5

Dosen Pengampu:

Prof. Dr. Ir. Sri Kumalaningsih, M. App.Sc
Prof. Dr. Ir. Wignyanto, MS
Dr. Ir. M. Hindun Pulungan, MS
Dr. Ir. Nur Hidayat, MP
Irnia Nurika, STP, MP, PhD
Sakunda Anggarini, STP, MP, MSc

Microbial Growth II

Agroindustrial Technology
Faculty of Agricultural Technology
University of Brawijaya 2015/ 2016

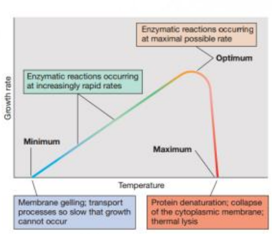
Effect of Environment on Growth

- The activities of microorganisms including growth are greatly affected by the **chemical** and **physical** state of their environment.
- Four key factors control the growth of all microorganisms: **temperature**, **pH**, **water availability**, and **oxygen**
- Other factors can potentially affect the growth of microorganisms: **pressure** and **radiation**
- it is important to remember that for the successful culture of any microorganism, both **medium** and **growth conditions** must be suitable

Effect of Temperature on Growth

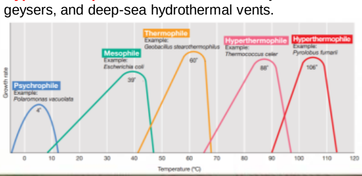
➢ **Cardinal Temperatures**

- o There 3 temperatures, called Cardinal temperature :
- \- a minimum temperature below which growth is not possible
- \- an optimum temperature at which growth is most rapid
- \- a maximum temperature above which growth is not possible
- o The cardinal temperatures of different microorganisms differ widely, some organisms have temperature optima as low as 4°C and some higher than 100°C



Effect of Temperature on Growth

- **Temperature Classes of Organisms**
  - **Mesophiles** are widespread in nature. They are found in warmblooded animals and in terrestrial and aquatic environments in temperate and tropical latitudes.
  - **Psychrophiles** and **thermophiles** are found in unusually cold and unusually hot environments, respectively.
  - **Hyperthermophiles** are found in extremely hot habitats such as hot springs, geysers, and deep-sea hydrothermal vents.



The temperature optimum of each example organism is shown on the graph

Microbial Growth at Cold Temperature

- **Cold Environments**

The oceans have an average temperature of 5ºC, and the depths of the open oceans have constant temperatures of 1–3ºC.

(Pict. a)

- the core is about 8 cm wide
- note the dense coloration due to pigmented microorganisms

(Pict. b)

- phase-contrast micrograph of phototrophic microorganisms from the core shown in part a.
- Most organisms are either diatoms or green algae (both eukaryotic phototrophs)

(a) A core of frozen seawater from McMurdo Sound, Antarctica.

(b)

Microbial Growth at Cold Temperature

- **Cold Environments**

(Pict. c)
-transmission electron micrograph of Polaromonas
-a gas vesiculate bacterium that lives in sea ice and grows optimally at 4°C
(Pict. d)
-the Lake is about 40 m deep
-remains permanently frozen and has an ice cover of about 5 m
-the water column remains near 0°C and contains both oxic and anoxic zones
-there are aerobic and anaerobic microorganisms
-no higher eukaryotic organisms inhabit Dry Valley lakes, making them uniquely microbial ecosystems

(c)

(d) Photo of the surface of Lake Bonney, McMurdo Dry Valleys, Antarctica

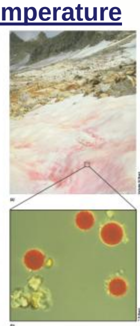
Microbial Growth at Cold Temperature

- **Psychrophilic Microorganisms (*psychrophiles*)**
  - optimal growth temperature of 15ºC or lower
  - max growth temperature below 20ºC
  - minimal growth temperature at 0ºC or lower
  - Psychrophilic microbial communities containing **algae** and **bacteria** grow in dense masses within and under sea ice (frozen seawater that forms seasonally) in polar regions

