# WATER RELATIONS OF PLANTS AND SOILS

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# Water Relations of Plants and Soils

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# Contents

| L | HISTORICAL REVIEW                                     |    |
|---|---|----|
|   | Introduction  | 1  |
|   | Early Research  | 1  |
|   | The Work of Stephen Hales                             | 2  |
|   | The Century after Hales                               | .3 |
|   | The Second Half of the 19th Century                   | 4  |
|   | Early Plant Physiology in the United States           | .5 |
|   | The 20th Century                                      | 6  |
|   | From Osmosis to Water Potential                       | 7  |
|   | The Permanent Wilting Percentage                      | 8  |
|   | The Absorption of Water                               | 8  |
|   | Some General Concepts                                 | 8  |
|   | Plant Water Balance                                   | 9  |
|   | Soil–Plant–Atmosphere Continuum and Ohm's Law Analogy | 9  |
|   | Klebs Concept   | 9  |
|   | The Situation Today                                   | 11 |
|   | Changing Viewpoints                                   | 11 |
|   | Increasing Emphasis at the Molecular Level            | 12 |
|   | Summary   | 13 |
|   | Supplementary Reading                                 | 14 |
|   | · ·   |    |

xiii

| •    | $\circ$ . |
|------|-----------|
| vi ( | Contents  |
|      |           |

| 2 | FUNCTIONS AND PROPERTIES OF WATER       |      |
|---|---|------|
|   | Introduction                            | 16   |
|   | Ecological Importance of Water          | 16   |
|   | Physiological Importance of Water       | 17   |
|   | Functions of Water in Plants            | 19   |
|   | Constituent                             | 20   |
|   | Solvent                                 | 21   |
|   | Reactant                                | 21   |
|   | Maintenance of Turgidity                | 21   |
|   | Properties of Water                     | 21   |
|   | Unique Physical Properties              | 21   |
|   | Explanation of Unique Properties        | 24   |
|   | Bound Water                             | 28   |
|   | Isotopes of Water                       | 29   |
|   | Unorthodox Views Concerning Water       | 29   |
|   | Properties of Aqueous Solutions         | 30   |
|   | Pressure Units                          | 31   |
|   | Vapor Pressure                          | .31  |
|   | Boiling and Freezing Points             | 32   |
|   | Osmotic Pressure or Osmotic Potential   | 33   |
|   | Chemical Potential of Water             | 35   |
|   | Summary                                 | 37   |
|   | Supplementary Reading                   | 37   |
|   | Appendix 2.1: The van't Hoff Relation   | 38   |
|   | Appendix 2.2: The Chemical Potential    | 39   |
|   | Appendix 2.3: Matric Potentials         | 41   |
| 3 | CELL WATER RELATIONS                    |      |
|   | Introduction                            | 42   |
|   | Structure                               | 42   |
|   | Osmosis                                 | 47   |
|   | Water Status                            | 49   |
|   | Measuring Water Status                  | 53   |
|   | Mechanism of Osmosis                    | .57  |
|   | Changes in Water Status                 | 61   |
|   | Water Transport                         | 63   |
|   | Significance of Reflection Coefficients | . 64 |
|   | Rates of Dehydration and Rehydration    | 68   |
|   | Osmotic Adjustment                      | 71   |
|   | Water Relations of Cells in Tissues     | 75   |
|   | Summary                                 | 79   |

| 0          | ••   |
|------------|------|
| Contents   | 1)11 |
| 0011001100 | ~~~  |

| Supplementary Reading  | 80 |
|--|----|
| Appendix 3.1: Preservation of Cell Ultrastructure for Electron |    |
| Microscopy   | 81 |
| Appendix 3.2: Osmotic Potential and Dehydration                | 81 |
| Appendix 3.3: Rates of Dehydration and Rehydration of Cells    | 82 |

### 4 SOIL AND WATER

| Introduction                               | 84  |
|--|-----|
| Important Characteristics of Soils         | 84  |
| Composition and Texture                    | 84  |
| Structure and Pore Space                   | 86  |
| Soil Profiles                              | 88  |
| Soil Water Terminology                     | 89  |
| Water Potential                            | 89  |
| Field Capacity                             | 91  |
| Permanent Wilting Percentage               | 92  |
| Readily Available Water                    | 92  |
| Water Movement within Soils                | 93  |
| Infiltration                               | 93  |
| Horizontal and Upward Movement             | 94  |
| Measurement of Soil Water                  | 97  |
| Soil Water Balance                         | 97  |
| Direct Measurement of Soil Water Content   | 98  |
| Indirect Measurement of Soil Water         | 99  |
| Other Methods                              | 101 |
| Measurement of Soil Water Potential        | 102 |
| Control of Soil Water                      | 105 |
| Irrigation                                 | 105 |
| Irrigation Scheduling                      | 107 |
| Irrigation Problems                        | 109 |
| Experimental Control of Soil Water Content | 110 |
| Summary                                    | 113 |
| Supplementary Reading                      | 114 |
| ROOTS AND ROOT SYSTEMS                     |     |
| Introduction                               | 115 |
| Functions of Poots                         | 115 |

