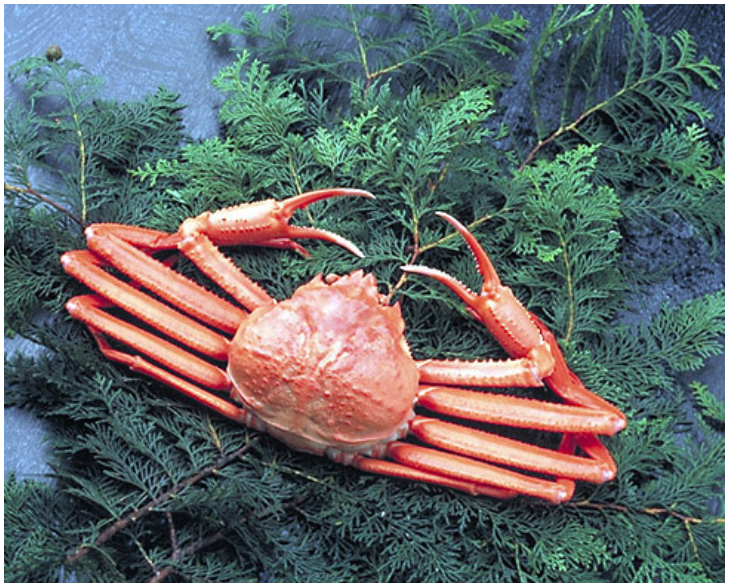
北海道海洋科学シンポジウム

海藻由来ハロゲン化酵素の特性

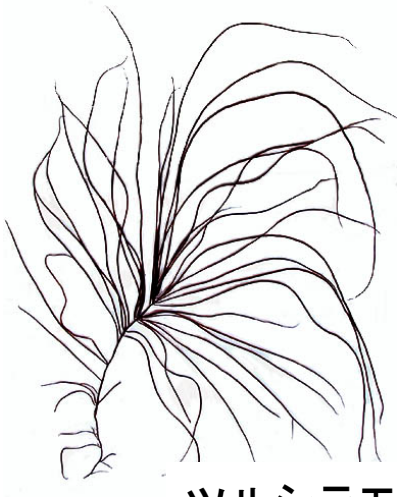
2010 年 11 月 5 日

鳥取大学大学院・工学研究科・化学・生物応用工学専攻
大城　隆



鳥取県ホームページより

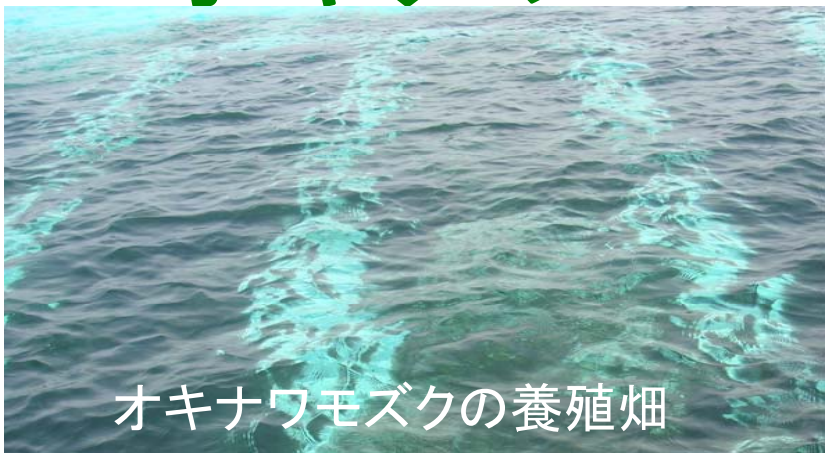
ヌネハノリ



ツルシラモ

トロロコンブ

オキナワモズク由来フコイダン

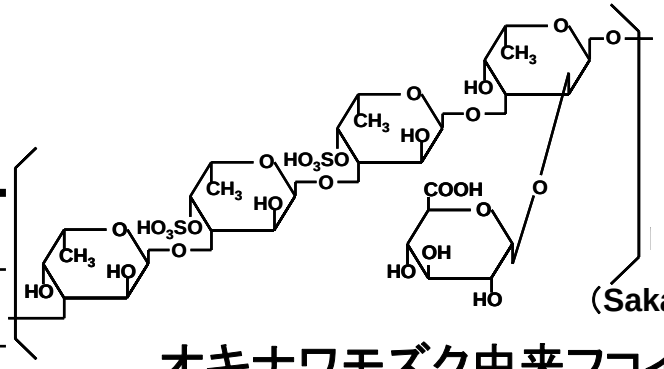


＜これまでに報告されているフコイダンの生理活性＞

- 抗腫瘍・抗ガン活性
- 抗ウイルス活性
- 抗凝血作用
- 抗ピロリ菌作用など

オキナワモズクは、他の海藻に比べてフコイダンの含有量が多く、化学構造もシンプルである。

海藻	フコイダン含有量 (%【w/w 乾燥海藻】)
ガゴメコンブ	4
ワカメ	1.5
ヒバマタ	7
オキナワモズク	25



（Sakai et al., 2002, 2003）

オキナワモズク由来フコイダン構造式

L-fucose : D-glucuronic acid : SO_3^-

4 : 1 : 2

日本では古くから多くの海藻を食料資源として利用

近年、海藻の持つ機能性に注目

→ 有効成分の単離

→ 生理機能解析

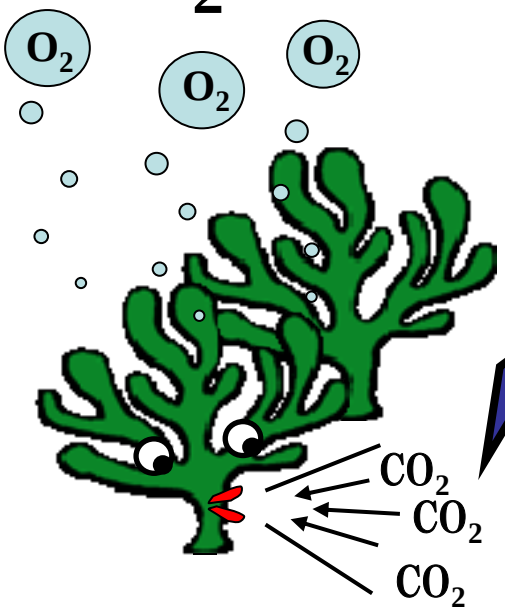
海藻の主な有効成分

高分子：アルギン酸、フコイダンなどの多糖類
低分子：遊離アミノ酸、抗酸化成分など
無機物質：微量元素

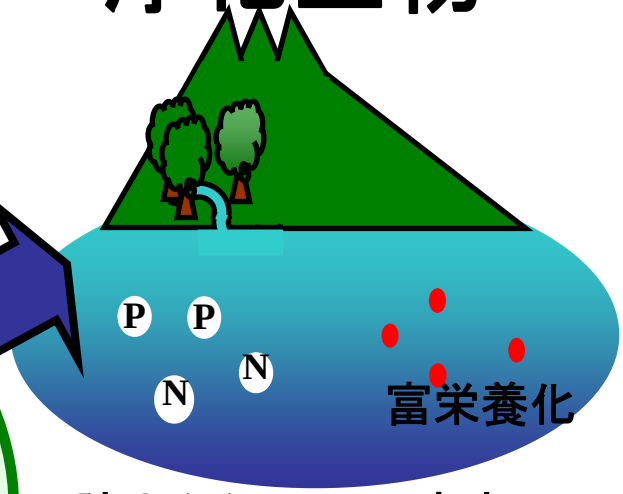
医薬品、化粧品、飼料、工業原料

海藻の応用

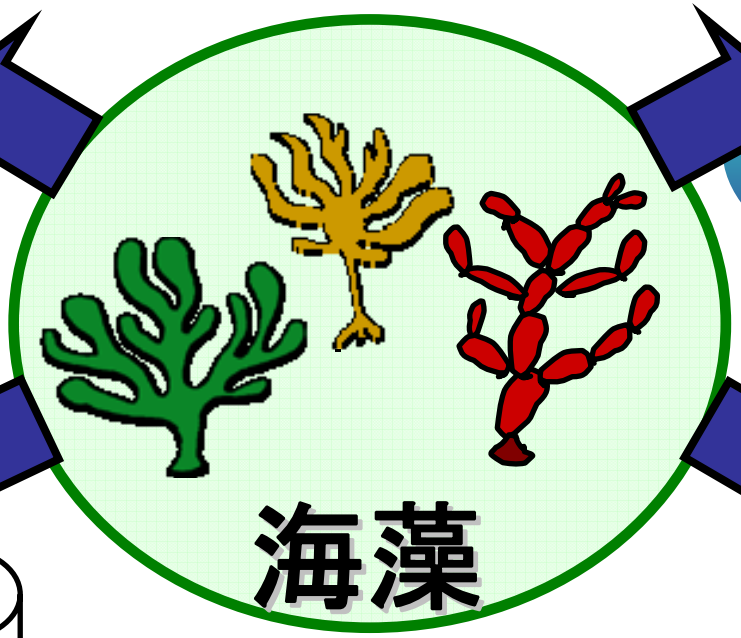
CO_2の削減



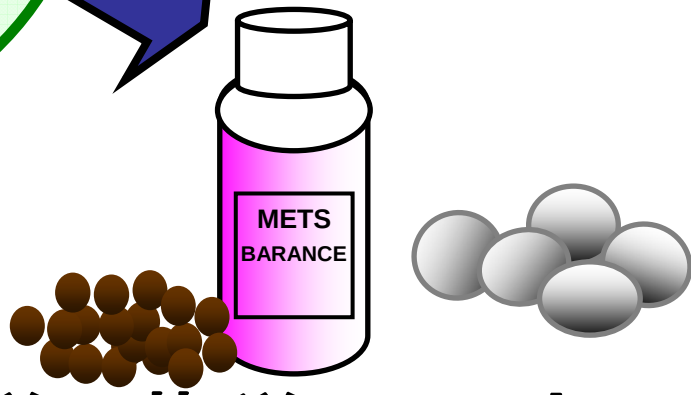
富栄養水質の浄化生物



陸上からのリン、窒素



健康食品、化粧品



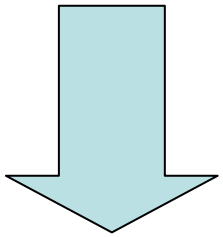
医学、薬学への応用

（アルギン酸等の硫酸化多糖類）

海藻由来の酵素の研究は進んでいない！

理由：1. 採集が困難
2. 人工増殖が困難
3. 藻体中の大量の多糖類、ポリフェノール類が生化学的解析を阻害

海藻が生産する物質の潜在的な機能は未だ未解明な点が多い！



海藻由来の酵素や機能性物質は新規でしかも実用性が高い可能性を秘めている！

海藻、海草とは？

海藻
(marine algae)

海草
(seagrass)

藻類

被子植物

緑藻類

褐藻類

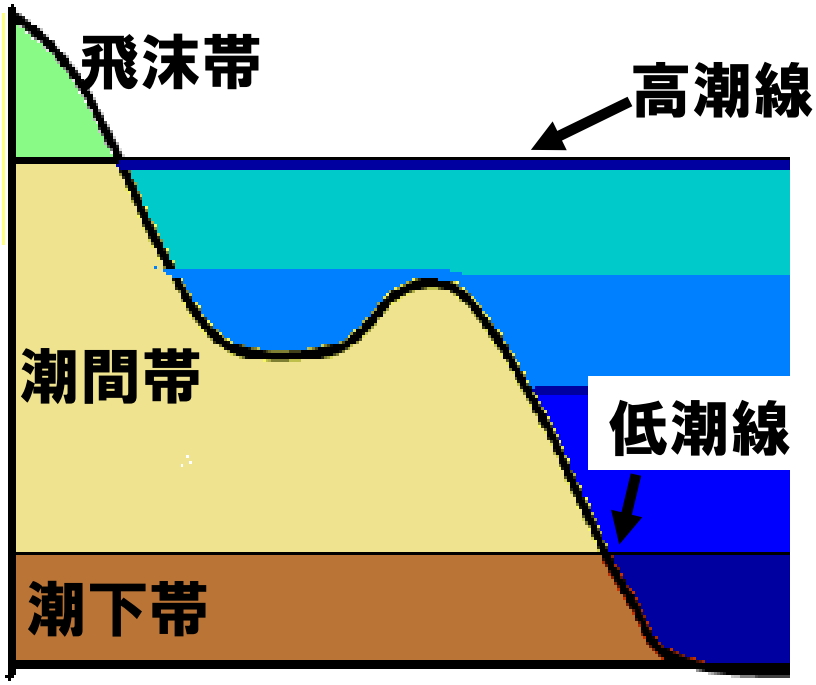
紅藻類

生理活性物質の研究が盛ん

生態分布に関する研究報告が主

しかしながら海藻、海草由来酵素についての研究報告は少ない！！

海藻類の生育帯ついて



- 潮間帯では通常１日２回の潮の干満により環境が激変。
- 潮間帯に住む海藻は，乾燥や紫外線に対する耐性が高い。

海藻類は様々なストレスにさらされていることから
海藻類由来の酵素はユニークな特徴を示すのではないか!？

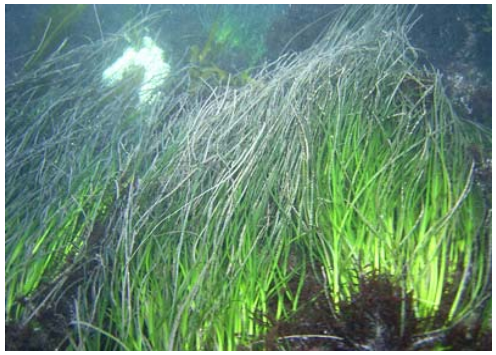
当研究室で研究対象にした海藻（草）由来酵素

酵素名	由来
ハロペルオキシダーゼ	*Corallina pilulifera*（紅藻、ピリヒバ）
	Ascophyllum nodosum（褐藻、和名なし）
	Ulvella lens（緑藻、アワビモ）
	Codium fragile（緑藻、ミル）
キチナーゼ	*Phyllospadix japonica*（海草、エビアマモ）
ホスファターゼ	*Phyllospadix japonica*（海草、エビアマモ）

