Plant
Biochemistry

*

BONNER

Plant Biochemistry

BY JAMES BONNER

Kerckhoff Laboratories of Biology,
California Institute of Technology,
Pasadena, California

FIRST EDITION
SECOND IMPRESSION

ACADEMIC PRESS INC., PUBLISHERS
NEW YORK 10, N. Y.
1950

Second Printing, 1952

PRINTED IN THE UNITED STATES OF AMERICA

PREFACE

The remarkable advances achieved in several branches of plant biochemistry in recent years have gone far toward establishing the basic similarity of the metabolic processes of higher plants to the metabolic processes of other groups of organisms. It is in fact becoming apparent that much of biochemistry is common to many kinds of living things and that metabolic pathways elucidated for, perhaps, a microorganism apply equally well to the mammal and to the higher plant. A familiar example is the way in which yeast studies have increased our knowledge of the steps involved in the glycolytic transformation of hexose to pyruvate—a metabolic pathway which we now know to be ubiquitous. More recently investigations of bacterial systems have held a key position in the discovery and study of heterotropic CO_2 fixation and have contributed greatly to our understanding of the role of energy-rich phosphate in energy transfer, both processes of the widest general significance in living organisms. The pathways of amino acid synthesis and interconversion, discovered and worked out with the fungus Neurospora, appear to have their counterparts also in other organisms and to be of value as a guide to studies with higher plants as well as with mammals.

Although living things now appear to operate along lines that are basically similar, still each group has its own special metabolic features superimposed on this basic metabolic pattern. In this discussion of the biochemistry of the plant we shall be concerned, not only with metabolic pathways which are well understood in other groups of organisms, but also with matters which peculiarly concern plants, such as the metabolism of starch and of the cell wall, the formation of certain typical secondary metabolic products, and the biochemistry of photosynthesis. It is the purpose of this book to bring together the scattered work on general biochemistry as it applies to plants as well as to summarize those fields of biochemistry pertaining to the plant.

This book is written for the student whose interest in biochemistry is especially directed toward the plant. It is based upon a course in plant biochemistry which the author has given for the past twelve years to students of the plant sciences as well as to students of the chemistry of natural products, and which in the absence of any appropriate text has been conducted solely by lectures and by readings in the original literature.

This volume is suitable as a text for courses in plant biochemistry given on the senior and early graduate level, provided that the student has a background of some organic chemistry, although not necessarily any previous course in biochemistry. Selections from the general reading appended to each chapter may serve as additional material for such courses, while the specific references may prove helpful to the advanced student or research worker who wishes to initiate a detailed study of a particular field.

The author believes that a book of this nature, in order to be useful, should not consist merely of a collection of facts or of an annotated bibliography, but should rather present a series of as well ordered and consistent pictures as are possible with the present state of our knowledge. Every effort has been made therefore to present the facts of each subject in such a manner as to bring some order out of the whole. This is by no means easy in the present unorganized state of our knowledge concerning the biochemistry of plants. Future work and future concepts will no doubt revise our notions as to the proper way in which to present and organize the information on this subject.

There is much work to be done in plant biochemistry. Our understanding of many basic metabolic pathways in the higher plant is lamentably fragmentary. While the emphasis in this book is on the higher plant, it will frequently be necessary to call attention to conclusions drawn from work with microorganisms or with higher animals. Numerous problems of plant biochemistry could undoubtedly be illuminated by the closer application of the information and the techniques which have been developed by those working with other organisms.

Biochemistry today is a rapidly expanding discipline and new facts as well as new concepts are being continuously brought forward. It is inevitable therefore that certain of the material contained in the present book will be superseded by new facts and broader concepts. In certain particularly active fields this has indeed occurred even during the preparation of the manuscript.

Certain important aspects of biochemistry have been entirely omitted from the present volume simply because of the lack of pertinent information from the domain of higher plants.

The author wishes to express thanks to his colleagues who have so generously helped him in the preparation of this book. To A. J. Haagen-Smit in particular the author wishes to express his appreciation not only for his unfailing and enthusiastic assistance with the present volume but also for his counsel over the years. The author is indebted to the students in his successive classes for aid in collection of much of the original material. Thanks are especially due to those who diligently checked the original references cited in the text: Francis Haskins, Herbert Hull, Leonard Jansen, Kenneth Paigen, Carl Price, Bernard Strauss, Albert Siegel, and Emanuel Windsor.