Microbial Growth at Cold Temperature

- **Psychrophilic Microorganisms (*psychrophiles*)**

(Pict. a)
-snow bank in the Sierra Nevada, California, with red coloration caused by the presence of snow algae
-pink snow such as this is common on summer snow banks at high altitudes throughout the world
(Pict. b)
-photomicrograph of red-pigmented spores of the snow alga *Chlamydomonas nivalis*
-the spores germinate to yield motile green algal cells
-some strains of snow algae are true psychrophiles but many are psychrotolerant, growing best at temperatures above 20°C
-from a phylogenetic standpoint, *C. nivalisis* a green alga



Microbial Growth at Cold Temperature

- **Psychrotolerant Microorganisms**
  - grow at 0ºC but have optima of 20–40ºC
  - **Psychrotolerant** microorganisms are more widely distributed in nature than are psychrophiles
  - they can be isolated from soils and water in temperate climates, as well as from meat, milk and other dairy products, cider, vegetables, and fruit stored at refrigeration temperatures (~4ºC)
  - Various *Bacteria*, *Archaea*, and microbial eukaryotes are psychrotolerant

Microbial Growth at Cold Temperature

- **Molecular Adaptations to Psychrophily**
  - Psychrophiles produce **enzymes** that function **optimally in the cold** and that may be denatured or otherwise **inactivated at even very moderate temperatures**
  - other molecular adaptations to cold include "cold-shock" proteins and cryoprotectants
  - cold-shock proteins: a series of proteins that have several functions including helping the cell maintain other proteins in an active form under cold conditions or binding to specific mRNAs and facilitating their translation
  - these mRNAs include, in particular, those that encode other cold-functional proteins, most of which are not produced when the cell is growing near its temperature optimum
  - **Cryoprotectants**: antifreeze proteins or specific solutes, such as glycerol or certain sugars to help prevent the formation of ice crystals that can puncture the cytoplasmic membrane

Microbial Growth at Cold Temperature

- **Freezing**
  - temperatures below -20ºC prevent microbial growth but microbial cells can **continue to metabolize** at temperatures far **beneath** that which will support growth
  - Example: microbial respiration as measured by CO_2 production has been shown in tundra soils at temperatures as low as -39ºC
  - The medium in which cells are suspended also affects their sensitivity to freezing
  - **cryoprotectants** (glycerol or dimethyl sulfoxide (DMSO)) can **depresses the freezing point and prevents ice crystal formation**
  - To freeze cells for **long-term preservation**, cells are typically suspended in growth medium containing **10% DMSO or glycerol** and quickly frozen at **-80ºC** (ultracold-freezer temperature) or **-196ºC** (liquid nitrogen temperature)

Microbial Growth at High Temperature

- **Thermal Environments**

Presently known upper temperature limits for growth of living organisms

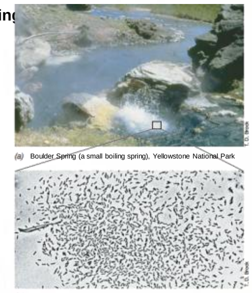
Group	*Upper temperature limits (°C)*
Macroorganisms	
Animals	
Fish and other aquatic vertebrates	38
Insects	45–50
Ostracods (crustaceans)	49–50
Plants	
Vascular plants	45 (60 for one species)
Mosses	50
Microorganisms	
Eukaryotic microorganisms	
Protozoa	56
Algae	55–60
Fungi	60–62
Prokaryotes	
Bacteria	
Cyanobacteria	73
Anoxygenic phototrophs	70–73
Chemoorganotrophs/chemolithotrophs	95
Archaea	
Chemoorganotrophs/chemolithotrophs	122

Microbial Growth at High Temperature

- **Hyperthermophiles in Hot Springs**

(Pict a)
-this spring is superheated, having a temperature 1–2°C above the boilingpoint
-The mineral deposits around the spring consist mainly of silica and Sulfur