C. pilulifera

A. nodosum

C. fragile



P. japonica

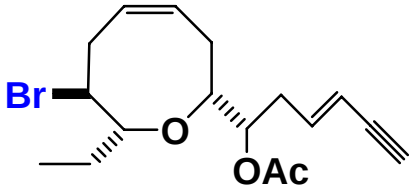
１．ピリヒバ由来ハロペルオキシダーゼ

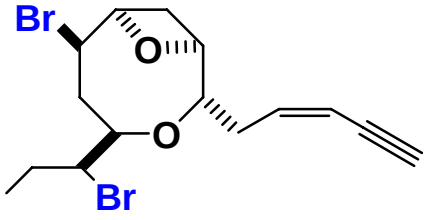
（I）酵素の精製、構造解析

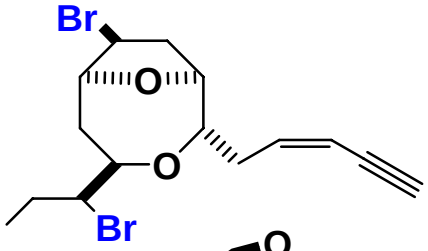
（II）安定性とカルシウム

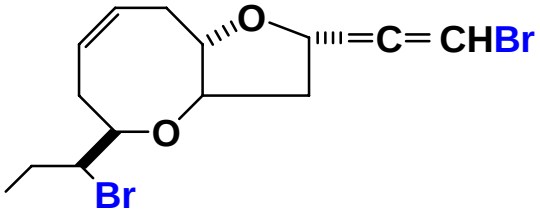
（III）変異酵素のハライドに対する活性

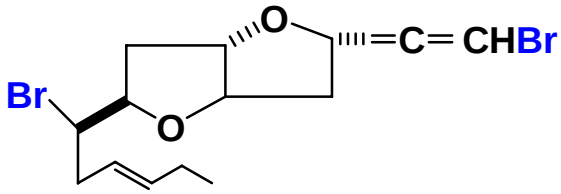
２．緑藻（アワビモ、ミル）由来ハロペルオキシダーゼ

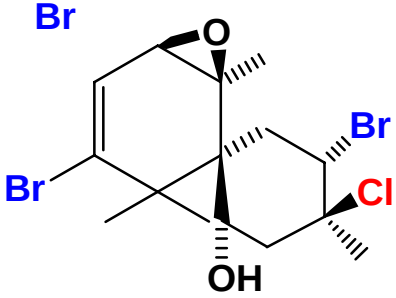


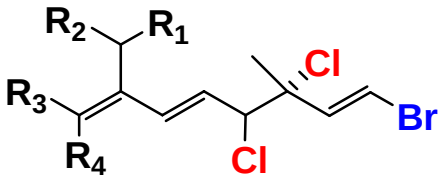




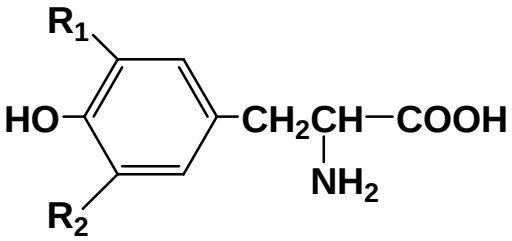




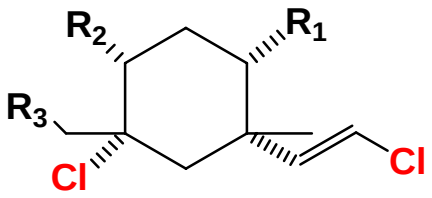




R_1	R_2	R_3	R_4
H	H	H	Br
H	H	Br	Br
Cl	Cl	H	Cl
Cl	Cl	Cl	H



R_1	R_2
H	I
I	I



R_1	R_2	R_3
Br	Br	H
Cl	Cl	Br
Cl	Br	Br

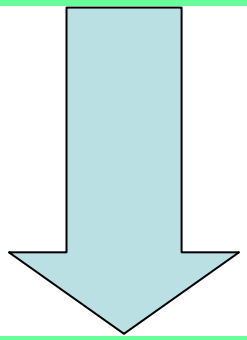
Halogenated Compounds Produced by Algae

Haloperoxidase

$$AH + X^- + H_2O_2 + H^+ \longrightarrow AX + 2H_2O$$

(A: nucleophilic cpds. ; X: Cl, Br, I)

多くの海藻がハロペルオキシダーゼを有し、高活性

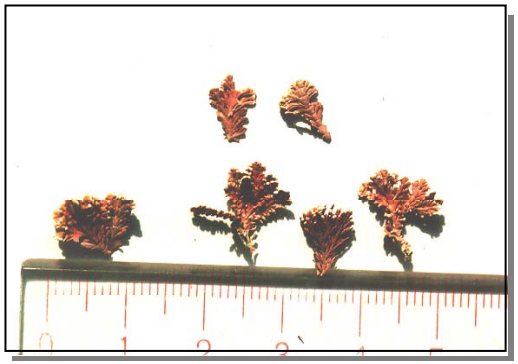


海藻由来の酵素の中では
最も研究が進んでいる酵素

Haloperoxidases Produced by Marine Algae and Microorganisms

Source	Prosthetic group	Halide
Algae		
brown algae		
Ascophyllum nodosum	vanadium	Br, I
Fucus distichus	vanadium	Br, I
Laminaria saccharina	vanadium	Br, I
Macrocystis pyrifera	vanadium	Br, I
red algae		
Corallina pilulifera	**Vanadium**	**Br, I**
Laurencia japonica	(ferriprotoporphyrin)	Br, I
green algae		
Penicillus capitatus	ferriprotoporphyrin IX	Cl, Br, I
Ulvella lens	(vanadium)	Br, I

Source	Prosthetic group	Halide
Microorganisms		
Fungi		
Caldariomyces fumago	ferriprotoporphyrin IX	Cl, Br, I
Curvularia inaequalis	vanadium	Cl, Br, I
Embellisia didymospora	vanadium	Cl, Br, I
Bacteria		
Pseudomonas pyrrocinia	ferriprotoporphyrin IX	Br, I
Pseudomonas pyrrocinia	zinc and iron	Cl, Br, I
Actinomycetes		
Streptomyces aureofaciens	unknown	Br, I
Streptomyces phaeochromogenes	unknown	Br, I



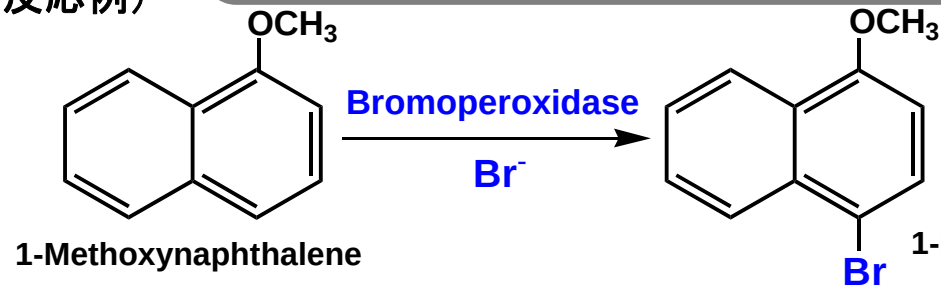
Corallina pilulifera

Haloperoxidase

$$AH + X^- + H_2O_2 + H^+ \longrightarrow AX + 2H_2O$$

(X: Cl, Br, I)

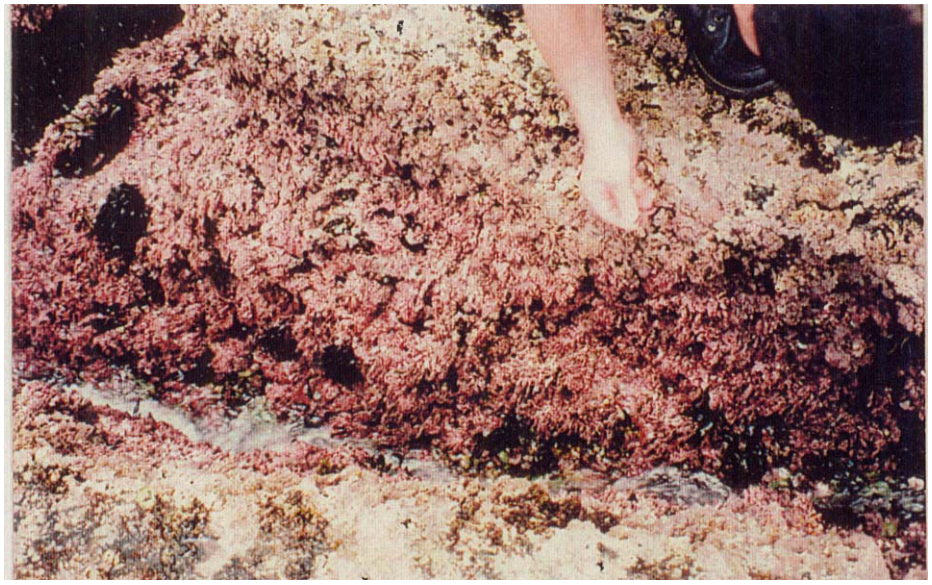
（反応例）



1-Methoxynaphthalene

1-Methoxy-4-bromo-naphthalene

Corallina pilulifera（ピリヒバ）



鳥取空港付近の海岸

Haloperoxidases Produced by Marine Algae and Microorganisms

Source	Prosthetic group	Halide
Algae		
brown algae		
Ascophyllum nodosum	**vanadium**	**Br, I**
Fucus distichus	vanadium	Br, I
Laminaria saccharina	vanadium	Br, I
Macrocystis pyrifera	vanadium	Br, I
red algae		
Corallina pilulifera	Vanadium	Br, I
Laurencia japonica	(ferriprotoporphyrin)	Br, I
green algae		
Penicillus capitatus	ferriprotoporphyrin IX	Cl, Br, I
Ulvella lens	(vanadium)	Br, I

Source	Prosthetic group	Halide
Microorganisms		
Fungi		
Caldariomyces fumago	ferriprotoporphyrin IX	Cl, Br, I
Curvularia inaequalis	vanadium	Cl, Br, I
Embellisia didymospora	vanadium	Cl, Br, I
Bacteria		
Pseudomonas pyrrocinia	ferriprotoporphyrin IX	Br, I
Pseudomonas pyrrocinia	zinc and iron	Cl, Br, I
Actinomycetes		
Streptomyces aureofaciens	unknown	Br, I
Streptomyces phaeochromogenes	unknown	Br, I

Ascophyllum nodosum

Haloperoxidase

$$AH + X^- + H_2O_2 + H^+ \longrightarrow AX + 2H_2O$$

(X: Cl, Br, I)

大堤防 Afsluitdijk（オランダ北部）

Ascophyllum nodosum の採集

1. ピリヒバ由来ハロペルオキシダーゼ

(I)酵素の精製、構造解析

(II)安定性とカルシウム

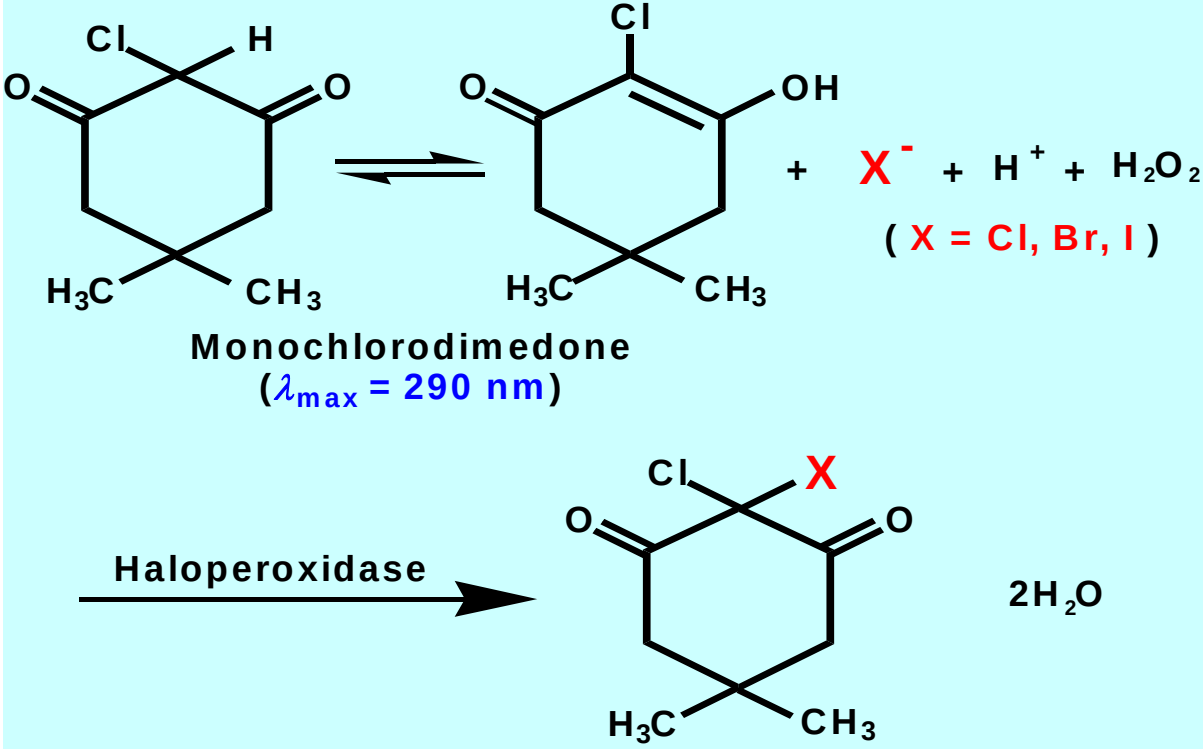
(III)変異酵素のハライドに対する活性

2. 緑藻(アワビモ、ミル)由来ハロペルオキシダーゼ

Haloperoxidase

$$AH + X^- + H_2O_2 + H^+ \longrightarrow AX + 2H_2O$$

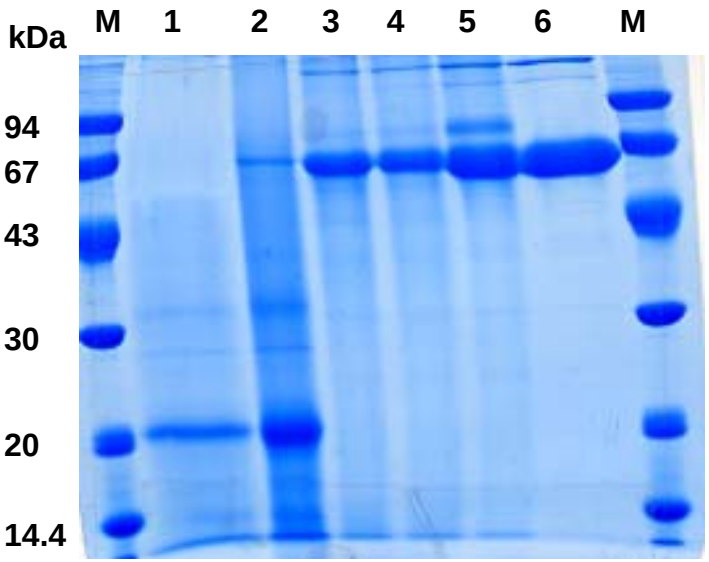
(A: nucleophilic cpds. ; X: Cl, Br, I)