Critical reading of various portions of the manuscript has been shared by A. A. Benson, R. H. Burris, Ray Dawson, Jacob W. Dubnoff, A. J. Haagen-Smit, W. Z. Hassid, James Henderson, Norman H. Horowitz, K. Markley, John Nance, Walton B. Sinclair, Emil Smith, Adrian Srb, W. Stepka, Paul K. Stumpf, Samuel G. Wildman and Laszlo Zechmeister. To each the author wishes to express his appreciation. Daniel E. Atkinson and Gerald Fling have contributed by their critical reading of the proof. It is improbable that this book could have been brought to completion without the untiring and expert editorial assistance of Betty Jean Wood, who has helped in all matters. The author wishes to also thank Harriet Bonner, who has done much of the proof reading and Shigeru Honda who has aided in the preparation of the illustrations. For the task of typing the successive versions of the manuscript the author is particularly indebted to Delores Craton and Kay Asakawa. A final note of appreciation is due to the directors of the Herman Frasch Foundation for Agricultural Chemistry, who in their policy of supporting basic work in plant biochemistry have done so much to promote study in this field, both at the California Institute of Technology and elsewhere.

JAMES BONNER

Pasadena, California
July 1950

CONTENTS

	Page
Preface	iii
CHAPTER	
1. AN INTRODUCTION TO PLANT BIOCHEMISTRY	1
Biochemistry of the Cell	1
Enzymes	4
Mode of Enzyme Action	7
Pathways of Plant Metabolism	10
General Reading	12
PART I	
CARBOHYDRATES AND CARBOHYDRATE METABOLISM	
2. THE MONOSACCHARIDES	15
The Hexoses	15
The Pentoses and Heptoses	21
General References	25
References	25
3. THE DISACCHARIDES	26
Maltose	27
Other Disaccharides of Glucose	29
Sucrose	30
Further Disaccharides Containing Two Different Sugars	30
Trisaccharides	31
Stachyose	32
General References	33
References	33
4. TRANSFORMATION OF THE SUGARS	34
Phosphorylation of Hexoses	34
Enolization of Hexoses	37
Formation of Galactose	37
Formation of Sucrose	38
Oxidation of Hexoses	41
Reduction of Sugars	42
Inositol	43
Ascorbic Acid	45
General References	46
References	47
5. STARCH	48
Structure of Starch	48
Iodine Complexes of Starch	55
The Starch Grain	57
Amylases	59
The Mechanism of Starch Synthesis	60

CHAPTER — Page
General References . . . 63
References . . . 64
6. INULIN AND THE WATER-SOLUBLE POLYSACCHARIDES . . . 66
Inulin . . . 66
The Water-Soluble Polysaccharides . . . 68
Water-Soluble Fructosans . . . 68
Water-Soluble Barley Glucosan . . . 69
Water-Soluble Mannosan . . . 69
General References . . . 69
References . . . 69

PART II

THE CELL WALL AND CELL WALL METABOLISM

7. CELLULOSE . . . 71
The Structure of Cellulose . . . 71
Crystallography of Cellulose . . . 72
Arrangement of a Cellobiose in the Unit Cell . . . 74
Molecular Weight of Cellulose . . . 75
Micellar Structure . . . 77
Orientation of Glucopyranose Chains in Cellulose Cell Walls . . . 84
Metabolism of Cellulose . . . 89
Determination of Cellulose . . . 89
General References . . . 91
References . . . 91
8. NONCELLULOSIC POLYSACCHARIDES . . . 93
Mannans and Galactans . . . 93
Xylans and Arabans . . . 95
General References . . . 98
References . . . 98
9. THE PECTIC SUBSTANCES . . . 99
Constitution of Pectic Acid . . . 99
Structure of Pectin . . . 101
Protopectin . . . 101
The Middle Lamella . . . 102
Pectic Enzymes . . . 103
Pectin in Fruits . . . 104
Pectin Jellies . . . 106
General References . . . 107
References . . . 107
10. THE POLYURONIDE HEMICELLULOSES . . . 109
Purification of Hemicellulose . . . 109
Composition of Hemicellulose . . . 110
Structure of Hemicellulose . . . 112
Determination of Hemicellulose . . . 113
General References . . . 113
References . . . 113
11. THE GUMS, MUCILAGES, AND GEL-FORMING SUBSTANCES . . . 115
Gum Arabic . . . 115
Mesquite Gum . . . 116

