  can rapidly respond to, and even become nuisances under, eutrophic conditions, while those with lower ratios are less responsive.

This illustrates the ecological relevance of  $V_{max}$  and  $K_s$ , allowing us to predict under what conditions various algae will thrive or become problematic, based on their morphology and nutrient uptake physiology.

## 4.7 The Three Phases of Nutrient Uptake

Now, considering active uptake, there are three phases to the process:

1. **The Surge Phase**
2. **The Internally Controlled Phase**
3. **The Externally Controlled Phase**

Let's discuss each in turn.

### 4.7.1 Surge Phase

The surge phase occurs immediately after a previously nutrient-deprived alga is introduced into nutrient-rich medium (for example, moving a seaweed from low-nutrient water into a beaker of enriched seawater). At time  $t = 0$ , there is ample nutrient outside but little inside the plant's vacuoles and cellular pools. This difference drives a rapid influx of nutrients—'surge uptake'—from the environment into these pools until the concentration gradients equilibrate and no further rapid uptake is possible. This phase is therefore very short and occurs at high external nutrient concentration.

Note: Be mindful that, on the typical uptake curve, time runs in the opposite direction to substrate concentration; do not confuse the two.

### 4.7.2 Internally Controlled Phase

Next is the internally controlled phase. Once the cellular nutrient pools are filled, the rate of converting these newly imported nutrients (from inorganic to organic forms, such as amino acids and macromolecules) is limited by the enzymatic processing capacity—this is,  $V_{max}$ . The rate of nutrient utilisation is set by the maximum rate of these metabolic pathways and is intrinsic to the species in question.

#### 4.7.3 Externally Controlled Phase

If the uptake experiment occurs in a closed system (e.g., seaweed in a beaker), and the algae continue to absorb nutrients, eventually the outer nutrient concentration drops as it is depleted from the water. At very low ambient concentrations, uptake is now determined by the concentration gradient and diffusion across the boundary layer is limiting—the ‘externally controlled phase.’ The steeper the concentration gradient, the greater the influx; as the gradient shallows, this uptake rate diminishes proportionately.

Two main factors affect the rate of nutrient movement across the boundary layer: - The concentration gradient between the external and internal environment, - The thickness of the boundary layer, which is itself influenced by water movement: rapid water flow yields a thin boundary layer and increased diffusion, whilst still water results in a thicker boundary layer and reduced diffusion.

#### 4.8 Influence of Morphology and Environmental Factors

Certain seaweeds with high surface area:volume ratios—those with flat, membranous, or highly branched forms—are optimised for rapid nutrient uptake. When placed in nutrient-rich medium, these forms respond almost instantly, with rapid increases in biomass, sometimes doubling mass within a day or two, given high  $V_{max}$  and sufficient nutrients.

On the other hand, seaweeds with significantly lower surface area:volume ratios respond more slowly. They may exhibit ‘luxury consumption,’ taking up nutrient amounts exceeding immediate growth requirements and storing these for future use when growth conditions permit.

Consequently, the physiological and morphological traits associated with fast uptake—high surface area:volume ratio, high  $V_{max}$ , and low  $K_s$ —are precisely those that predispose certain species to become nuisance algae under eutrophic conditions.

#### 4.9 Factors Affecting Nitrogen (and Other Nutrient) Uptake

To summarise, several factors determine nutrient uptake rates:

- **Physical environment:** The concentration of nutrients in the water and the thickness of the boundary layer, affected by water motion.
- **Form of nutrient:** For example, ammonium is absorbed much more rapidly than nitrate. Nitrate must be taken up by active transport, whilst ammonium can diffuse passively into the cell.
- **Nutritional state of the plant:** Nutrient-starved plants will take up nutrients rapidly when re-exposed, while replete plants will not show a significant response.
- **Growth environment:** Higher light intensities and temperatures increase metabolic rates, raising  $V_{max}$  and thus enhancing nutrient uptake.
- **Morphology:** As discussed, a higher surface area to volume ratio increases both diffusion and uptake capacities.
- **Uptake mechanism:** Combinations of uptake mechanisms (active, passive, facilitated) determine overall absorption rates.

All of these factors interact to control the rate at which nitrogen, phosphorus, or any other macronutrient can be absorbed from the environment.

## **5 Lecture Transcript: Nutrient Uptake Mechanisms in Seaweeds**

### **5.1 Introduction**

Good morning, everyone. Today is our last lecture, so I would just like to wrap up a few more slides. It's not going to be a very long lecture. What we need to talk about today are the two remaining kinds of uptake mechanisms. We spoke at length about active uptake, which is characterised by the Michaelis-Menten equation, but there are also other kinds of uptake mechanisms, primarily passive uptake and facilitated uptake, and today we're going to quickly talk about both of those.

The reason why we have different kinds of uptake mechanisms is because there are various different forms of nitrogen available in the environment. For some of the more complex molecules, such as nitrate, active uptake is necessary. However, there are more simple molecules also available that make up the total dissolved inorganic nitrogen (DIN) pool, and in this instance, we talk about the molecule ammonium or ammonia.