Purification of BPO Produced by *Cor. pilulifera*

Step	Total activity (U)	Total protein (mg)	Specific activity (U/mg)	Purification (fold)	Yield (%)
Cell-free extract	35,000	4,240	8.25	1	100
$(NH_4)_2SO_4$ fractionation	35,700	4,230	8.44	1.02	102
DEAE-Sepharose	22,600	188	120	14.5	64.6
1st Q-Sepharose	9,230	57.6	160	19.4	26.4
Sepharose CL-4B	7,360	25.9	284	34.4	21.0
2nd Q-Sepharose	4,560	11.6	393	47.6	13.0

SDS-PAGE of BPO from *Cor. pilulifera*



M. Marker proteins

1. Cell-free extract
2. $(NH_4)_2SO_4$ fractionation
3. DEAE-Sepharose
4. 1st Q-Sepharose
5. Sepharose CL-4B
6. 2nd Q-Sepharose

Comparison of Properties between BPOs from *Cor. pilulifera* and *A. nodosum*

	Cor. pilulifera	*A. nodosum*
Molecular weight	680 kDa	90 kDa
Subunit weight	64 kDa × 12	40 kDa x 2
Optimum temp.	65ºC	N.D*
Optimum pH	6	6.5
Heat stability	85ºC (90% 20 min)	70ºC (38%, 20 min)
pH stability	5-13	N.D*
Specific activity	393 U/mg (BPO)	87.5 U/mg (BPO)
K_m value	0.12 mM (H_2O_2)	
	8.4 mM (KBr)	12.7 mM (KBr)

*Not determined

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BPO1    MGIPADNLQSRAKASFDTRVAAAELALNRGVVPSFANGEELLYRNPDPDNTDPSFIASFT  60
BPO2    ..........................A.................CETG--.........  58

BPO1    KGLPHDDNGAIIDPDDFLAFVRAINSGDEKEIADLTLGPARDPETGLPIWRSDLANSLEL 120
BPO2    ........................................................... 118

BPO1    EVRGWENSSAGLTFDLEGPDAQSIAMPPAPVLTSPELVAEIAELYLMALGREIEFSEFDS 180
BPO2    ......................V........M....I.............D........ 178

BPO1    PKNAEYIQFAIDQLNGLEWFNTPAKLGDPPAEIRRRRGEVTVGNLFRGILPGSEVGPYLS 240
BPO2    ....AF.RS..ER.............................................. 238

BPO1    QYIIVGSKQIGSATVGNKTLVSPNAADEFDGEIAYGSITISQRVRIATPGRDFMTDLKVF 300
BPO2    ..................F..................................... 298

BPO1    LDVQDAADFRGFESYEPGARLIRTIRDLATWVHFDALYEAYLNACLILLANGVPFDPNLP 360
BPO2    .....G..................................................... 358

BPO1    FQQEDKLDNQDVFVNFGSAHVLSLVTEVATRALKAVRYQKFNIHRRLRPEATGGLISVNK 420
BPO2    .........H................................................. 418

BPO1    IAPQKG-ESIFPEVDLAVEELGDILEK-AEISNRKQNIADGDPDPDPSFLLPMAFAEGSP 478
BPO2    .KSFLA.SDI.....SEL....SS..DDV..-..E...R...IVS..K........... 477

BPO1    FHPSYGSGHAVVAGACVTILKAFFDSGIEIDQVFEVDKDEDKLVKSSFKGTLTVAGELNK 538
BPO2    ........................ANFQ..K.....T.................... 537