CHAPTER Page
Damson Gum 117
Gum Tragacanth 117
Microbial Gums 118
Mucilages 118
The Gel-Forming Substances 119
General References 121
References 121
12. LIGNIN 122
Methods for Obtaining Lignin 122
General Properties of Lignin 123
Degradation Products of Lignin 124
Sulfonation of Lignin 125
Structure of Lignin 126
Metabolism of Lignin 129
General References 129
References 129
13. COMPOSITION OF THE CELL WALL 130
Primary Cell Walls 134
Cell Wall Composition of Woody Species 136
Cell Wall Composition of Straws and Grasses 137
References 138

PART III

PLANT ACIDS AND PLANT RESPIRATION

14. THE ORGANIC ACIDS OF PLANTS 140
Nature and Distribution of Plant Acids 140
Determination of the Plant Acids 143
The Krebs Cycle 146
Metabolism of Organic Acids in Leaves 149
Carbon Dioxide Fixation 150
Metabolism of Succulents 154
Acid-Base Balance 159
Relation of Nitrogen Nutrition to Organic Acid Content 161
Aromatic Acids of Plants 162
General References 165
References 165
15. PLANT RESPIRATION 167
Introduction 167
Early Work 168
The Nature of Oxidation 169
Oxidative Enzymes 171
The Dehydrogenases 171
The Flavoproteins 175
Porphyrin Proteins 178
Copper Proteins 181
Enzymes of CO_2 Evolution 183
Succinic Dehydrogenase 185
Initial Breakdown of Carbohydrates 187
Oxidation of Pyruvate: The Krebs Cycle 192

CHAPTER Page
Pyruvate Oxidation in Higher Plants 197
The Terminal Oxidase 200
The Energetics of Respiration 203
Transfer of Energy in Biological Systems 207
General References 215
References 215

PART IV

METABOLISM OF NITROGENOUS COMPOUNDS

16. SYNTHESIS AND METABOLISM OF AMINO ACIDS 219
Nitrate Reduction 222
Transamination 230
Special Cases of Amino Acids Synthesis 234
Amino Acid Decarboxylation 241
Conclusions 242
General References 242
References 242
17. THE PLANT PROTEINS 245
General 245
Seed Proteins of the Cereals 251
Proteins of Seeds Other than Cereals 253
The Leaf Proteins 254
Chloroplastic Protein 256
The Cytoplasmic Proteins 260
The Nucleoproteins 266
Structure of Ribonucleic Acid 267
Structure of Desoxyribonucleic Acid 269
Molecular Size and Form of Nucleic Acids 271
Protein Portion of Nucleoproteins 271
Nuclear Nucleoprotein 272
Enzymes Which Attack Nucleic Acids 273
Virus 274
General References 279
References 280
18. THE PLANT PROTEOLYTIC ENZYMES 283
General 283
Proteases 283
Peptidases 286
Peptide Bond Formation 289
General References 291
References 292
19. NITROGEN METABOLISM OF SEEDLINGS 293
Proteolysis 293
Amide Formation 294
General References 298
References 298
20. NITROGEN METABOLISM OF LEAVES 299
Behavior of Excised Leaves 299
Regulation of Protein Level in Leaves 308

CHAPTER Page
General References . . . 317
References . . . 317
21. PURINES AND PYRIMIDINES . . . 319
THE PURINES . . . 319
Biosynthesis of Purines . . . 321
Purine Oxidation . . . 322
The Methylated Purines . . . 323
Metabolism of the Methylated Purines . . . 324
Biosynthesis of the Methylated Purines . . . 324
THE PYRIMIDINES . . . 324
Biosynthesis of Pyrimidines . . . 325
General References . . . 327
References . . . 327
22. ALKALOIDS . . . 328
NICOTINE . . . 328
Site of Nicotine Synthesis . . . 328
Biosynthesis of Nicotine . . . 330
Biogenesis of Nicotinic Acid . . . 331
Relation of Nicotine to Nornicotine and Anabasine . . . 331
Function of Nicotine . . . 332
ATROPINE AND HYOSCYAMINE . . . 332
FUNCTION OF ALKALOIDS . . . 333
General References . . . 334
References . . . 334
23. NITRIFICATION AND NITROGEN FIXATION . . . 335
NITRIFICATION . . . 335
NITROGEN FIXATION . . . 337
Nonsymbiotic Nitrogen Fixation . . . 338
Symbiotic Nitrogen Fixation . . . 340
Nodules . . . 342
Hemoprotein in Nodules . . . 344
Factors Influencing Symbiotic Fixation of Nitrogen . . . 344
Excretion of Nitrogen by Legumes . . . 346
Biochemistry of Nitrogen Fixation . . . 346
General References . . . 350
References . . . 351