### **5.2 Passive Uptake Mechanism**

Right, so the passive uptake mechanism is one that, when we talk about nitrogen uptake, is going to be mostly applicable to the uptake of ammonium from seawater into the seaweed itself.

If you want to know a little bit more about nutrient uptake in seaweeds—and it's definitely recommended that you do—you can read that paper I wrote about 18 years ago, in 2002, that discusses nutrient uptake. It examines the nutrient uptake of ammonium and nitrate at various rates of external water movement and different temperatures in one particular kind of seaweed. So have a look; it's going to give you additional information that might make the difference in your exams, enabling you to write an answer worth 100% versus one worth 80%. Every little bit of extra work you do by reading additional papers and so on is going to count in your favour.

The uptake of ammonium is established in the same way as nitrate uptake. In other words, we apply either multiple flask experiments or perturbation experiments, we establish a depletion curve, and from the depletion curve, we derive  $V$  versus  $S$ , that is, the uptake kinetics graph. For ammonium, when you plot the uptake kinetics graph, you'll notice that a straight line best describes the relationship between uptake rate and substrate concentration. Here, we see a nice straight line going through all the points.

But in the case below, when we look at the uptake of nitrate, also done by first establishing a depletion curve, and we translate those data into our uptake graph, we see a Michaelis-Menten-type curve is much better fitted. A linear relationship no longer describes the relationship between  $V$  and  $S$  for nitrate. In passive uptake, when we relate  $V$  to  $S$ , we always find a linear relationship. That's the primary difference in uptake kinetics between active uptake and passive uptake.

Passive uptake, in the case of ammonium, is always going to give us, when we relate  $V$  to  $S$ , a linear relationship. This implies that in passive uptake, no expenditure of metabolic energy is necessary, because the entire uptake process can be described by diffusion, and these usually involve the movement of uncharged molecules.

Nitrate is a charged molecule, as it has a negative charge, with extra electrons. Ammonia, on the other hand, is a non-charged, uncharged molecule, as is  $\text{CO}_2$ , as is oxygen. So, uncharged molecules usually diffuse from the external environment into the plant, down the concentration gradient—that is, from where there's plenty of it in the external culture medium, to where there's less of it inside the plant. So it goes down the concentration gradient.

In active uptake, uptake typically goes against the concentration gradient, hence the necessity to use energy to drive that process. Here, the entire thing relies mostly on diffusion; therefore, external factors such as the rate of water movement, which affects the thickness of the boundary layer outside the thallus, are very important in affecting the rate at which uptake can take place.

### 5.3 Uptake Kinetics and the Affinity Coefficient

So, when we have a linear relationship—for example, in passive uptake—at no point along our increasing range of external substrate concentrations is there any evidence that the rate of uptake slows down. In active uptake, the rate of uptake reaches a maximum, which is  $V_{\max}$ , but in passive uptake, there's no  $V_{\max}$ , because it's a straight line. If you increase the substrate concentration from 40 to 80 to 120, the line will just continue to go up, which means that the rate of uptake is proportional to the amount of nitrogen present in the external environment.

A higher external concentration sets up a steeper concentration gradient, and when we have a steeper concentration gradient, the rate of diffusion increases. This is why, in a linear relationship, we cannot, as we do in the case of Michaelis-Menten kinetics, calculate the parameters  $K_s$  or  $V_{\max}$ , because enzymes at no point, internal to the plant, influence the maximum rate of uptake in these cases. And the  $K_s$  relationship—that is, the substrate concentration at which uptake rate is half of  $V_{\max}$ —also cannot be calculated, because in order to calculate  $K_s$ , we need a  $V_{\max}$ .

However, we can calculate a parameter called  $\alpha$ , and  $\alpha$ , in the case of a linear relationship, is simply the slope of that line. The slope of the line is directly equal to  $\alpha$ , so by calculating the slope from a linear regression, we can know what  $\alpha$  is. Alpha has the same meaning as in the case of active uptake: it tells us about the affinity of the plant for a particular nutrient.

So, the steeper the  $\alpha$ , the more rapidly the uptake rate increases with a change in nutrient concentration. By contrast, with a low  $\alpha$ , or a very shallow slope, you need a far greater change in nutrient concentration to produce the same change in uptake rate.

Seaweeds with a steep  $\alpha$ —that is, a steep curve—are able to take up nutrients efficiently, even when the amount of nutrients in the external environment is low. Seaweeds with a low  $\alpha$ —a shallow slope—will not take up nutrients effectively in low-nutrient environments. So, given a particular low nutrient concentration, if you put a seaweed with a low  $\alpha$  next to one with a high  $\alpha$  in the same water, the one with the high  $\alpha$  will better sustain its nutritional needs and enable continued growth in those conditions.