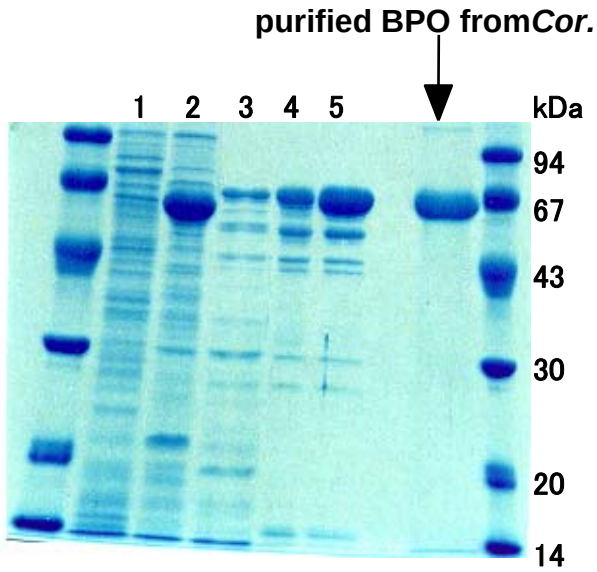
BPO1    LADNIAIGRNMAGVHYFSDQFESLLLGEQVAIGILEEQSLTYGENFFFNLPKFDGTTIQI 598
BPO2    .....V......................I........................... 597
```

Alignment of the Amino Acid Sequences of BPOs, BPO1 and BPO2 from *Cor. pilulifera*

	Protein (mg)	Total activity (U)	Specific activity (U/mg)
1. Cell-free extracts	17600	—	—
2. DEAE-Sepharose	264	613	2.32
3. Phenyl-Sepharose	9.92	363	36.6
4. Source 30Q	1.66	159	95.9
5. Superdex	0.341	97.5	286

発現量低い

無細胞抽出液中で
活性測定できない



***N*-Terminal amino acid sequence**

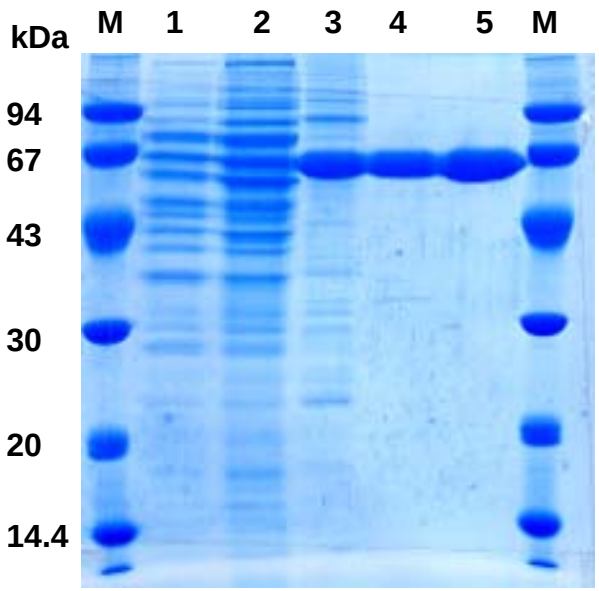
G-I-P-A-D-N-L-Q-S-R-A-K-A-S-F-D

Purification of BPO from the Recombinant *E. coli*

Purification of BPO Produced by *Saccharomyces cerevisiae* BJ1991/pTNT30

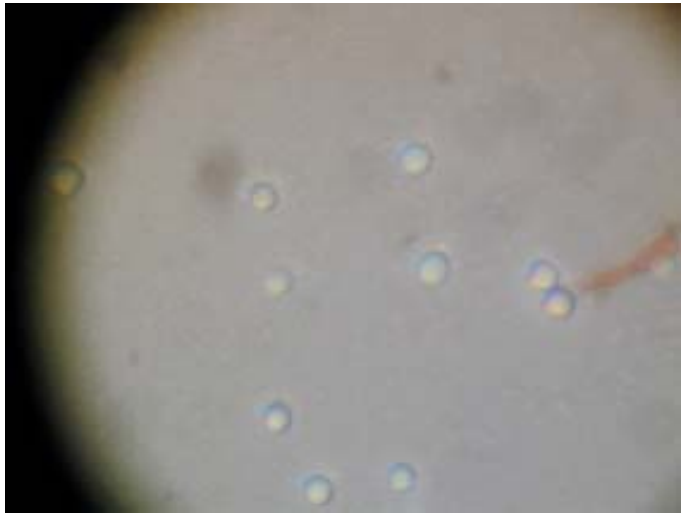
Step	Total activity (U)	Total protein (mg)	Specific activity (U/mg)	Purification (fold)	Yield (%)
Cell-free extract	225,000	10,300	21.8	1	100
$(NH_4)_2SO_4$ fractionation	213,000	5,730	37.2	1.71	94.7
DEAE-Sepharose	160,000	627	255	11.7	71.1
Q-Sepharose	65,700	162	406	18.6	29.2
Sepharose CL-4B	63,000	146	432	19.8	28.0

SDS-PAGE of BPO from *S. cerevisiae* BJ1991/pTNT30



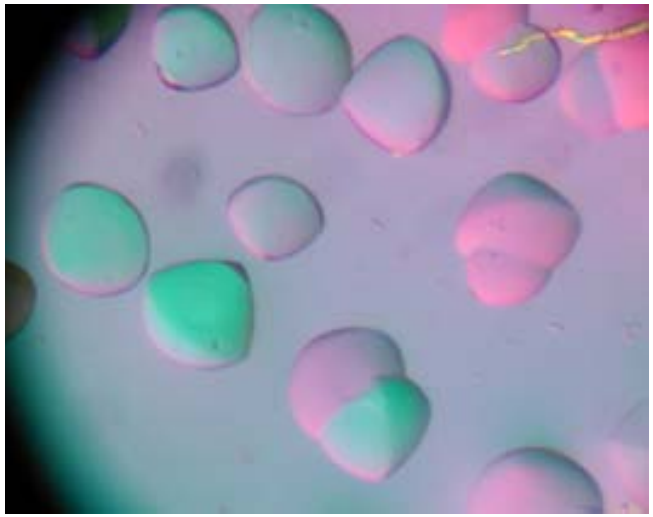
M. Marker proteins

1. Cell-free extract
2. $(NH_4)_2SO_4$ fractionation
3. DEAE-Sepharose
4. Q-Sepharose
5. Sepharose CL-4B



1.8 M Ammonium dihydrogenphosphate

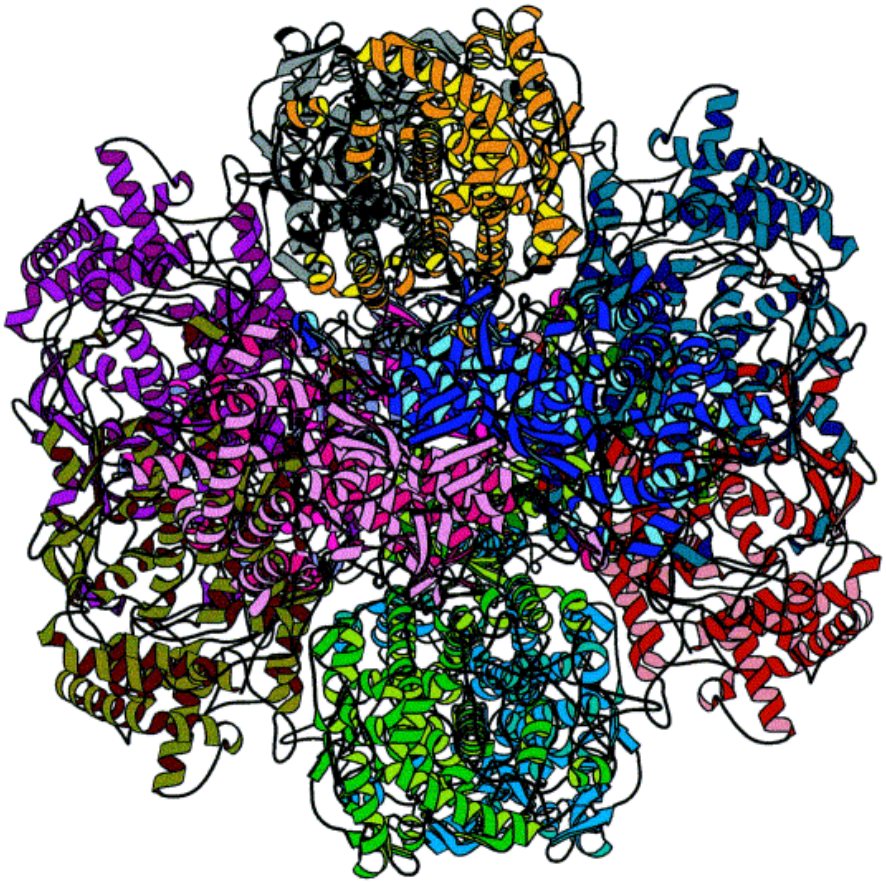
0.1 M Tris-HCl buffer, pH 5.0 (1 day)



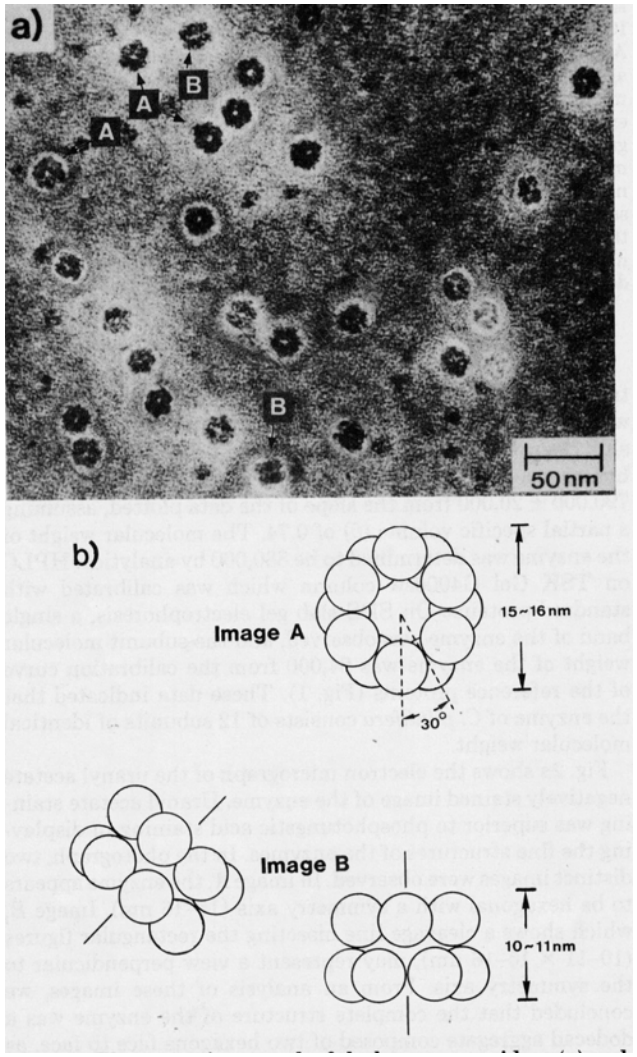
1.8 M Ammonium dihydrogenphosphate

0.1 M Tris-HCl buffer, pH 5.0 (6 days)

Photomicrographs of Crystalline BPO from *S. cerevisiae* BJ1991/pTNT30



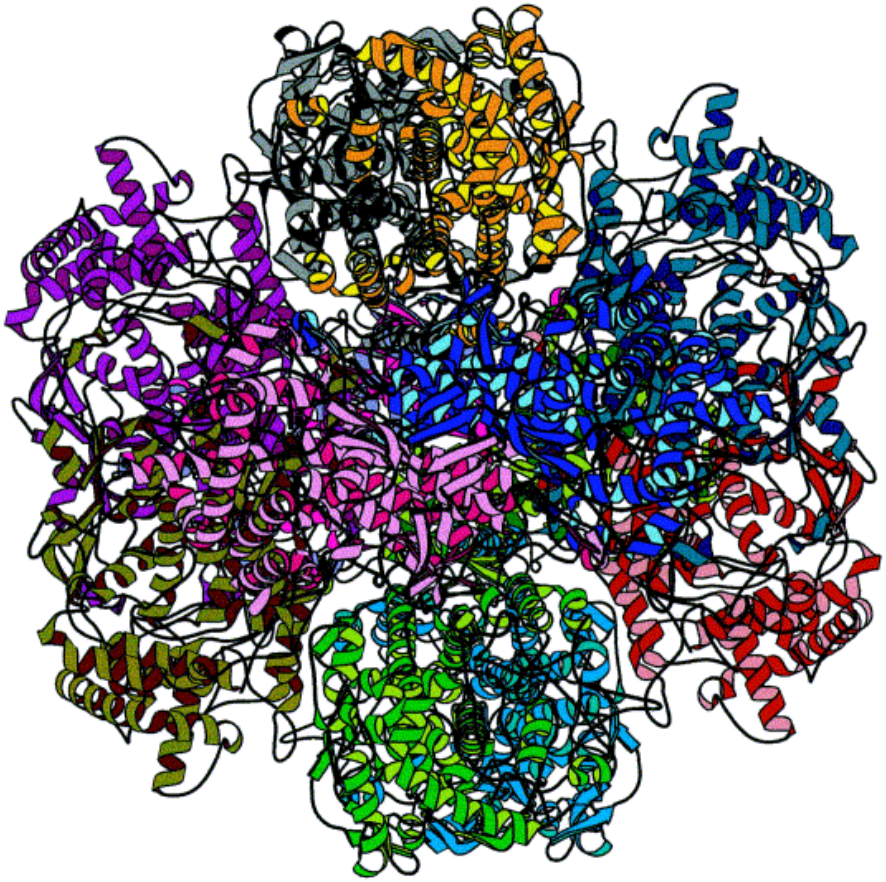
Coordination Chemistry Reviews, 237, 65-76 (2003)



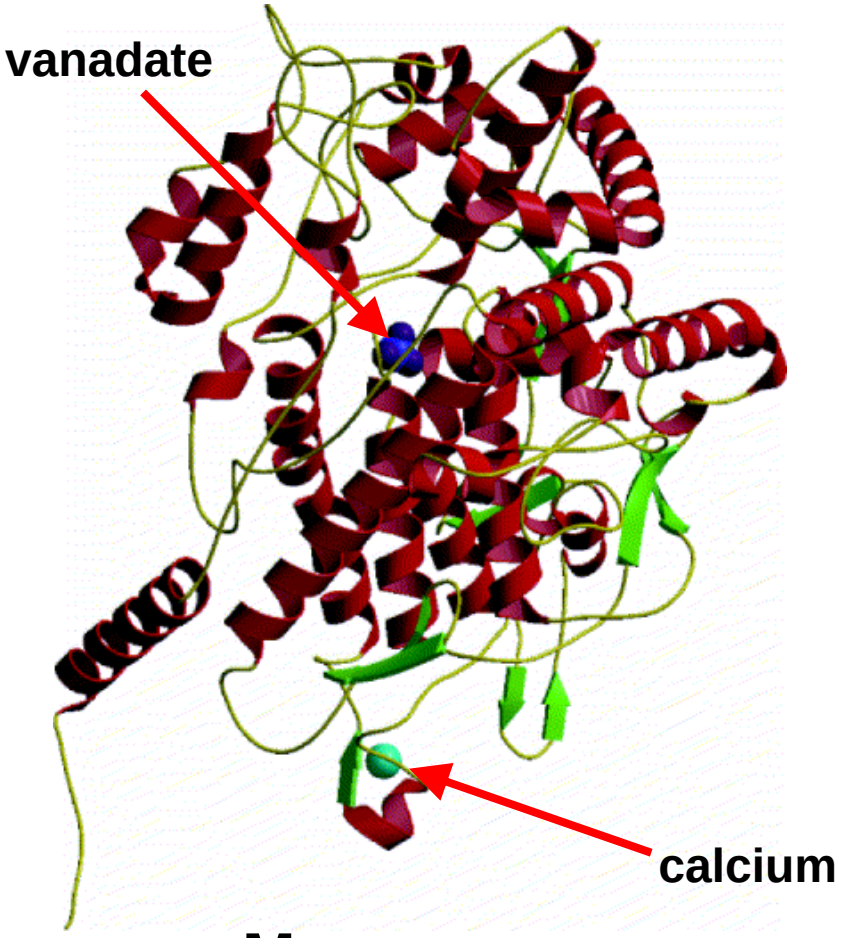
Electron Micrograph

J.B.C., 261, 5194-5200 (1986)

Dodecamer Structure of the *Cor.pilulifera* BPO