PART V

SECONDARY PLANT PRODUCTS

24. LIPIDS AND LIPID METABOLISM . . . 352
Classification of the Lipids . . . 352
Separation of Lipids . . . 353
Occurrence of Fats . . . 354
The Fatty Acids . . . 355
Separation of Fatty Acids . . . 358
Distribution of Fatty Acids in Plant Fats . . . 359
Structure of the Fats . . . 364
The Plant Waxes . . . 365
The Biosynthesis of Fats and Fatty Acids . . . 368

Chapter		Page
	The Mobilization of Fats	372
	Pathways of Fat Metabolism	374
	THE PHOSPHOLIPIDS	378
	Phosphatidic Acids	378
	Lecithin and Cephalin	378
	Lipositols	380
	Separation of Phospholipids	380
	Distribution and Metabolism	380
	Enzymes Attacking Phosphatides	380
	General References	382
	References	382
25.	ESSENTIAL OILS	384
	Introduction to the Terpenes	384
	Essential Oils	385
	Monoterpenes	387
	Sesquiterpenes	390
	Diterpenes	391
	Triterpenes	392
	Extraction and Separation of the Lower Terpenes	392
	Metabolism of the Lower Terpenes	393
	Function of the Lower Terpenes	394
	General References	396
	References	396
26.	THE CAROTENOIDS	397
	Chemistry of the Carotenoids	397
	Stereoisomerism in the Carotenoids	401
	Biogenesis of the Carotenoids	405
	Function of the Carotenoids in Plants	406
	Physiology of the Carotenoids	407
	General References	409
	References	410
27.	RUBBER	411
	Natural Distribution of Rubber	411
	Latex	411
	Chemistry of Rubber	414
	Biosynthesis of Rubber	417
	The Role of Rubber	419
	General References	419
	References	420
28.	THE ANTHOCYANINS AND ANTHOXANTHINS	421
	Chemistry of the Anthocyanidins	421
	Chemistry of the Anthocyanins	424
	Factors Affecting Color	426
	Factors Affecting Anthocyanin Production	426
	Chemistry of the Anthoxanthins	428
	Résumé of Structural Relations of Anthocyanin and Related Pigments	429
	Genetics of the Anthocyanins and Anthoxanthins	432
	Biogenesis of the Anthocyanins and Anthoxanthins	434
	General References	437
	References	437

Part VI

CERTAIN ASPECTS OF PLANT GROWTH

Chapter — Page

29. The Plant Growth Substances . . . 438
    Introduction . . . 438
    Responses to Growth Substances . . . 439
    Chemistry and Identification of the Native Plant Growth Substances . . . 442
    Biogenesis of Indoleacetic Acid . . . 447
    Destruction of Growth Substance . . . 450
    Growth Substance Complexes . . . 453
    Survey of the Known Forms of Growth Substance . . . 455
    Mechanism of Growth Substance Action . . . 457
    Pharmacology of the Growth Substances . . . 459
    Metabolic Antagonists of Growth Substances . . . 461
    Formative Effects . . . 464
    General References . . . 465
    References . . . 465
30. Photosynthesis . . . 468
    Introduction . . . 468
    Chemistry of Chlorophyll . . . 468
    Chloroplast Structure and Development . . . 473
    Biogenesis of Chlorophyll . . . 475
    Chlorophyll Destruction . . . 477
    Formulation of Photosynthesis . . . 478
    Evolution of Oxygen . . . 480
    Quantum Yield . . . 481
    Path of Carbon in Photosynthesis . . . 483
    General References . . . 490
    References . . . 490