| Functions of Roots               | 115 |
|----------------------------------|-----|
| Anchorage                        | 116 |
| Roots as Absorbing Organs        | 116 |
| Synthetic Functions              | 116 |
| Roots as Sensors of Water Stress | 117 |

viii Contents

| Root Growth   | 118  |
|---|------|
| Epidermis and Root Hairs                              | 120  |
| Endodermis  | 123  |
| Secondary Growth                                      | 124  |
| Root Contraction                                      | 124  |
| Rate and Periodicity of Root Growth                   | 125  |
| Depth and Spread of Roots                             | 126  |
| Longevity of Roots                                    | 128  |
| The Absorbing Zone of Roots                           | 128  |
| Absorption through Suberized Roots                    | 130  |
| Mycorrhizae   | 130  |
| Development of Root Systems                           | 134  |
| Root-Shoot Interrelationships                         | 136  |
| Root Grafting   | 140  |
| Metabolic Cost of Root Systems                        | 142  |
| Environmental Factors Affecting Root Growth           | 143  |
| Soil Texture and Structure                            | 143  |
| Soil Moisture   | 145  |
| Soil Aeration   | 147  |
| Soil Temperature                                      | 157  |
| Root Competition                                      | 158  |
| Allelopathy   | 1.59 |
| The Replant Problem                                   | 160  |
| Biochemistry of Competition and Infection             | 160  |
| Atmospheric Conditions                                | 161  |
| Miscellaneous Effects                                 | 161  |
| Methods of Studying Root Systems                      | 162  |
| Summary   | 164  |
| Supplementary Reading                                 | 165  |
|   |      |
| THE ABSORPTION OF WATER AND ROOT                      |      |
| AND STEM PRESSURES                                    |      |
| Introduction  | 167  |
| Absorption Mechanisms                                 | 167  |
| Passive Absorption by Transpiring Plants              | 168  |
| Osmotic Absorption and Root Pressure                  | 170  |
| Relative Importance of Osmotic and Passive Absorption | 172  |
| Characteristics of Root Pressure Exudation            | 173  |
| Species Differences                                   | 173  |
| Guttation   | 176  |
|   |      |

6

|   | Stem Pressures   | 178  |
|---|--|------|
|   | Maple Sap Flow   | 170  |
|   | Uther Stem Pressures   | 181  |
|   | Latex and Oleoresins<br>Abcomption of Daw and Eog through Leaves | 181  |
|   | Restors Affecting Water Absorption through Roots                 | 182  |
|   | Efficiency of Root Systems in Absorption                         | 183  |
|   | Resistances to Water Movement in the Soil–Plant System           | 187  |
|   | Environmental Factors  | 190  |
|   | Efflux of Water from Roots and Hydraulic Lift                    | 198  |
|   | Summary  | 199  |
|   | Supplementary Reading  | 199  |
| 7 | TRANSPIRATION AND THE ASCENT OF SAP                              |      |
|   | Introduction   | 201  |
|   | The Importance of Transpiration                                  | 201  |
|   | The Process of Transpiration                                     | 204  |
|   | Evaporating Surfaces   | 204  |
|   | Driving Forces and Resistances                                   | 205  |
|   | Energy Relations   | 207  |
|   | Vapor Pressure Gradients   | 209  |
|   | Resistances to Diffusion   | 211  |
|   | Other Factors Affecting Transpiration                            | 214  |
|   | Leaves   | 214  |
|   | Disease  | 223  |
|   | Measurement of Transpiration and Evaporation                     | 223  |
|   | Measurement of Transpiration of Plants and Leaves                | 224  |
|   | Evapotranspiration from Stands of Plants                         | 230  |
|   | The Ascent of Sap  | 234  |
|   | The Conducting System  | 234  |
|   | The Mechanism of Sap Rise  | 249  |
|   | Conduction in Leaves   | 251  |
|   | Use of Xylem Sap by Parasites                                    | 253  |
|   | Summary  | 253  |
|   | Supplementary Reading  | 255  |
| 8 | STOMATA AND GAS EXCHANGE   |      |
|   | Introduction   | 2.57 |
|   | Historical Review  | 2.57 |
|   | Occurrence and Frequency   | 2.58 |