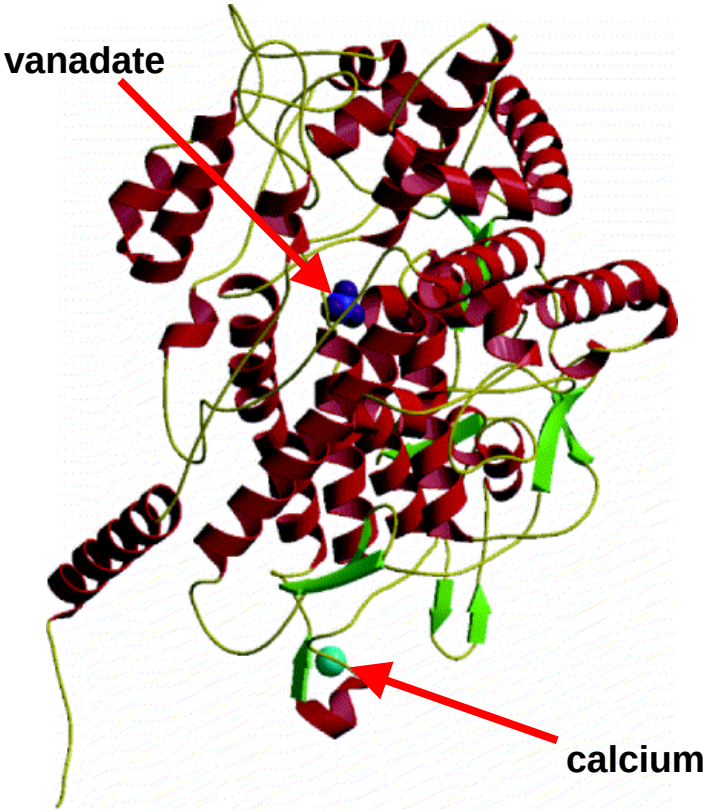
Dodecamer



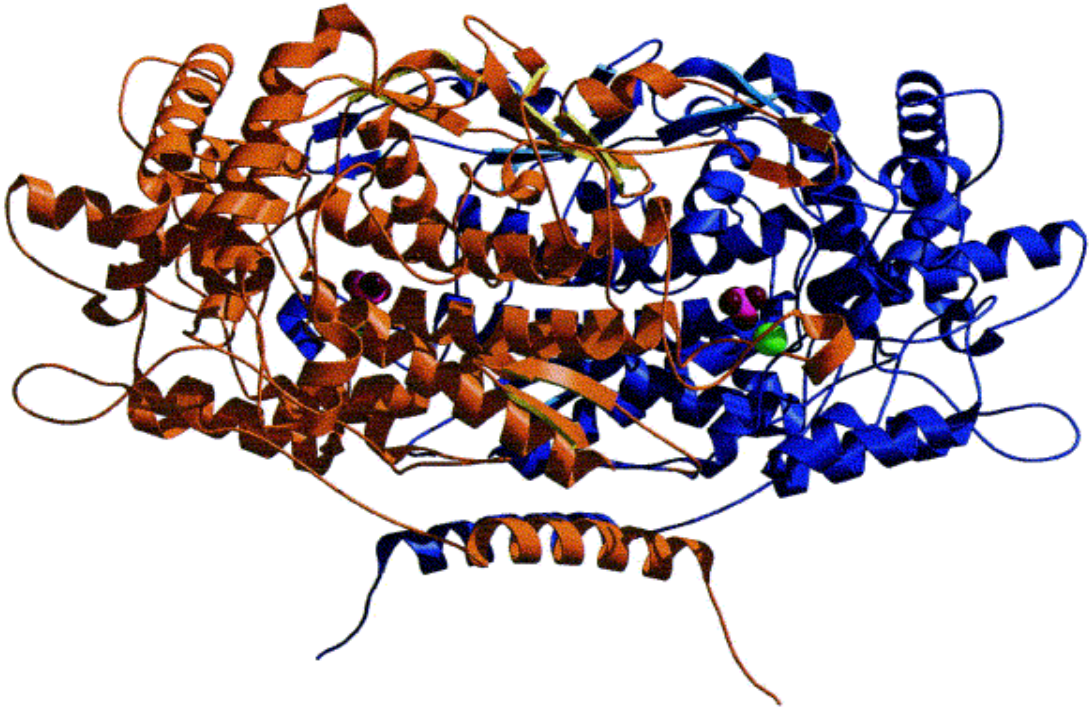
Monomer

Structure of the *Cor. pilulifera* BPO

バナジン酸が位置する活性中心から離れた場所にカルシウムが存在



Monomer



Monomer + Monomer

Structure of the *Cor. pilulifera* BPO

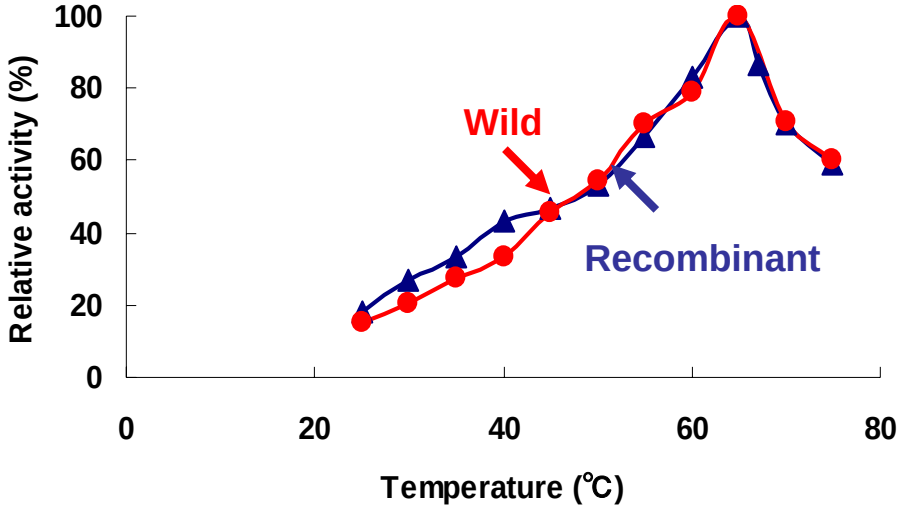
1. ピリヒバ由来ハロペルオキシダーゼ

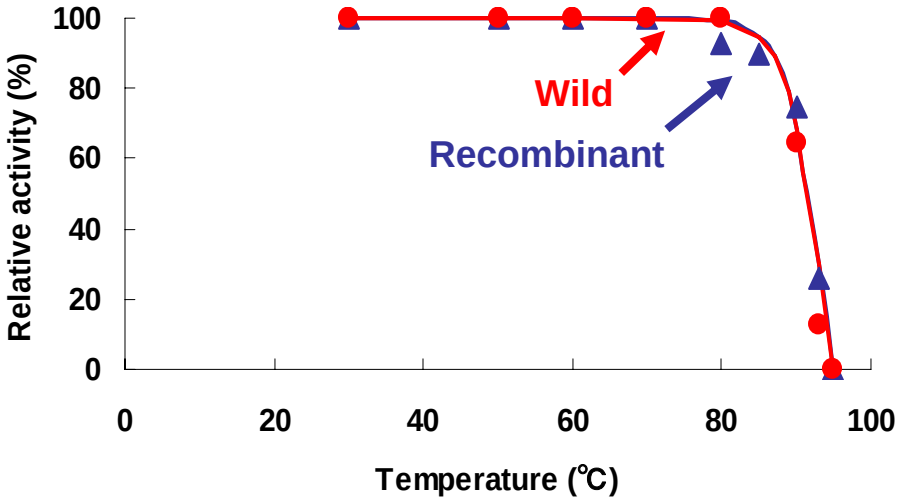
(I)酵素の精製、構造解析

(II)安定性とカルシウム

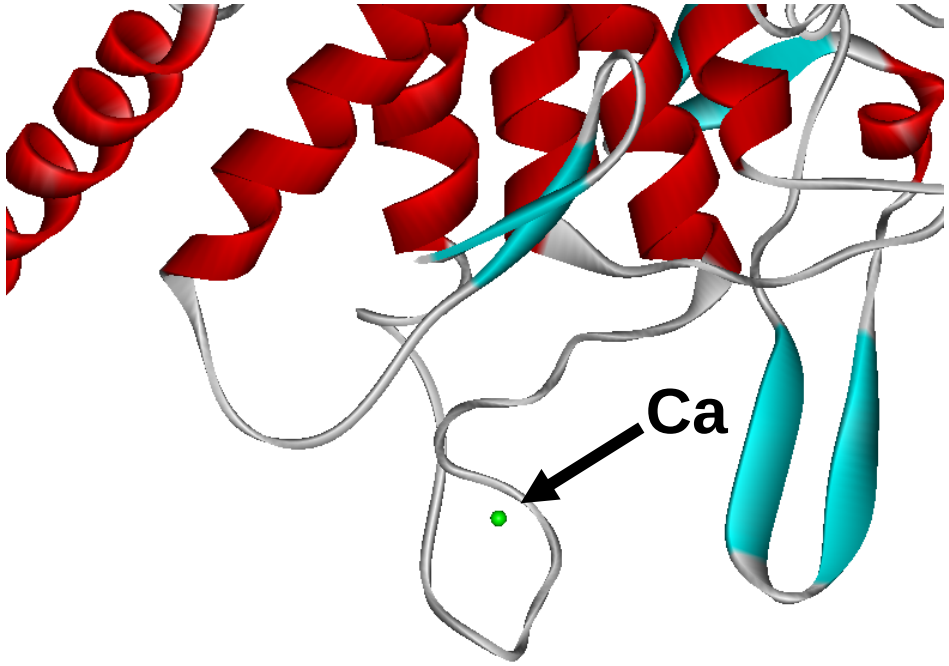
(III)変異酵素のハライドに対する活性

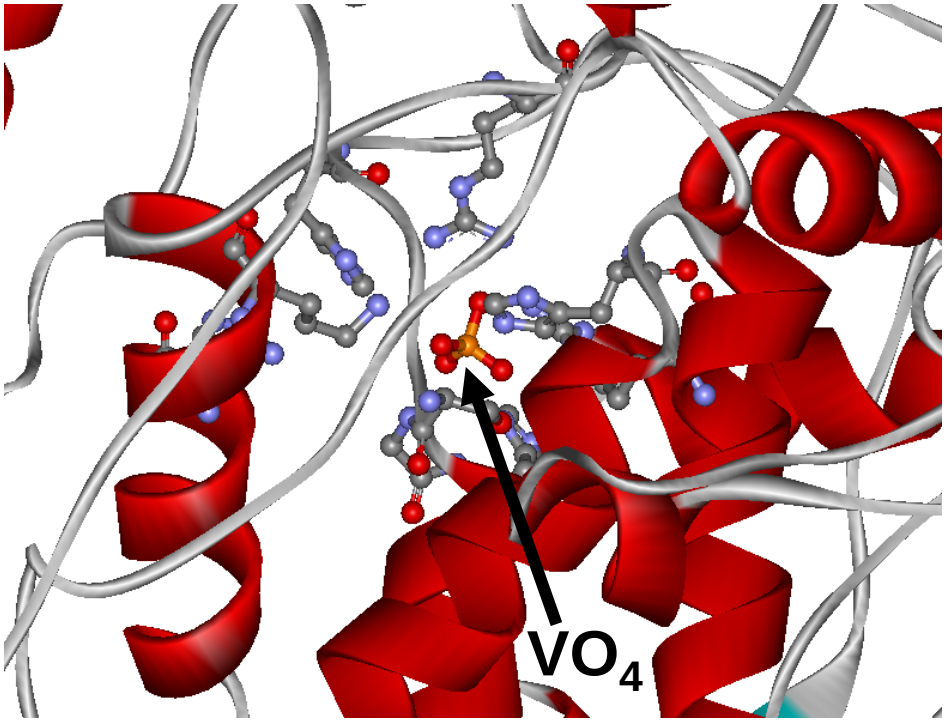
2. 緑藻(アワビモ、ミル)由来ハロペルオキシダーゼ





Effects of Temperature on Wild or Recombinant BPO Activity and Stability





Structure of the Calcium Binding Site of BPO from *Cor. pilulifera*

Structure of the Vanadate Binding Site of BPO from *Cor. pilulifera*

Determination of Calcium in BPO by Inductively Coupled Plasma (ICP) Emmision Spectrometry

	Wild	Recombinant	Apo	
			Wild	Recombinant
mol Ca/mol subunit	0.976	0.828	N.D.	0

N.D. : not determined

Enzymes from *Cor. pilulifera* and the recombinant yeast

- dialyzed against 10 mM EDTA/
  100 mM citric acid-potassium dihydrogenphosphate buffer
  (pH 3.8) for 24 h
- dialyzed against 50 mM Tris-SO_4 buffer (pH 7.4) for 24 h

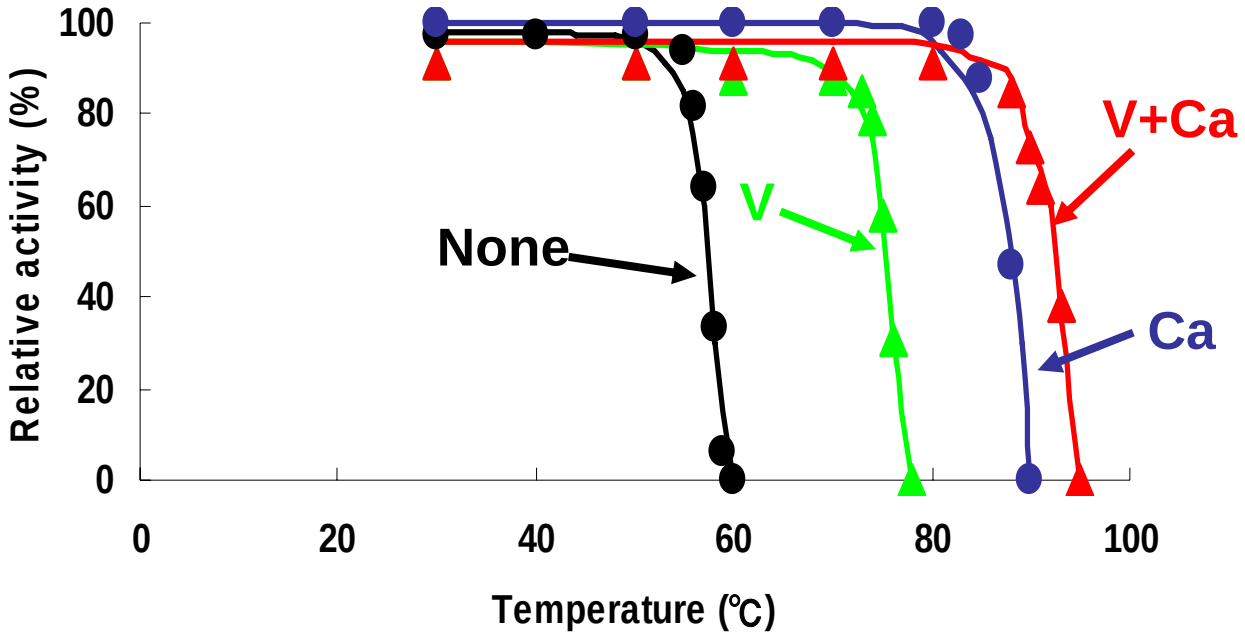
Apo-enzymes

- preincubated with 1 mM Na_3VO_4 and/or 1 mM various metal salts
  at 30°C for 12 h

Holo-enzymes

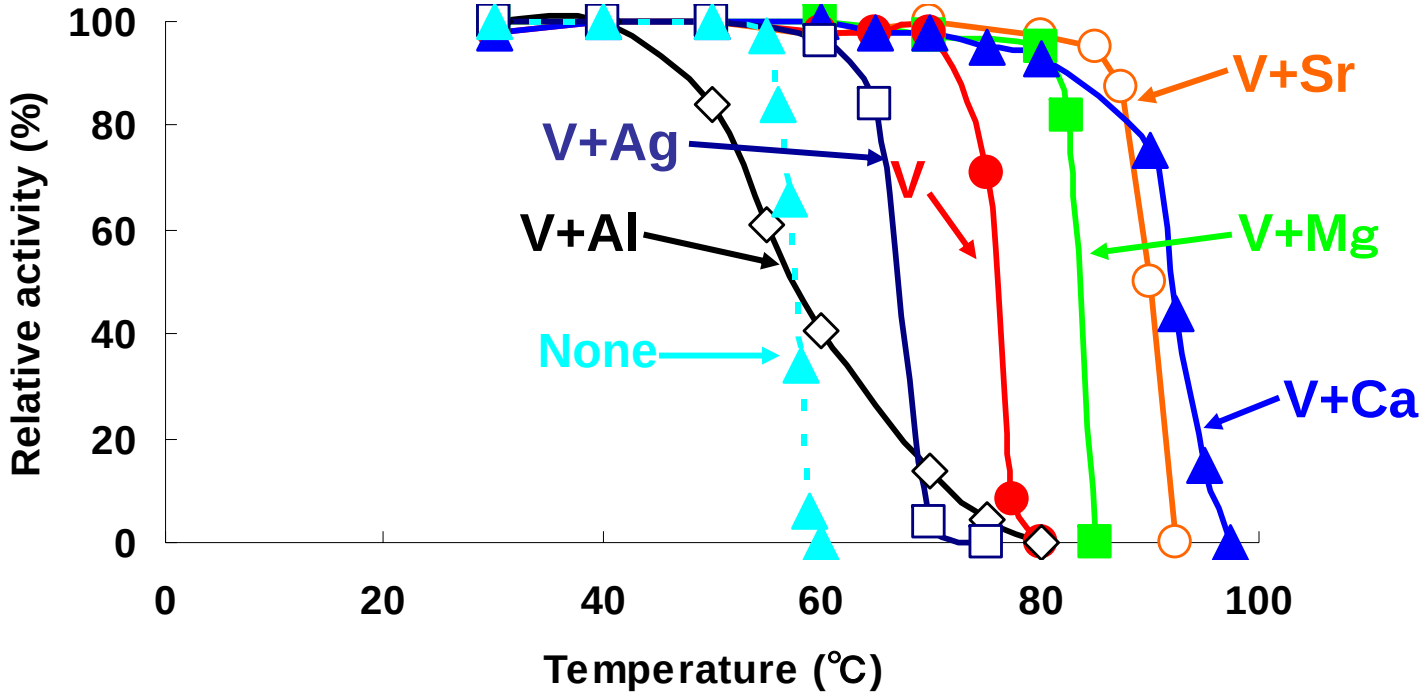
- heat treatment (20 min)
- measure BPO activity

Scheme of Formation of Apo-enzyme and Holo-enzyme



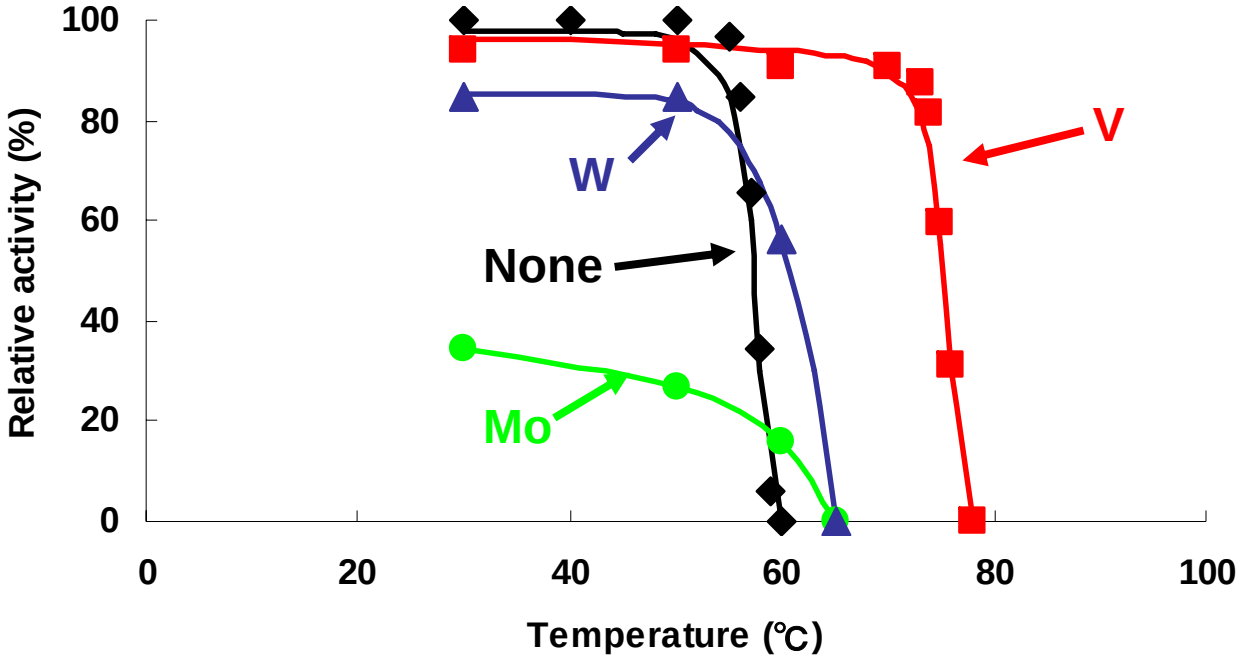
Effects of Vanadate and Calcium Ions on Thermostability of Apo-BPO

Ca が熱安定性に関与、V も多少関与



Effects of Various Metal Ions on Thermostability of Apo-BPO

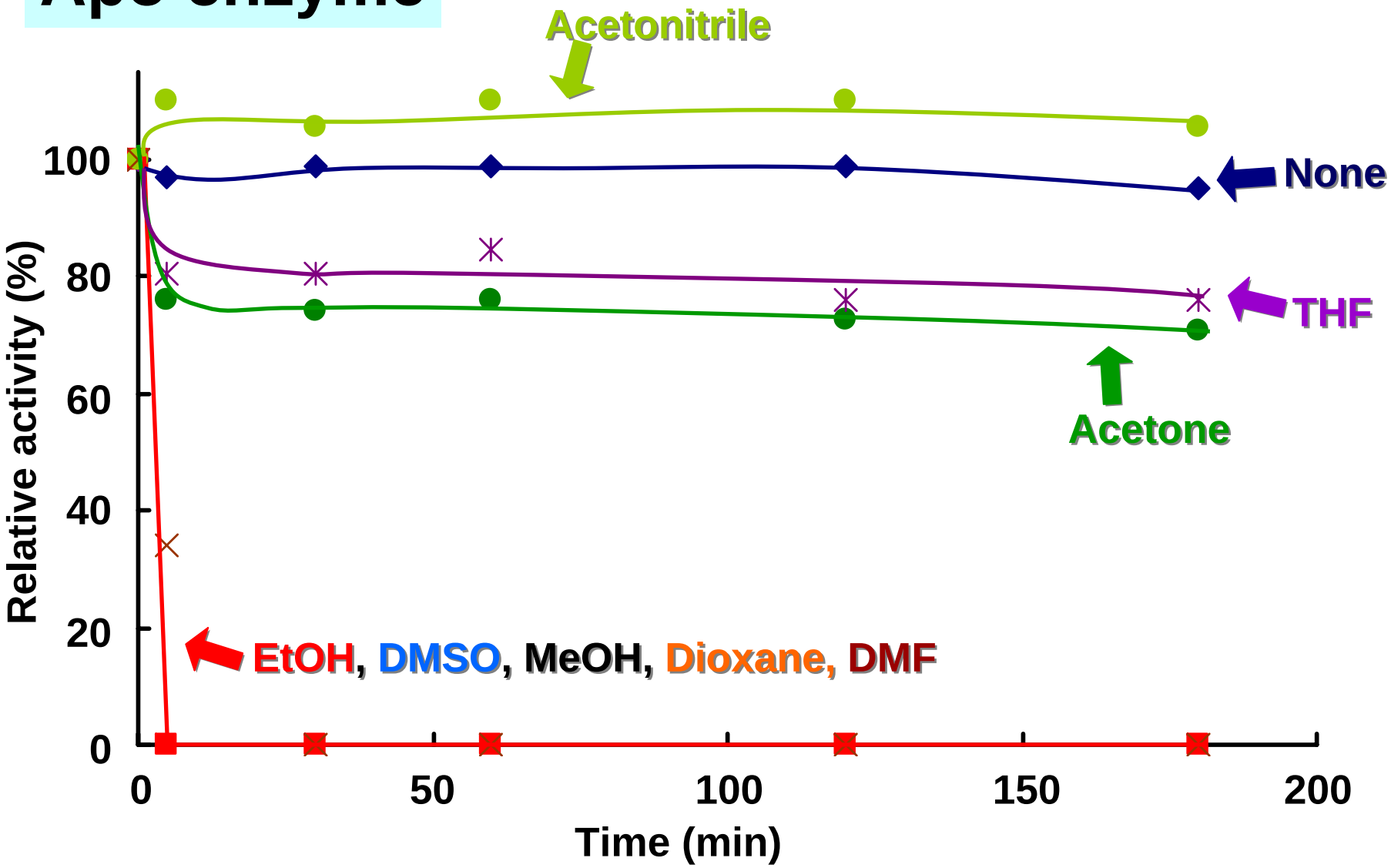
Mg, Sr に Ca の代替効果有り



Effects of Tungstate Ion and Molybdate Ions on Thermostability of Apo-BPO

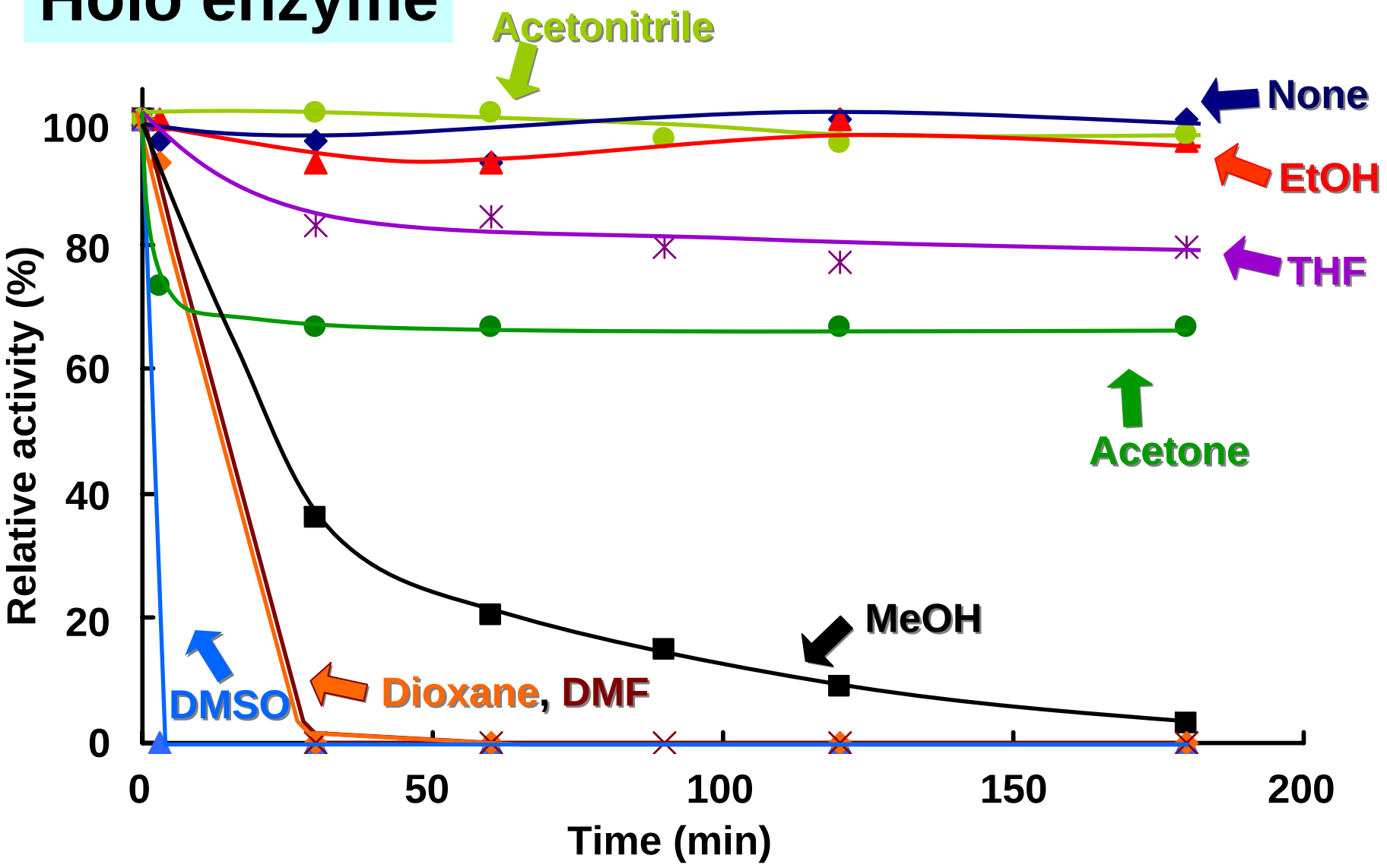
VO_4^{3-} MoO_4^{2-} WO_4^{2-}