(Pict b)
-Photomicrograph of a micro-colony of prokaryotes that developed on a microscope slide immersed in such a boiling spring


(a) Boulder Spring (a small boiling spring), Yellowstone National Park
(b)

Microbial Growth at High Temperature

- **Hyperthermophiles in Hot Springs**
  - a variety of morphological and physiological types of both *Bacteria* and *Archaea* are known.
  - some hyperthermophilic Archaea have growth-temperature optima above 100 C, while no species of Bacteria are known to grow
  - the most heat-tolerant of all known *Archaea* is *Methanopyrus*, a methanogenic organism capable of growth at 122^{o}C above 95^{o}C

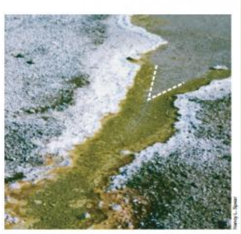
Microbial Growth at High Temperature

Thermophiles

-Many thermophiles (optima 45–80^{o}C) are also present in hot springs and other thermal environments.

-In hot springs, as boiling water overflows the edges of the spring and flows away from the source, it gradually cools, setting up a thermal gradient

-Along this gradient, various microorganisms grow, with different species growing in the different temperature ranges (Figure)


Growth of thermophilic cyanobacteria in a hot spring in Yellowstone National Park

Microbial Growth at High Temperature

Thermophiles

1. prokaryotic organisms are able to grow at far higher temperatures than are eukaryotes

2. the most thermophilic of all prokaryotes are certain species of Archaea

3. nonphototrophic organisms can grow at higher temperatures than can phototrophic organisms

Microbial Growth at High Temperature

Protein Stability at High Temperatures

How do thermophiles and hyperthermophiles survive at high temperature?

First, their enzymes and other proteins are much more heat-stable than are those of mesophiles and actually function optimally at high temperatures.

How is heat stability achieved?

- ✓ studies of several heat-stable enzymes have shown that they often differ very little in amino acid sequence from heat-sensitive forms of the enzymes that catalyze the same reaction in mesophiles
- ✓ It appears that critical amino acid substitutions at only a few locations in the enzyme allow the protein to fold in such a way that it is heat-stable.

Microbial Growth at High Temperature

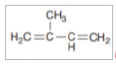
Protein Stability at High Temperatures

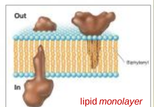
- ✓ Heat stability of proteins in hyperthermophiles is also bolstered by an increased number of ionic bonds between basic and acidic amino acids and their often highly hydrophobic interiors; the latter property is a natural resistance to unfolding in an aqueous cytoplasm.
- ✓ Finally, solutes such as di-inositol phosphate, diglycerol phosphate, and mannosylglycerate are produced at high levels in certain hyperthermophiles, and these may also help stabilize their proteins against thermal degradation.

Microbial Growth at High Temperature

Membrane Stability at High Temperatures

- **thermophiles** typically have lipids rich in saturated fatty acids
- this feature allows the membranes to remain stable and functional at high temperatures
- saturated fatty acids form a stronger hydrophobic environment than do unsaturated fatty acids, which helps account for membrane stability
- **hyperthermophiles**, most of which are Archaea, do not contain fatty acids in their membranes but instead have C_{40} hydrocarbons composed of repeating units of isoprene bonded by ether linkage to glycerol phosphate
- the architecture of the cytoplasmic membranes of **hyperthermophiles** takes a unique twist: The membrane forms a lipid *monolayer* rather than a lipid *bilayer*


isoprene

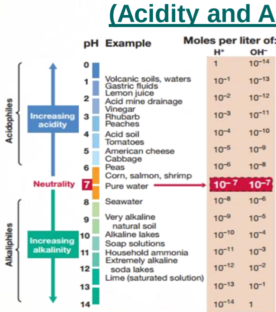


lipid *monolayer*

Microbial Growth at High Temperature

- **Thermophily and Biotechnology**
  - ✓ Thermophiles and hyperthermophiles: these organisms offer some major advantages for industrial and biotechnological processes, many of which can be run more rapidly and efficiently at high temperatures
  - ✓ Example: enzymes from thermophiles and hyperthermophiles are widely used in industrial microbiology
  - ✓ Such enzymes can catalyze biochemical reactions at high temperatures and are in general more stable than enzymes from mesophiles, thus prolonging the shelf life of purified enzyme preparations
  - ✓ A classic example of a heat-stable enzyme of great importance to biology is the DNA polymerase isolated from *Taq aquaticus*