Contents

| Stomatal Functioning                             | 260 |
|--|-----|
| Guard Cells                                      | 260 |
| Stomatal Behavior                                | 262 |
| Mechanism of Stomatal Opening and Closing        | 263 |
| Factors Affecting Stomatal Aperture              | 265 |
| The Role of Light                                | 265 |
| Carbon Dioxide                                   | 267 |
| Humidity   | 268 |
| Temperature                                      | 269 |
| Wind   | 270 |
| Mineral Nutrition                                | 271 |
| Stomata and Air Pollution                        | 271 |
| Stomata and Fungi                                | 272 |
| Internal Factors Affecting Stomata               | 272 |
| Anomalous Behavior of Stomata                    | 273 |
| Cycling  | 273 |
| Heterogeneity in Stomatal Response               | 274 |
| Optimization                                     | 276 |
| Diffusive Capacity of Stomata                    | 277 |
| Bulk Flow in Leaves                              | 277 |
| Measurement of Stomatal Aperture and Conductance | 277 |
| Visual Observations                              | 279 |
| Infiltration                                     | 279 |
| Porometers                                       | 280 |
| Summary  | 281 |
| Supplementary Reading                            | 282 |

| 9 | ION TRANSPORT AND NITROGEN METABOLISM  | 1   |
|---|--|-----|
|   | Introduction                           | 283 |
|   | Ion Uptake and Transport               | 285 |
|   | Optimum Conditions                     | 285 |
|   | Effects of Dehydrating Conditions      | 290 |
|   | Nitrogen Metabolism                    | 291 |
|   | Nitrogen Fixation                      | 294 |
|   | Nitrate Metabolism                     | 298 |
|   | Protein Synthesis                      | 301 |
|   | Dehydration and Root/Shoot Signals     | 304 |
|   | Dehydration and Enzyme Activity        | 306 |
|   | Direct Enzyme Effects                  | 306 |
|   | Regulator Hypothesis of Enzyme Control | 308 |

#### x

|    |   | Contents | xi  |
|----|---|----------|-----|
|    | Summary   |          | 310 |
|    | Supplementary Reading                             |          | 312 |
| 10 | PHOTOSYNTHESIS AND RESPIRATION                    |          |     |
|    | Introduction                                      |          | 313 |
|    | Photosynthesis and Water Availability             |          | 315 |
|    | Flooding and Dehydration of Soil                  |          | 315 |
|    | Mechanisms of the Photosynthesis Response         |          | 319 |
|    | Respiration Changes                               |          | 319 |
|    | Substrate Starvation                              |          | 321 |
|    | Metabolic Inhibition                              |          | 328 |
|    | Plant Signals That Trigger the Metabolic Response |          | 332 |
|    | Acclimation                                       |          | 336 |
|    | Recovery  |          | 337 |
|    | Translocation                                     |          | 340 |
|    | Summary   |          | 341 |
|    | Supplementary Reading                             |          | 342 |
| 11 | GROWTH  |          |     |
|    | Introduction                                      |          | 344 |
|    | Growth of Single Cells                            |          | 346 |
|    | Growth in Complex Tissues                         |          | 351 |
|    | Growth-Induced Water Potentials                   |          | 353 |
|    | Gradients in Water Potential during Growth        |          | 354 |
|    | Transpiration and Growth                          |          | 358 |
|    | Growth at Low Water Potentials                    |          | 360 |
|    | Primary Signals                                   |          | 363 |
|    | Metabolic Changes                                 |          | 366 |
|    | Ecological and Agricultural Significance          |          | 372 |
|    | Summary   |          | 374 |
|    | Supplementary Reading                             |          | 375 |
| 12 | EVOLUTION AND AGRICULTURAL WATER USE              |          |     |
|    | Introduction                                      |          | 377 |
|    | Measuring Evolutionary Pressures                  |          | 378 |
|    | Environmental Limitations on Yield                |          | 380 |
|    | Water Use Efficiency                              |          | 383 |
|    | Measuring Water Use Efficiency                    |          | 387 |
|    | Drought Tolerance                                 |          | 390 |
|    | Improvement of Drought Tolerance                  |          | 391 |
|    | Water Deficits and Reproduction                   |          | 395 |

xii Contents

| Desiccation           | 398 |
|-----------------------|-----|
| Antitranspirants      | 400 |
| Summary               | 402 |
| Supplementary Reading | 403 |
| References            | 405 |
|                       | 105 |

Index

482

## Preface

Everyone who grows plants, whether a single geranium in a flower pot or hundreds of acres of corn or cotton, is aware of the importance of water for successful growth. Water supply not only affects the yield of gardens and field crops, but also controls the distribution of plants over the earth's surface, ranging from deserts and grasslands to rain forests, depending on the amount and seasonal distribution of precipitation. However, few people understand fully why water is so important for plant growth. This book attempts to explain its importance by showing how water affects the physiological processes that control the quantity and quality of growth. It is a useful introduction for students, teachers, and investigators in both basic and applied plant science, including botanists, crop scientists, foresters, horticulturists, soil scientists, and even gardeners and farmers who desire a better understanding of how their plants grow. An attempt has been made to present the information in terms intelligible to readers with various backgrounds. If the treatment of some topics seems inadequate to specialists in certain fields, they are reminded that the book was not written for specialists, but as an introduction to the broad field of plant water relations. As an aid in this respect, a laboratory manual is available with detailed instructions for some of the more complex methods (I. S. Bover in "Measuring the Water Status of Plants and Soils," Academic Press, San Diego, 1995).