Apo enzyme

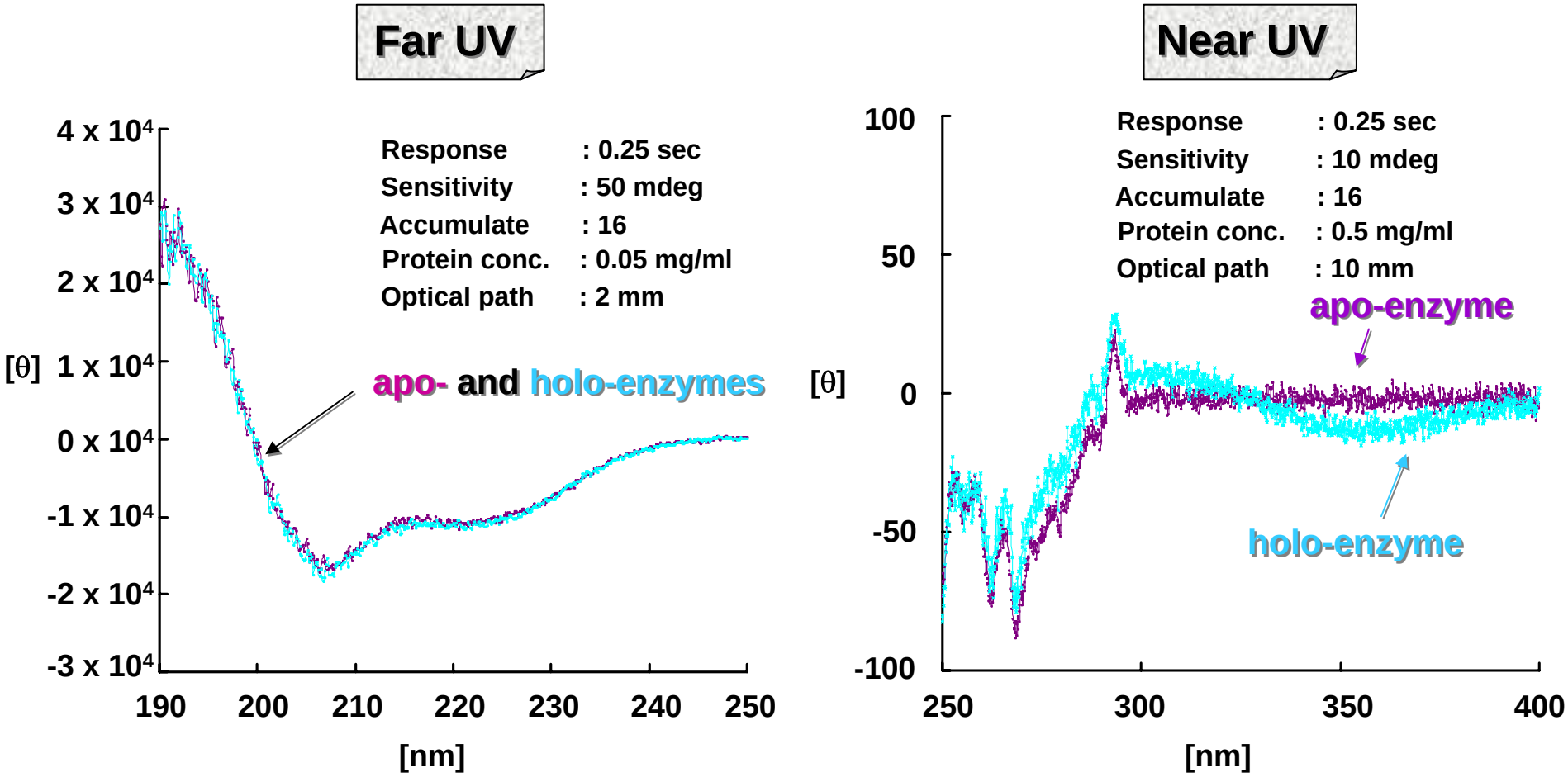


Effects of Polar Organic Solvents on the Stability of Apo-BPO

Holo enzyme



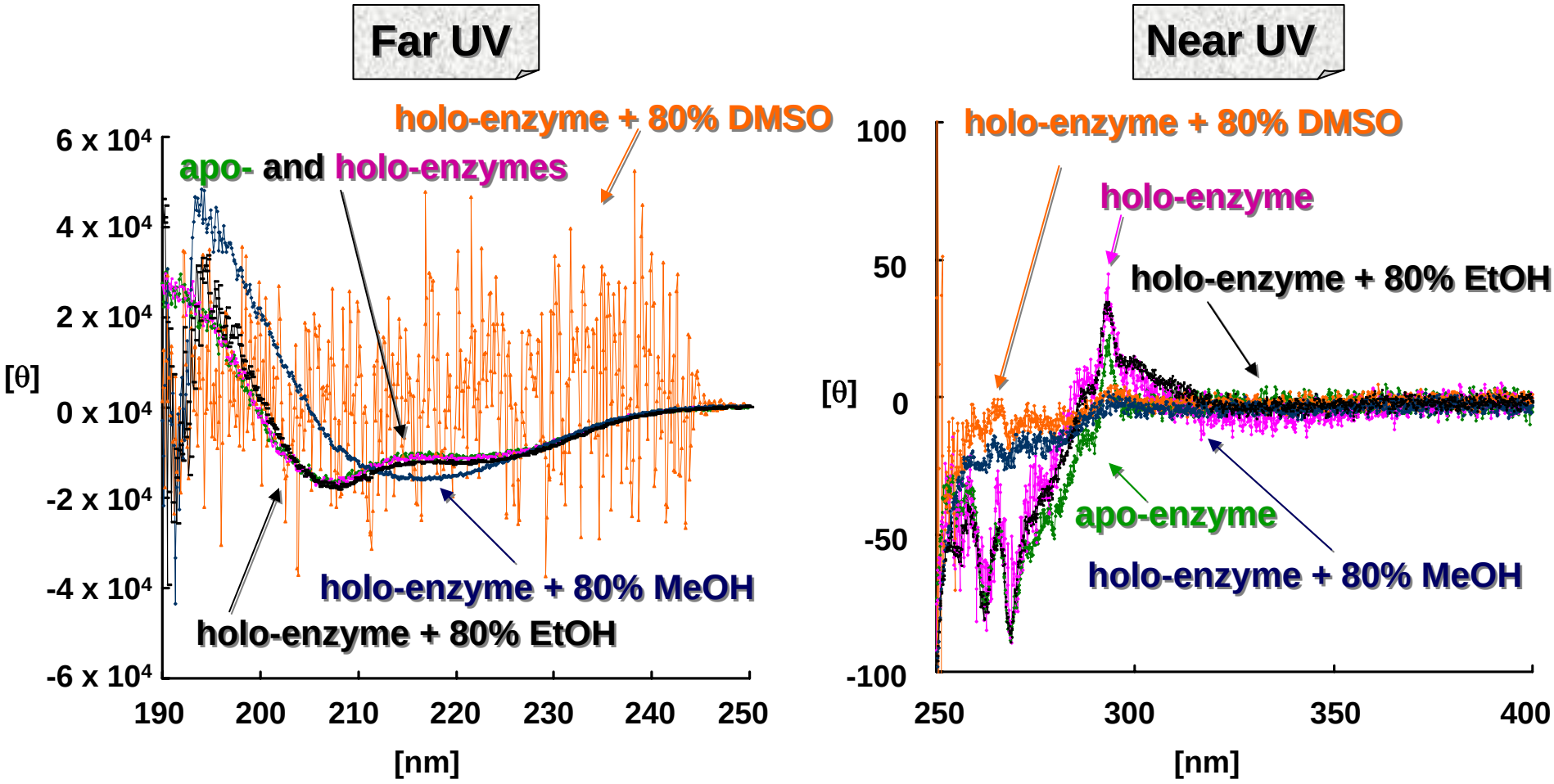
Effects of Polar Organic Solvents on the Stability of Holo-BPO



Analysis of CD Spectrometry of Apo- and Holo-enzymes

アポ型、ホロ型酵素の CD スペクトルに大差なし

→ アポ型、ホロ型酵素で極端な構造変化なし



Analysis of CD Spectrometry of Holo-enzymes in 80% Organic Solvents

エタノール添加では構造変化なし、
メタノール添加で 195 nm～230 nm の CD 波形にずれ

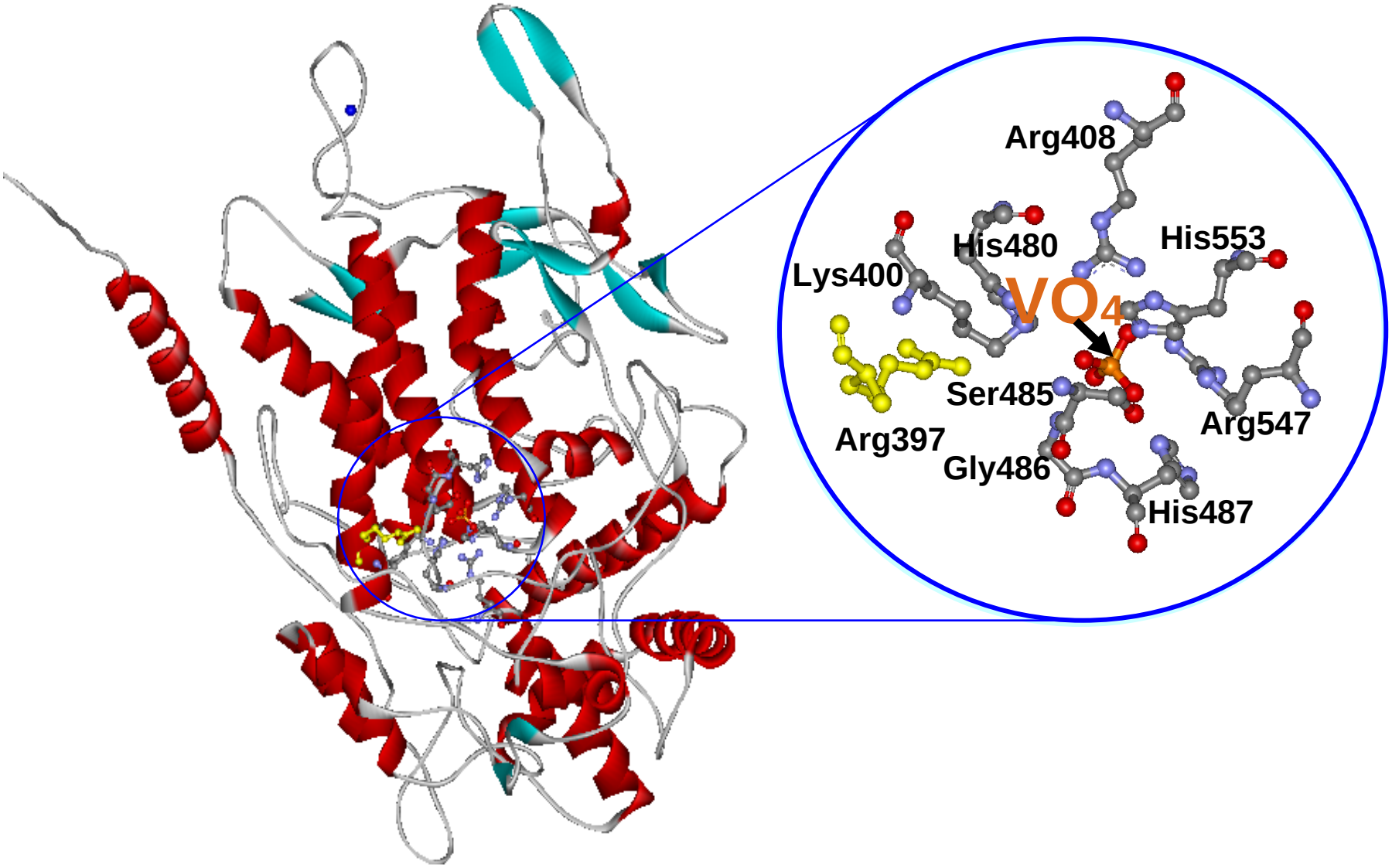
1. ピリヒバ由来ハロペルオキシダーゼ

(I)酵素の精製、構造解析

(II)安定性とカルシウム

(III)変異酵素のハライドに対する活性

2. 緑藻(アワビモ、ミル)由来ハロペルオキシダーゼ



Structure and Active Site of the BPO Subunit from *Cor. pilulifera*

Haloperoxidases Produced by Marine Algae and Microorganisms

Source	Prosthetic group	Halide
Algae		
brown algae		
Ascophyllum nodosum	vanadium	Br, I
Fucus distichus	vanadium	Br, I
Laminaria saccharina	vanadium	Br, I
Macrocystis pyrifera	vanadium	Br, I
red algae		
Corallina pilulifera	Vanadium	Br, I
Laurencia japonica	(ferriprotoporphyrin)	Br, I
green algae		
Penicillus capitatus	ferriprotoporphyrin IX	Cl, Br, I
Ulvella lens	(vanadium)	Br, I
Microorganisms		
Fungi		
Caldariomyces fumago	ferriprotoporphyrin IX	Cl, Br, I
Curvularia inaequalis	vanadium	Cl, Br, I
Embellisia didymospora	vanadium	Cl, Br, I
Bacteria		
Pseudomonas pyrrocinia	ferriprotoporphyrin IX	Br, I
Pseudomonas pyrrocinia	zinc and iron	Cl, Br, I
Actinomycetes		
Streptomyces aureofaciens	unknown	Br, I
Streptomyces phaeochromogenes	unknown	Br, I

Haloperoxidase

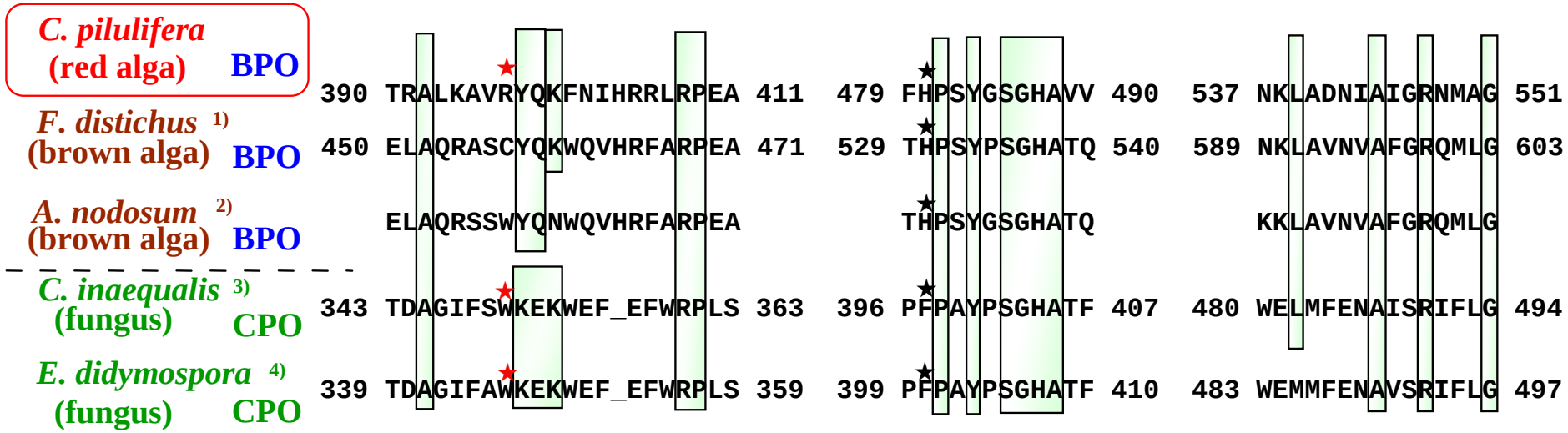
$$AH + X^- + H_2O_2 + H^+ \longrightarrow AX + 2H_2O$$

(X: Cl, Br, I)

Comparison of Properties between BPO from *Cor. pilulifera* and CPO from *Cur. inaequalis*

	BPO	CPO
Molecular weight	680 kDa	67 kDa
Subunit weight	64 kDa × 12	67 kDa
Optimum temp.	65ºC	N.D*
Optimum pH	6	5.5
Heat stability	85ºC (90% 20 min)	80ºC (73%, 5 min)