Microbial Growth at Low and High pH (Acidity and Alkalinity)



- **Acidophiles**
  organisms that grow best below pH 5.5
- **Alkaliphiles**
  Microorganisms showing growth pH optima of 8 or higher

The pH scale
Although some microorganisms can live at very low or very high pH, the cell's internal pH remains near neutrality

Microbial Growth at Low and High pH (Acidity and Alkalinity)

Physiological class (optima range)	Appoximate pH optimum for growth	Example organism[a]
Neutrophile (pH >5.5 and <8)	7	*Escherichia coli*
Acidophile (pH <5.5)	5 3 1	*Rhodopila globiformis* *Acidithiobacillus ferrooxidans* *Picrophilus oshimae*
Alkaliphile (pH ≥8)	8 9 10	*Chloroflexus aurantiacus* *Bacillus firmus* *Natronobacterium gregoryi*

[a] *Picrophilus* and *Natronobacterium* are *Archaea*; all others are *Bacteria*.

Relationships of microorganisms to pH

Microbial Growth at Low and High pH (Acidity and Alkalinity)

- **Internal Cell pH**
  - The optimal pH for growth of any organism is a measure of the pH of the extracellular environment only
  - The intracellular pH must remain relatively close to neutrality to prevent destruction of macromolecules in the cell
  - For the majority of microorganisms whose pH optimum for growth is between pH 6 and 8, organisms called neutrophiles, the cytoplasm remains neutral or very nearly so
  - in acidophiles and alkaliphiles the internal pH can vary from neutrality
  - This is because DNA is acid-labile and RNA is alkaline-labile; if a cell cannot maintain these key macromolecules in a stable state, it obviously cannot survive

Microbial Growth at Low and High pH (Acidity and Alkalinity)

- **Buffers**
  - buffers are frequently added to microbial culture media to keep the pH relatively constant
  - a given buffer works over only a narrow pH range, hence, different buffers must be used at different pH values
  - for near neutral pH ranges, potassium phosphate (KH2PO4)and calcium carbonate (CaCO3) are good buffers
  - many other buffers for use in microbial growth media or for the assay of enzymes extracted from microbial cells are available, and the best
  - buffering system for one organism or enzyme may be considerably different from that for another.

Osmotic Effects on Microbial Growth

- **Water Activity and Osmosis**

Water activity (a_w)	Material	Example organisms[a]
1.000	Pure water	*Caulobacter, Spirillum*
0.995	Human blood	*Streptococcus, Escherichia*
0.980	Seawater	*Pseudomonas, Vibrio*
0.950	Bread	Most gram-positive rods
0.900	Maple syrup, ham	Gram-positive cocci such as *Staphylococcus*
0.850	Salami	*Saccharomyces rouxii* (yeast)
0.800	Fruit cake, jams	*Saccharomyces bailii, Penicillium* (fungus)
0.750	Salt lakes, salted fish	*Halobacterium, Halococcus*
0.700	Cereals, candy, dried fruit	*Xeromyces bisporus* and other xerophilic fungi

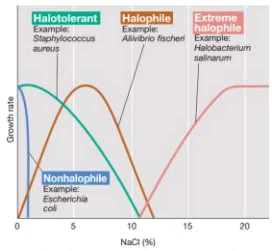
[a]Selected examples of prokaryotes or fungi capable of growth in culture media adjusted to the stated water activity.