Author Index . . . 493
Subject Index . . . 505

Chapter 1

AN INTRODUCTION TO PLANT BIOCHEMISTRY

Biochemistry is concerned with the chemical operation of living things, and this book treats therefore the chemical operation of plants. We will discuss the manner in which plants synthesize some of their many chemical constituents, the functions of these constituents in the plant, and the ways in which these constituents may be again broken down or altered into still other constituents; in fact, we will discuss, in so far as it is possible, the metabolism of the plant. Biochemistry merges imperceptibly into the related field of the organic chemistry of natural products. It can readily be sensed that this must be so since we must evidently be aware at least of some of the exact chemical compounds present in a plant before we are able to initiate any study of their metabolism. A study of the biochemistry of plant growth for example must first entail finding out what chemical substances constitute the growth increment. It is not surprising therefore that the great bulk of the chemical work thus far carried out with plants has concerned the isolation, identification, and structure determination of some of the vast number of compounds synthesized by and occurring in higher plants. This book is not intended to be a general catalog of the chemical compounds found in plants. On the contrary, such information is tabulated in several excellent works which are listed at the end of this chapter and which should be consulted for details concerning the phylogenetic distribution, amounts, isolation, and structure determinations of particular plant products. Since biochemistry is, however, the study of metabolic changes in chemical structure it will be necessary for us to discuss in some detail the chemistry of the particular plant materials with which we shall be concerned. In this discussion of individual plant components we should not however lose sight of the relationship which these individual components bear to the structure of the plant cell as a whole.

Biochemistry of the Cell. The generalized plant cell is made up of a thin layer of protoplasm which surrounds the large vacuole and which is in turn surrounded by the characteristic cell wall. From the point of view of cell volume, the vacuole is all important. Viewed physiologically, the vacuole is also doubtless of great significance, particularly as to its osmotic role in the water relations of the plant. From the standpoint of dry weight, however, the vacuole is relatively insignificant since its contents are made up so largely of water. Metabolically also the vacuole is not of great interest since few if any important metabolic processes take place within this portion of the cell. The wall of the plant cell ordinarily makes up a much smaller portion of the total volume than the vacuole, although in certain cases very massive secondary walls may occupy the bulk of the cell lumen. Even in the generalized cell, however, the cell wall tends to make up a quarter to a half or more of the total dry weight, and is then the largest single item in the overall cellular constitution. The remaining dry matter of the cell is shared among the components which go to make up the cytoplasm and its inclusions, the nucleus, starch grains, fat droplets, the various granules and, particularly in the case of the cells of green leaves, the chloroplasts. What now can we say about the chemical composition and the metabolic functions of these different portions of the plant cell?

The cell wall consists primarily of polysaccharides and polysaccharide derivatives (Part II), and although there are a few special cases in which the cell wall is made up largely of a single polysaccharide, still in the more usual case, several distinct and different compounds are intimately intermingled in its structure. Pores in this structure permit the ready exchange of smaller molecules and it is undoubtedly the protoplasmic membrane rather than the cell wall which constitutes the semipermeable barrier in the plant cell. Cell wall constituents are evidently formed by processes which take place in the protoplasm, although we have but little evidence on this point. In any case, the cell wall once laid down is relatively inert and its constituents ordinarily reenter the metabolism of the plant sluggishly if at all. The cell wall is, however, subject to at least two striking and important transformations, related respectively to cell elongation (Chapter 7) and to fruit ripening (Chapter 9). In both of these cases as in cell wall growth itself, the secondary transformations of the wall constituents are undoubtedly mediated by metabolic processes carried out within the protoplasm of the cell.

The nonaqueous constituents of the vacuole appear to consist principally of substances of low molecular weight including water soluble pigments (Chapter 28) and possibly other glycosides, in addition to inorganic ions, sugars (Chapters 2 and 3), and organic acids (Chapter 14). Proteins if they occur in the vacuole at all are present only in small amounts, and enzymes have been located with certainty in the vacuole only in latex vessels where vacuolar and protoplasmic contents are inextricably mixed.