pH stability	5-13	N.D*
Specific activity	432 U/mg (BPO)	48 U/mg (BPO)
	0.65 U/mg (CPO)	14 U/mg (CPO)
K_m value	0.12 mM (H_2O_2)	1 μM (H_2O_2)
	8.4 mM (KBr)	
	N.D* (KCl)	0.25 mM (KCl)

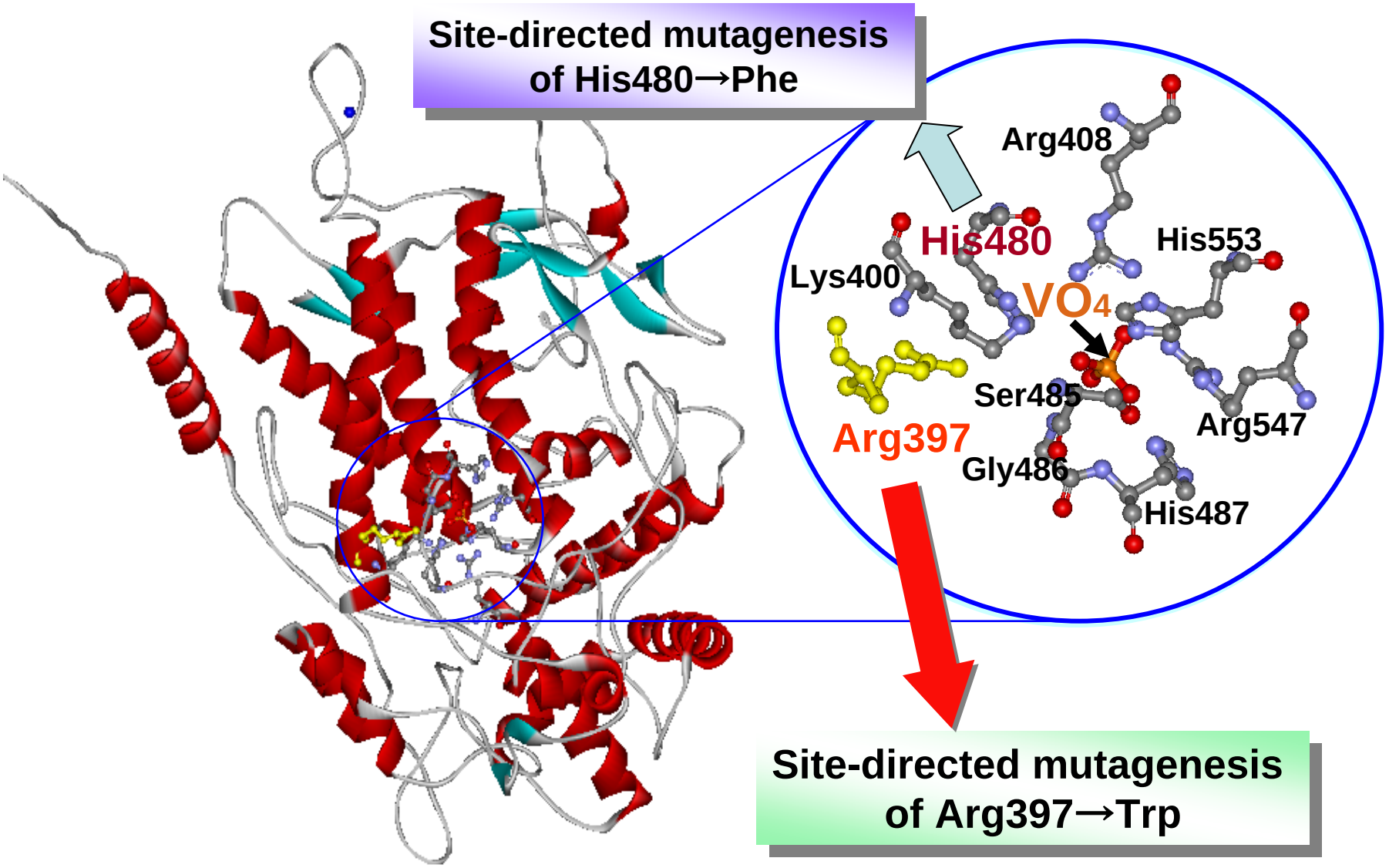
*Not determined



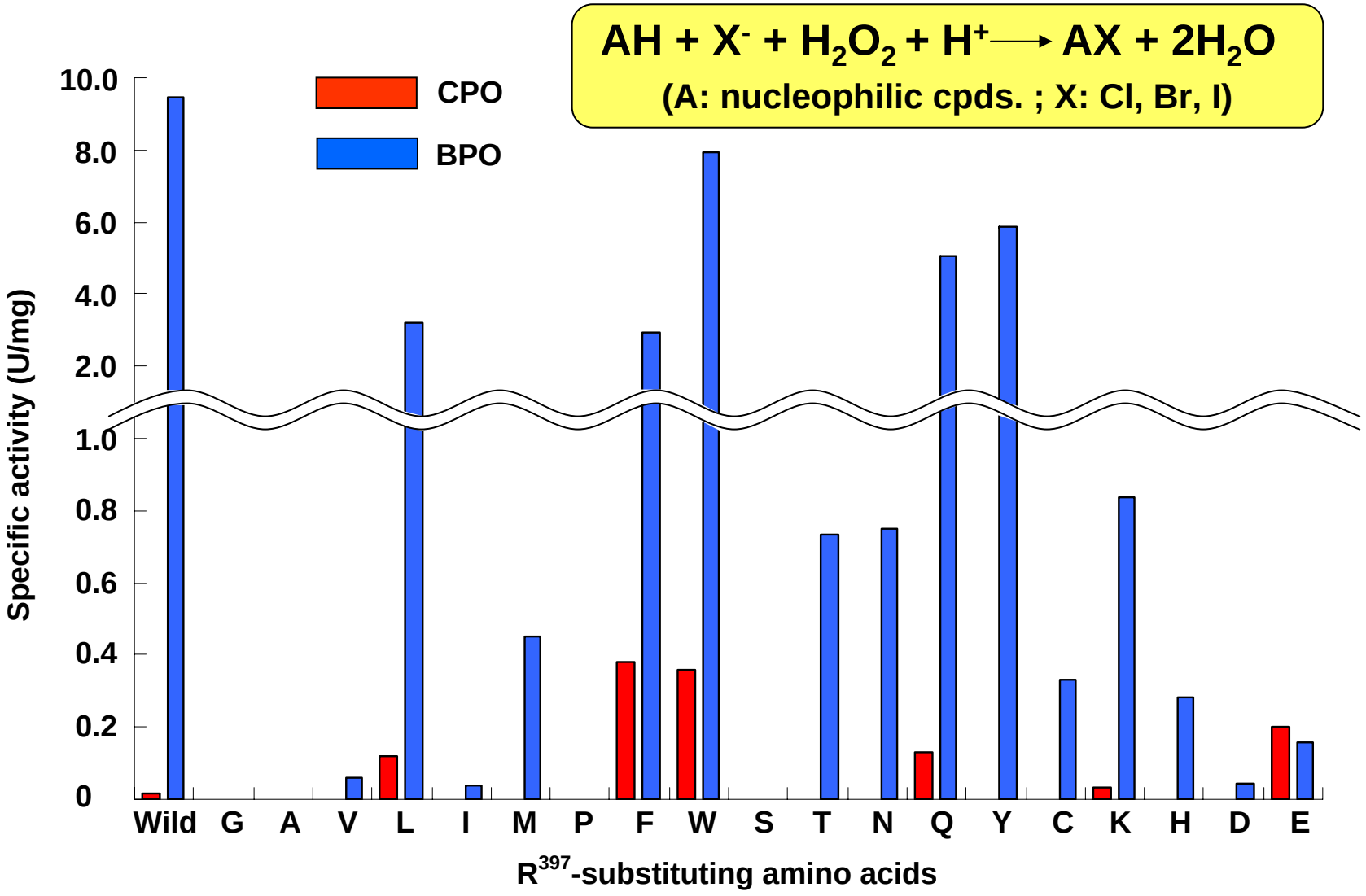
Alignment of the Amino Acid Sequences of Vanadium-dependent Haloperoxidases from Algae and Microorganisms

***C. pilulifera*: *Corallina pilulifera*, *F. distichus*: *Fucus distichus*,**
***A. nodosum*: *Ascophyllum nodosum*, *C. inaequalis*: *Curvularia inaequalis*,**
E. didymospora*: *Embellisia didymospora

1) The sequence was submitted to the GenBank Data Bank under the accession number AF053411 (1998).
2) The partial amino acid sequence was determined.
3) Eur. J. Boichem., 229 , 566-574 (1995).
4) J. Biol. Chem., 273 , 23381-23387 (1998).



Structure and Active Site of the BPO Subunit from *Cor. pilulifera*

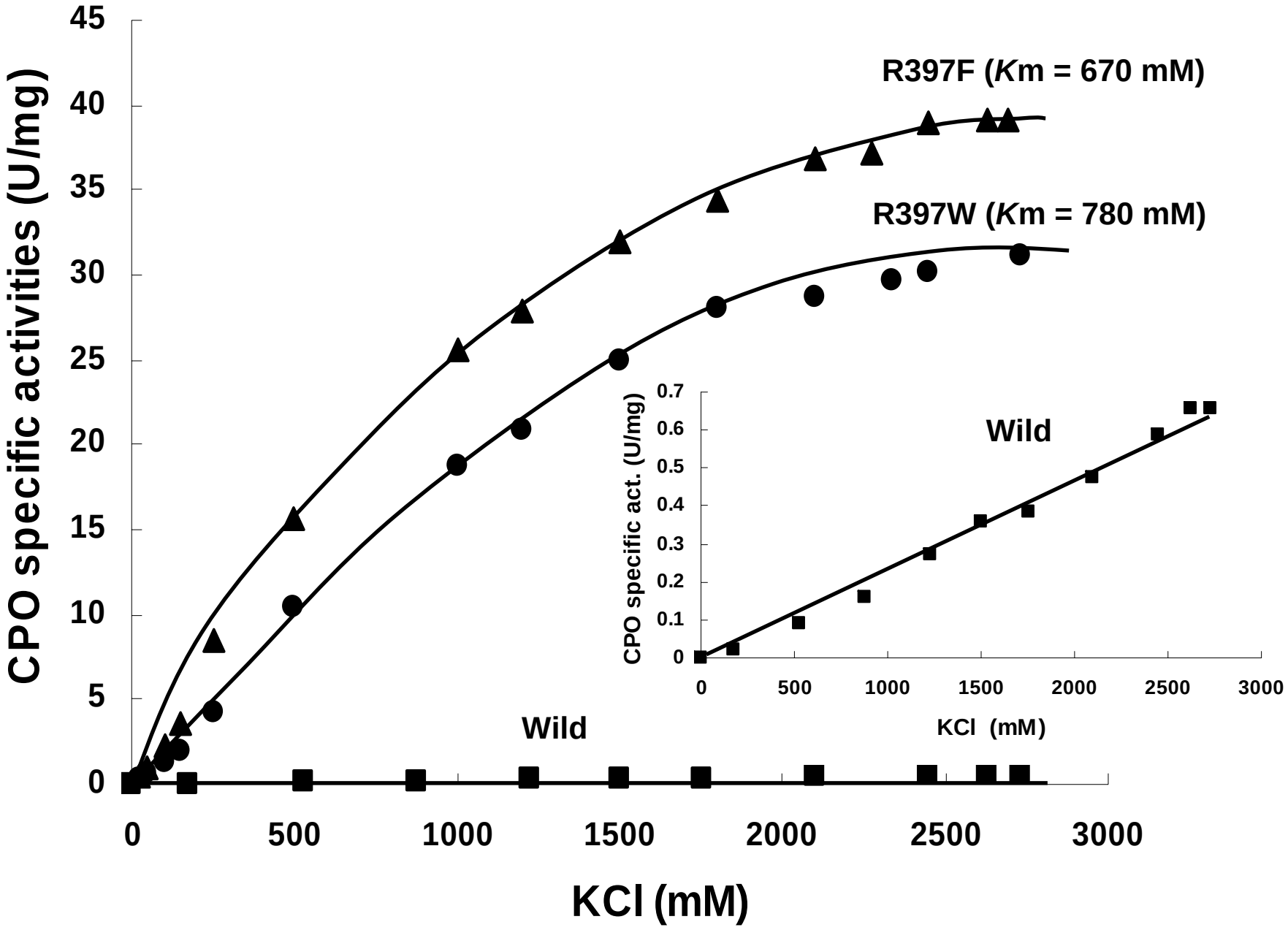


Activities of Mutant Enzymes in Cell-free Extracts

Comparison of Properties among Recombinant Wild Type BPO, Mutant BPOs (R397W and R397F)

	Wild	R397W	R397F
Molecular weight	680 kDa	680 kDa	680 kDa
Subunit weight	64 kDa × 12	64 kDa × 12	64 kDa × 12
Optimum temp.	65ºC	65ºC	65ºC
Optimum pH	6	6	6
Heat stability (20 min)	85ºC (90%)	85ºC (90%)	85ºC (90%)
pH stability	5-13	3-13	5-13
Specific activity	432 U/mg (BPO)	469 U/mg (BPO)	459 U/mg (BPO)
	0.65 U/mg (CPO)	25.1 U/mg (CPO)	32.0 U/mg (CPO)
K_m value	0.12 mM (H_2O_2)	0.13 mM (H_2O_2)	0.081 mM (H_2O_2)
	8.4 mM (KBr)	7.1 mM (KBr)	4.25 mM (KBr)
	N.D* (KCl)	780 mM (KCl)	670 mM (KCl)
Inhibitor	Cu^{2+}, 8-quinolinol	Cu^{2+}, 8-quinolinol	Cu^{2+}, 8-quinolinol
	Iodoacetate	Iodoacetate	Iodoacetate
		Sodium azide	Sodium azide

*Not determined



Measuring *K*m Values with KCl Concentrations

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- (I)酵素の精製、構造解析