Water activity of several substances

- ✓ Water availability is expressed in physical terms as **water activity**
- ✓ Water activities in agricultural soils generally range between 0.90 and 1

Osmotic Effects on Microbial Growth

- **Halophiles and Related Organisms**
  - ✓ In nature, osmotic effects are of interest mainly in habitats with high concentrations of salts
  - ✓ Seawater contains about 3% sodium chloride (NaCl) plus small amounts of many other minerals and elements.
  - ✓ Marine microorganisms usually have a specific requirement for NaCl and grow optimally at the water activity of seawater (*Figure*)
  - ✓ Such organisms are called halophiles

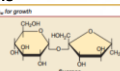


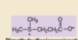
Effect of sodium chloride (NaCl) concentration on growth of microorganisms of different salt tolerances or requirements. The optimum NaCl concentration for marine microorganisms such as *Aliivibrio fischeriis* about 3%; for extreme halophiles, it is between 15 and 30%, depending on the organism.

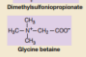
Osmotic Effects on Microbial Growth

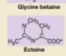
- **Halophiles and Related Organisms**

Organism	Major cytoplasmic solute(s)	Minimum a_w for growth
Nonphototrophic *Bacteria*/freshwater cyanobacteria	Amino acids (mainly glutamate or proline[a])/sucrose, trehalose[b]	0.98–0.90
Marine cyanobacteria	α-Glucosylglycerol[b]	0.92
Marine algae	Mannitol,[b] various glycosides, dimethylsulfoniopropionate	0.92
Salt lake cyanobacteria	Glycine betaine	0.90–0.75
Halophilic anoxygenic phototrophic purple *Bacteria*	Glycine betaine, ectoine, trehalose[b]	0.90–0.75
Extremely halophilic *Archaea* and some *Bacteria*	KCl	0.75
Dunaliella (halophilic green alga)	Glycerol	0.75
Xerophilic and osmophilic yeasts	Glycerol	0.83–0.62
Xerophilic filamentous fungi	Glycerol	0.72–0.61


Sucrose


Dimethylsulfoniopropionate


Glycine betaine


Ectoine


Glycerol

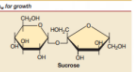
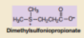
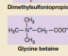
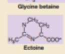
[a] See Figure 6.29 for the structures of amino acids.
[b] Structures not shown. Like sucrose, trehalose is a C_{12} disaccharide; glucosylglycerol is a C_9 alcohol; mannitol is a C_6 alcohol.

Compatible solutes of microorganisms

- ✓ Organisms able to live in environments high in sugar as a solute are called **osmophiles**, and those able to grow in very dry environments (made dry by lack of water rather than from dissolved solutes) are called **xerophiles.**
- ✓ For example look at table

Osmotic Effects on Microbial Growth

- **Compatible Solutes of Microorganisms**

Organism	Major cytoplasmic solute(s)	Minimum a_w for growth	
Nonphototrophic *Bacteria*/freshwater cyanobacteria	Amino acids (mainly glutamate or proline[a])/sucrose, trehalose[b]	0.98–0.90	 Sucrose
Marine cyanobacteria	α-Glucosylglycerol[b]	0.92	
Marine algae	Mannitol,[b] various glycosides, dimethylsulfoniopropionate	0.92	 Dimethylsulfoniopropionate
Salt lake cyanobacteria	Glycine betaine	0.90–0.75	 Glycine betaine
Halophilic anoxygenic phototrophic purple *Bacteria*	Glycine betaine, ectoine, trehalose[b]	0.90–0.75	 Ectoine
Extremely halophilic *Archaea* and some *Bacteria*	KCl	0.75	
Dunaliella (halophilic green alga)	Glycerol	0.75	 Glycerol
Xerophilic and osmophilic yeasts	Glycerol	0.83–0.62	
Xerophilic filamentous fungi	Glycerol	0.72–0.61	

[a] See Figure 6.29 for the structures of amino acids.
[b] Structures not shown. Like sucrose, trehalose is a C_{12} disaccharide; glucosylglycerol is a C_9 alcohol; mannitol is a C_6 alcohol.