This is a useful way to use knowledge of the steepness of that slope—in other words, the mathematical relationship that relates uptake rate to nutrient concentration in the water. This knowledge tells us about the ecological competitiveness of two different seaweeds with different alphas, in the same nutrient medium. It also tells us something about seaweeds likely to become nuisance species under eutrophic conditions. Those with a high  $\alpha$  can respond rapidly to increased nutrient availability, and may become nuisance species when eutrophication occurs.

## 5.4 Factors Modifying Uptake Rates

There are various things that can complicate the relationship between  $V$  and  $S$ . For example, seaweeds that have been exposed to high nutrient concentrations over time will show a slower rate of uptake, as their nutritional requirements have already been met. But if you take a seaweed from oligotrophic (low nutrient) conditions and move it into water with more nutrients, it will show a very rapid rate of uptake.

In the case of active uptake, this can increase  $V_{\max}$ . In passive uptake, this influences the steepness of the line— $\alpha$ . The more deprived a seaweed is of nutrients, the greater the response in uptake when exposed to higher nutrient levels.

Another important factor is the light environment. For both linear (passive) and active uptake, a greater light environment—that is, more light—generally means more rapid photosynthesis. Photosynthesis takes up inorganic carbon and converts it into organic forms. In order to produce organic molecules inside the plant, nitrogen is also required to accompany carbon, hydrogen, oxygen, and sometimes phosphorus, in the molecule.

So, under higher light, the plant takes up more carbon, which increases demand for nitrogen. Typically, then, plants in high light environments will have a higher nutrient uptake rate than plants in low light.

Related to this is photoperiod—that is, the ratio of day to night, or how long light is present. The enzyme nitrate reductase, which converts nitrate into ammonium (before it can be incorporated into amino acids), is closely coupled to the photoperiod. The more light there is, the more active nitrate reductase is, and the faster the rate of nitrate uptake during daylight.

Temperature is another key factor. As you may recall from discussions of  $Q_{10}$ , the metabolic rate typically doubles for every 10 °C increase in temperature. As metabolic rate increases, more organic carbon can be formed, which requires more nitrogen uptake to support the synthesis of organic molecules. Temperature effects, though, are ion-specific and depend on the species, and will differ for uptake of nitrate or ammonium, for example.

Other influences include surface area to volume ratio. You need to know, in detail, how the surface area to volume ratio modulates different physiological responses in seaweeds.

Environmental factors such as desiccation, the type, and the concentration of nutrients also play a role. For instance, the type of nutrient—ammonium versus nitrate—dictates uptake mechanism: ammonium shows a linear, passive mechanism, while nitrate shows a Michaelis-Menten active mechanism.

Some nutrients interact in their uptake. If ammonium and nitrate are both present in culture medium, seaweeds will preferentially take up ammonium; nitrate uptake does not occur until all ammonium has been depleted.

Biological interactions, such as multiple species of plants or algae growing together, can influence nutrient uptake rates. Additionally, intrinsic adaptive factors, such as the production of hairlike hairs (small protrusions from the algal thallus), can increase surface area to volume ratio and thereby increase nutrient affinity, which is especially useful under low nutrient conditions.

The reproductive state matters too; reproductive seaweeds require greater nutrient uptake to sustain gamete and spore production. As a thallus ages and its growth slows, nutrient uptake decreases. Morphological changes—such as in seaweeds exhibiting heteromorphic alternation of generations—also affect nutrient uptake responses. Within the same species, genetic variation can also influence uptake kinetics.

## 5.5 Facilitated Uptake Mechanism

The third type of uptake, after active and passive, is facilitated uptake. Facilitated uptake resembles passive uptake in that it moves nutrients down a concentration gradient—the external concentration is greater than inside the cell.

However, unlike passive uptake, which relies entirely on diffusion, facilitated uptake uses a particular membrane protein that spans the cell membrane. This protein has an orientation across the membrane; its active site is external to the plant and specific for a particular molecule—say, for instance, sulfate. It binds to the sulfate outside, then flips around and releases it inside the cell.

In short, a protein collects something from outside, flips its conformation, and releases the molecule inside the cell—this is facilitated uptake. It is similar to passive uptake in being down the concentration gradient, but it is also similar to active uptake in showing a saturation response. That is, there is a maximum external concentration beyond which the transport protein cannot increase the rate of transport further—there is a  $V_{\max}$ . Facilitated uptake is also very specific to particular nutrients, and is susceptible to competitive and non-competitive inhibition. For example, another molecule may compete with the primary substrate (such as sulfate) for the active site, displacing sulfate and preventing its uptake.

That's essentially what facilitated uptake is about, and I will not go any further on that point.

## 5.6 Conclusion

If you need to know more about seaweed nutrient uptake, or nutrient uptake more generally (which can be generalised to plants), do look at the references provided. At the very least, I would like you to read the paper I wrote, as everything I have lectured on around this section is based on those experiments.

And that brings me to the end of this nutrient uptake lecture, and indeed to the end of BDC223 as far as the plant component is concerned.

## Bibliography