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2. 緑藻(アワビモ、ミル)由来ハロペルオキシダーゼ

PERGAMON

Phytochemistry 52 (1999) 1211–1215

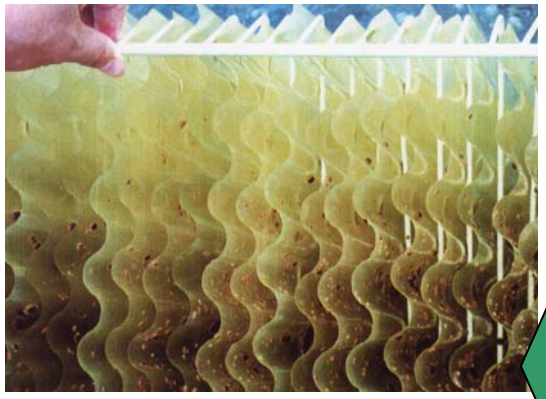
PHYTOCHEMISTRY

アワビモ（*Ulvella lens*）由来ハロペルオキシダーゼ

Occurrence of bromoperoxidase in the marine green macro-alga, *ulvella lens*, and emission of volatile brominated methane by the enzyme

Takashi Ohshiro[a], Satoru Nakano[b], Yoshinori Takahashi[b], Minoru Suzuki[b], Yoshikazu Izumi[b,*]

[a]*Department of Biotechnology, Tottori University, Tottori 680-8552, Japan*
[b]*Division of Material Science, Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan*



ウニの人工養殖において、幼生の着底、変態誘起にアワビモが用いられている

↓

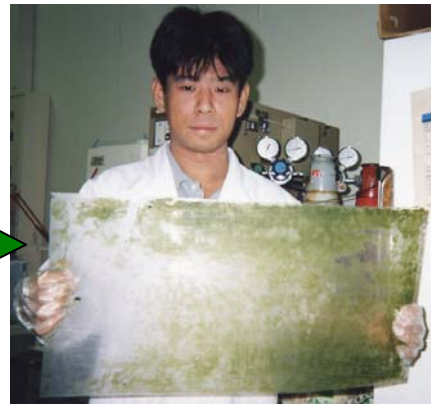
ハロメタンが関与??

↓

アワビモ由来ハロペルオキシダーゼを精製するため、アクリル板上に付着したアワビモを、北海道栽培漁業振興公社より送っていただいた。

↓

活性を確認、金属依存型酵素（特にコバルト）、オキザロ酢酸からブロモメタンの生成を確認



海藻ミル（*Codium fragile*）の無細胞抽出液調製

藻体12.1 kg

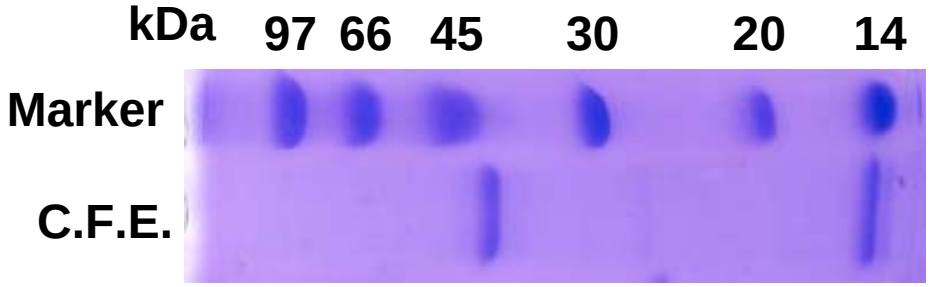
液体窒素で凍結

ミキサーで破砕

10 mM Tris-HCl buffer (pH 7.0)

遠心分離
（8,000 rpm、60 min、4℃）

無細胞抽出液

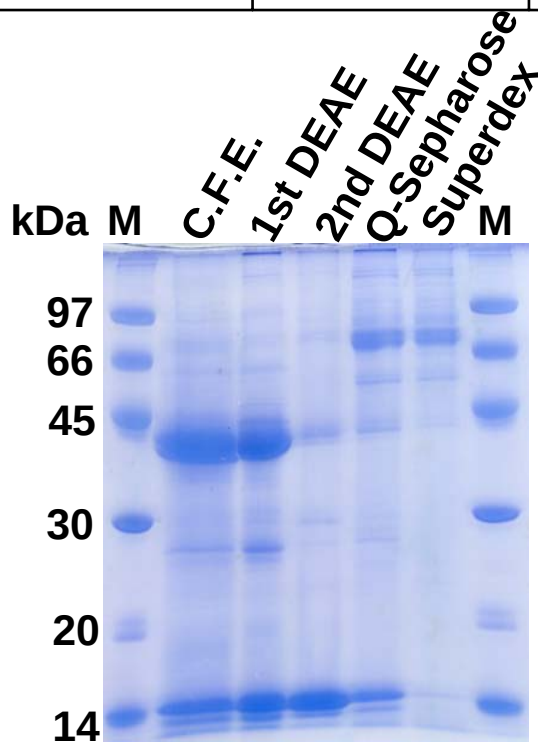


総タンパク質量　1,217 mg

海藻ミル由来ハロペルオキシダーゼの精製

	Total protein (mg)	Total activity (U)	Specific activity (U/mg)	Purification (fold)	Yield (%)
ミルC.F.E.	768	212	0.277	1	100
1st DEAE	238	32	0.136	0.5	15
2nd DEAE	94	18.8	0.200	0.7	8.9
Q-Sepharose	3.5	4.3	1.24	4.5	2.0
Superdex	0.18	0.64	3.56	12.9	0.3

ミル藻体 10 kg（湿重量）から酵素精製



- 金属（Ca、Mn）で活性増大
- ピリヒバ由来酵素に比べ、
  熱安定性は低い
  （60℃、20 min 処理で失活）

海藻ミル由来ハロペルオキシダーゼの諸性質

	至適 pH	K_m [H_2O_2] (mM)	K_m [KBr] (mM)	分子量 (kDa)
C. fragile (緑藻)	6.0	0.015	35	72 [1], 417 [2]
P. capitatus (緑藻)	4.0	0.125	30	52 [2]
P. lamourouxii (緑藻)	4.0	0.125	15	48 [2]
C. pilulifera (紅藻)	6.0	0.092	11	67 [1], 790 [2]
A. nodosum (褐藻)	6.0	0.034	13	40 [1], 90 [2]

1) subunit 2) native

本酵素は他の緑藻由来ハロペルオキシダーゼと
異なる特性を有する！

ハロゲン化酵素の現状と今後の課題

- ピリヒバ由来の酵素は、他のハロペルオキシダーゼよりも高い熱安定性、溶媒耐性、比活性
- クロロ活性が低い

さらに機能改変された変異酵素の構築

実際のハロゲン化反応への適用