We begin with a brief review of the research on plant water relations from Aristotle to the 20th century, including the development of such basic concepts as plant water balance, the soil-plant-atmosphere continuum, and the Klebs concept showing that both genetic potentialities and environmental factors

#### xiv Preface

modify growth through their effects on physiological processes and conditions. Some current questions, such as the role of roots as sensors of water stress and the increasing importance of investigations at the cellular and molecular level, are mentioned briefly in preparation for later discussion. Succeeding chapters are devoted to the unique properties of water and to cell water relations, providing an opportunity to define some of the terminology and units used in later chapters. Cell water relations are discussed in detail because they are basic to later discussions of plant water relations. Soil is discussed as a reservoir for water and a medium for root growth, root structure and growth are discussed with respect to the absorption of water and minerals, and the transport of water to the transpiring shoots is discussed in detail. Considerable attention is given to transpiration and the role of stomata in controlling it because transpiration often dominates plant water relations. Finally, we discuss the effects of water deficits on various physiological processes that control growth and yield of plants.

There is considerable cross referencing among chapters but there is also some repetition of material in various chapters. This is intended to make each chapter a fairly complete unit that can be read without excessive referral to other chapters, facilitating use of the book as a reference.

The need for a book summarizing modern views on plant water relations has been increased by the large volume of publications and the changes in viewpoint that have occurred in recent years. A number of books on plant water relations have appeared, but most of them are collections of papers on special topics. This book attempts to present the entire field of water relations in an organized manner, using current concepts and a consistent, simple terminology. Emphasis is placed on the interdependence of various processes. For example, the rate of water absorption is closely linked to the rate of transpiration by the sap stream in the vascular system, and it also is affected by resistance to water flow into roots and by soil factors affecting the availability of water. The rate of transpiration depends primarily on the energy supply, the stomatal opening, and the leaf water supply. Proper functioning of the physiological processes involved in growth requires a favorable water balance, which is controlled by relative rates of water absorption and water loss by transpiration. These complex interrelationships are discussed and described in modern terminology.

The large volume of publications in recent years makes it impossible to cite all of the relevant literature and many good papers have been omitted. Nevertheless, the bibliography is extensive enough to serve as an introduction to the literature in most areas of plant water relations research.

The present lively research activity is producing significant changes in explanations of various phenomena, and some long held views may have to be modified or abandoned. Examples of new trends are the recent emphasis on roots rather than leaves as primary sensors of water stress, the role of cell wall metabolism versus turgor in cell expansion, questions concerning the validity of water potential as a measure of plant water status, and the importance of osmotic adjustment. Even the cohesion theory of the ascent of sap is being questioned. Another new concept is the ecological importance of "hydraulic lift," or the supplying of water to shallow rooted plants by deeper rooted plants. Research at the molecular level is providing a better understanding of the reasons for such phenomena as differences in drought tolerance among species and cultivars. It also suggests the possibility of increasing plant drought tolerance by the genetic engineering of crop plants to minimize the effects of water stress.

Differences in opinion among various investigators are discussed, and in some instances the authors have indicated their preference, but it is pointed out that in many instances more research is needed before conclusions can be reached. We hope the uncertainty about some phenomena will challenge investigators to develop better explanations. Readers are reminded that so-called scientific facts often are merely the most logical explanations that can be developed from the available information. As additional research provides more information, it frequently becomes necessary to revise generally accepted explanations, and some that seem logical today may become untenable later.

This book owes more to interactions with other scientists than can be easily identified. We are indebted to our many graduate students and postdoctoral research associates and to our colleagues for their valuable suggestions. We especially acknowledge E. L. Fiscus, M. R. Kaufmann, J. S. MacFall, and C. D. Raper, Jr., for their useful comments on several chapters. We also acknowledge the assistance of Peggy Conlon in Dr. Boyer's office in typing several chapters and in preparing the bibliography, Dr. An-Ching Tang for preparing the artwork in several chapters, and the secretaries in the Duke University Department of Botany office who patiently typed and revised several chapters so many times.

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