Oxygen as a Factor in Microbial Growth

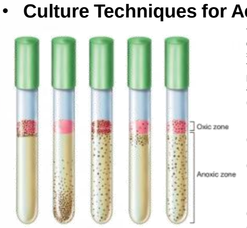
- **Oxygen Classes of Microorganisms**

Group	Relationship to O_2	Type of metabolism	Example[a]	Habitat[b]
Aerobes				
Obligate	Required	Aerobic respiration	*Micrococcus luteus* (B)	Skin, dust
Facultative	Not required, but growth better with O_2	Aerobic respiration, anaerobic respiration, fermentation	*Escherichia coli* (B)	Mammalian large intestine
Microaerophilic	Required but at levels lower than atmospheric	Aerobic respiration	*Spirillum volutans* (B)	Lake water
Anaerobes				
Aerotolerant	Not required, and growth no better when O_2 present	Fermentation	*Streptococcus pyogenes* (B)	Upper respiratory tract
Obligate	Harmful or lethal	Fermentation or anaerobic respiration	*Methanobacterium formicicum* (A)	Sewage sludge, anoxic lake sediments

[a] Letters in parentheses indicate phylogenetic status (B, *Bacteria*; A, *Archaea*). Representative of either domain of prokaryotes are known in each category. Most eukaryotes are obligate aerobes, but facultative aerobes (for example, yeast) and obligate anaerobes (for example, certain protozoa and fungi) are known.
[b] Listed are typical habitats of the example organism.

Oxygen as a Factor in Microbial Growth

- **Culture Techniques for Aerobes and Anaerobes**



Growth versus oxygen (O_2) concentration

The position of microbial colonies (depicted here as black dots) within tubes of thioglycolate broth culture medium. A small amount of agar has been added to keep the liquid from becoming disturbed. The redox dye, resazurin, which is pink when oxidized and colorless when reduced, has been added as a redox indicator.

(a) Aerocic, O_2 penetrates only a short distance into the tube, so obligate aerobes grow only close to the surface
(b) Anaerobes, being sensitive to O2, grow only away from the surface
(c) Facultative aerobes are able to grow in either the presence or the absence of O2and thus grow throughout the tube. However, growth is better near the surface because these organisms can respire
(d) Microaerophiles grow away from the most oxic zone
(e) Aerotolerant anaerobes grow throughout the tube. Growth is not better near the surface because these organisms can only ferment

Oxygen as a Factor in Microbial Growth

- **Culture Techniques for Aerobes and Anaerobes**

Incubation under anoxic condition

(a) Anoxic jar. A chemical reaction in the envelope in the jar generates H_2+CO_2. The H_2 reacts with O_2 in the jar on the surface of a palladium catalyst to yield H_2O; the final atmosphere contains N_2, H_2, and CO_2

(b) Anoxic glove bag for manipulating and incubating cultures under anoxic conditions. The airlock on the right, which can be evacuated and filled with O_2-free gas, serves as a port for adding and removing materials to and from the glove bag.

Oxygen as a Factor in Microbial Growth

Toxic Forms of Oxygen

▪**Oxygen Chemistry**

✓Oxygen in its ground state is called triplet oxygen ($^3O_2$)

✓However, other electronic configurations of oxygen are possible, and most are toxic to cells.

✓One major form of toxic oxygen is singlet oxygen ($^1O_2$), a higher-energy form of oxygen in which outer shell electrons surrounding the nucleus become highly reactive and can carry out spontaneous and undesirable oxidations within the cell

✓Singlet oxygen is produced both photochemically and biochemically, the latter through the activity of various peroxidase enzymes

✓Organisms that frequently encounter singlet oxygen, such as airborne bacteria and phototrophic microorganisms, often contain colored pigments called carotenoids, which function to convert singlet oxygen to nontoxic forms

Oxygen as a Factor in Microbial Growth

Toxic Forms of Oxygen

•**Superoxide and Other Toxic Oxygen Species**

Besides singlet oxygen, many other toxic forms of oxygen exist, including superoxide anion(O_2^-), hydrogen peroxide(H_2O_2), and hydroxyl radical(OH•). All of these are produced as by-products of the reduction of O_2 to H_2O in respiration