The full complexity of the plant cell is achieved only in the protoplasm, of which proteins are the principal and characteristic components. Of the protoplasmic protein, which may constitute a fourth to one-half of the total dry weight of a typical leaf cell, approximately one-half goes to make up the soluble cytoplasmic fraction while the remaining half is contained in various particulate inclusions, the nucleus, chloroplasts, and other granules. Many different and chemically individual proteins are undoubtedly concerned in the composition of these different cellular components and further cytochemical differentiation between the various cellular structures is found in the distribution of still other materials. Thus chlorophyll and the carotenoid pigments are restricted in higher plants to the plastid, desoxyribonucleic acid to the nucleus, and ribonucleic acid largely to the cytoplasm. This cytochemical differentiation is associated with important biochemical differentiation in metabolic function. Thus we know that the synthesis of certain proteins, the desoxyribonucleoproteins, occurs in the nucleus and there are indications that the nucleus may also directly synthesize other proteins which are then liberated into the cytoplasm. It is probable also that the synthesis and degradation of the starch grains and of the fat droplets which occur as particulate inclusions in the cytoplasm are reactions which take place in or on the surface of these particles. It is the chloroplast, however, which most clearly carries on chemical processes quite different in kind from those of the cytoplasm in which the chloroplast is imbedded. Thus the typical reaction of photosynthesis, the light-induced splitting of water, is a process confined in the higher plant to chloroplasts. The terminal stages of chlorophyll synthesis as well as the synthesis of the associated carotenoid pigments appear also to occur only within the chloroplast structure. Recent work indicates that much of the active respiratory system of the plant cell may be included in the particulate structure. What then is left to the cytoplasm proper by way of biochemical function? What synthetic and what degradative reactions are typically cytoplasmic processes? We cannot yet answer this with certainty, although it seems probable that there are biochemical reactions which are cytoplasmic in occurrence and which may include among other processes the formation and transformation of the simple carbohydrates and the synthesis of particular amino acids.

The point to be stressed is this. Biochemists have long tended to treat the cell as a homogeneous mixture of catalysts and substrates, the whole capable of carrying out the manifold activities of living things. Biologists on the contrary have been deeply concerned with the description of the structures which may be observed within the cell. We now know that each cellular structure, the nucleus, the chloroplast, and the other particulate inclusions, is concerned with its own typical and characteristic aspect of the overall metabolism. The concept of the cellular granule or particle as a metabolic unit has emerged with particular clarity from work on the animal enzyme systems responsible for such processes as pyruvate or fatty acid oxidation. Respiratory pyruvate oxidation takes place (Chapter 15) through an orderly sequence of reactions involving at least fifteen different kinds of enzymes. These enzymes are not distributed randomly among the cytoplasmic proteins of the cell but are combined into one large highly organized particle. It has been known for many years that certain types of biochemical reactions, including respiration, are dependent on cellular structure and are lost when cellular structure is destroyed. Just what aspect of cellular structure is it which is essential to such a process? It now seems probable that the answer to this question is somewhat as follows. Biochemical reactions in which an orderly sequence of reactions are required frequently take place only in the presence of highly organized particles made up of the required array of enzymes. The proper functioning of this metabolic particle may also require the presence of components of the cytoplasm such as coenzymes, energy acceptors, or other enzymes. The proper functioning of a cell as a whole undoubtedly requires the appropriate functioning of many different kinds of these metabolic units, all suspended in and interacting through the same cytoplasm. In this book we shall in general talk about metabolic processes as occurring in a particular kind of cell or tissue and will not be able from sheer lack of information to define more closely the exact nature of the cellular units involved in the particular reaction. It should be borne in mind however that any full elucidation of a biochemical process will necessarily include definition of the cellular units concerned.

Enzymes. Cellular metabolism consists essentially in the chemical alteration of substrate molecules by reactions which take place to an appreciable extent only in the presence of individual and specific enzymes. It is appropriate therefore to include in this introduction some discussion of the general nature and properties of enzymes. It will be assumed that the reader of this book is acquainted with the fact that the majority of biological reactions are catalyzed by enzymes and that all enzymes thus ar isolated in pure form are protein in nature. Since each enzyme pecifically catalyzes only one reaction or one type of reaction and since he cells of many tissues are known to be able to carry out many different inds of reactions, it is clear that each cell must contain a great many diferent kinds of enzymes. Sumner and Somers have, in fact, calculated hat the animal cell may contain of the order of 1000 different enzymes. While nowhere near this number have as yet been detected in any single kind of cell or tissue, a total of several hundred different enzymes is known in all. Although in a few cases a particular enzyme may make up a moderate proportion of the total dry weight of a cell, for example phoskhatase of leaves (several per cent) or urease of jack bean (ca. 0.1%),