Reactants	Products	
$O_2 + e^- \rightarrow$	O_2^-	(superoxide)
$O_2^- + e^- + 2H^+ \rightarrow$	H_2O_2	(hydrogen peroxide)
$H_2O_2 + e^- + H^+ \rightarrow$	H_2O + OH•	(hydroxyl radical)
$OH\bullet + e^- + H^+ \rightarrow$	H_2O	(water)

Outcome:
$O_2 + 4e^- + 4H^+ \rightarrow 2H_2O$

Four-electron reduction of O_2 to H_2O by stepwise addition of electrons. All the intermediates formed are reactive and toxic to cells, except for water, of course

Oxygen as a Factor in Microbial Growth

Toxic Forms of Oxygen

•Superoxide Dismutase and Other Enzymes That Destroy Toxic Oxygen

$H_2O_2 + H_2O_2 \rightarrow 2\,H_2O + O_2$

(a) **Catalase**

$H_2O_2 + NADH + H^+ \rightarrow 2\,H_2O + NAD^+$

(b) **Peroxidase**

$O_2^- + O_2^- + 2\,H^+ \rightarrow H_2O_2 + O_2$

(c) **Superoxide dismutase**

$4\,O_2^- + 4\,H^+ \rightarrow 2\,H_2O + 3\,O_2$

(d) **Superoxide dismutase/catalase in combination**

$O_2^- + 2\,H^+ + rubredoxin_{reduced} \rightarrow H_2O_2 + rubredoxin_{oxidized}$

(e) **Superoxide reductase**

Enzymes that destroy toxic oxygen species

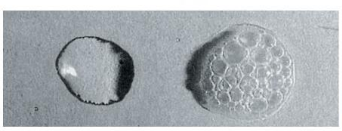
(a)Catalases
(b)peroxidases are porphyrin-containing proteins, although some flavoproteins may consume toxic oxygen species as well
(c)Superoxide dismutases are metal-containing proteins, the metals being copper and zinc, manganese, or iron
(d)Combined reaction of superoxide dismutase and catalase
(e)Superoxide reductase catalyzes the one-electron reduction of O_2-to H_2O_2

fppt.com

Oxygen as a Factor in Microbial Growth

Toxic Forms of Oxygen

•Superoxide Dismutase and Other Enzymes That Destroy Toxic Oxygen


T. D. Brock

- ✓ Method for testing a microbial culture for the presence of catalase
- ✓ A heavy loopful of cells from an agar culture was mixed on a slide (right) with a drop of 30% hydrogen peroxide
- ✓ The immediate appearance of bubbles is indicative of the presence of catalase
- ✓ The bubbles are O_2 produced by the reaction $H_2O_2 + H_2O_2 \rightarrow 2\,H_2O + O_2$.

fppt.com

Oxygen as a Factor in Microbial Growth

Toxic Forms of Oxygen

- **Superoxide Reductase**
  - ✓ Another means of superoxide disposal is present in certain obligately anaerobic *Archaea*
  - ✓ In the hyperthermophile *Pyrococcus furiosus*, for example, superoxide dismutase is absent, but a unique enzyme, superoxide reductase, is present and functions to remove O_2-
  - ✓ Superoxide reductases are present in many other obligate anaerobes as well, such as sulfate-reducing bacteria (*Bacteria*) and methanogens (*Archaea*), as well as in certain microaerophilic species of *Bacteria*, such as *Treponema*
  - ✓ Thus these organisms, previously thought to be O_2-sensitive because they lacked superoxide dismutase, can indeed consumesuperoxide
  - ✓ The sensitivity of these organisms to O_2 may therefore be for entirely different and as yet unknown reasons

fppt.com

Reference

Madigan, M. T. 2012. Brock Biology of Microorganism 13th ed. Pearson Education, Inc. San Francisco.