# Contents

## Chapter 1 Contexts, Perspectives, and Principles

| Plant interactions with the atmosphere, hydrosphere, and geosphere underpin terrestrial ecosystems         | 1  |
|--|----|
| Schimizing human impact on ecosystems and<br>achieving global food security are significant<br>challenges  | 3  |
| Proximate and ultimate questions elucidate how and why plants interact with the environment                | 5  |
| Resources, stressors, and toxins affect plant biomass production and quality                               | 6  |
| Environmental factors that affect plant growth are<br>interacting but independent variables                | 10 |
| Many reference soil groups are a product of<br>interacting environmental variables                         | 10 |
| Spatial and temporal analyses provide insights into plant responses to environmental variation             | 11 |
| Plants process information about environmental<br>pariation using signaling networks                       | 14 |
| Deferences in gene expression and in the genes<br>expressed underpin a hierarchy of plant adaptations      | 14 |
| Environmental plant physiology is ecologically useful<br>in defining plant traits and niches               | 19 |
| Studying plant-environment interactions can help to<br>increase agricultural efficiency and sustainability | 20 |
| Modeling is improving our understanding of plant-  | 21 |
| Summary  | 21 |
| Further reading  | 22 |
|  |    |

## Chapter 2 Light

| <b>In plants</b> , ancient photosynthetic systems provide<br><b>the chemical</b> energy for terrestrial ecosystems | 23 |
|--|----|
| Photosystems, cytochromes, and ATP synthases   | 25 |
| Terrestrial plants have to adapt to a generally high and very variable light regime                                | 28 |
| Plants can adjust quickly to variation in PAR using non-photochemical quenching                                    | 31 |
| Plants can adjust electron flows to help them to withstand variable light intensities                              | 34 |
| PSII repair is important in plants that tolerate high light intensities  | 36 |
| Chloroplast movements can be used to adjust fairly rapidly the amount of light absorbed                            | 37 |
| Photosystems, grana, and thylakoids adapt to   |    |
| differences in light regime  | 39 |

| Leaf optical properties are adapted to long-term variation in light regimes                 | 41 |
|---|----|
| Adjustments in leaf position and plant architecture adapt plants to different light regimes | 44 |
| Photoinhibition is most severe in alpine  | 10 |
| environments  | 46 |
| Summary   | 48 |
| Further reading   | 49 |
|   |    |

### Chapter 3 Carbon Dioxide 51 CO<sub>2</sub> fixation underpins the primary production of biomass 51 Variation in the supply of CO<sub>2</sub> to plants is significant and affected by human activity 53 The regulation of rubisco activity controls CO<sub>2</sub> entry into the Calvin-Benson cycle 56 Oxygenation of RuBP decreases growth but provides rapid metabolic flexibility 58 When there is a sustained low CO<sub>2</sub> supply, C<sub>4</sub> plants maintain a high CO<sub>2</sub>:O<sub>2</sub> ratio in the vicinity of rubisco 60 C<sub>3</sub>-C<sub>4</sub> intermediates and C<sub>4</sub> plants show distinct responses to chronic differences in the environment 63 Crassulacean acid metabolism adapts plants to chronically difficult CO2-fixation conditions 66 Long-term increased CO2 levels can increase plant growth, but limiting factors can moderate this effect 69 Plant responses to increasing CO<sub>2</sub> levels will affect the hydrological cycle and Earth's climate 72 An understanding of CO<sub>2</sub> fixation by plants is important for sustainable food production and ecosystem conservation 73 75 Summary Further reading 75

## Chapter 4 Water

23

| Plant-water relations affect physiological processes from a cellular to a global scale   | 77 |
|--|----|
| Water management is vital for ensuring global food<br>security and minimizing the impact of human<br>activity on the environment | 80 |
| Water potential gradients drive water movement,<br>including transpiration in trees over 100 m tall                              | 83 |
| Short-term adjustments of resistance to water flux allow water homeostasis   | 85 |

77

#### viii CONTENTS

| water deficit   | 88  |
|---|-----|
| Extended water deficit induces changes in root growth                                       | 90  |
| Leaf adaptations aid drought survival and provide alternative ways of capturing water       | 92  |
| Succulent xerophytes are physiologically decoupled from their chronically arid environments | 94  |
| Resurrection plants cope with complete desiccation  | 95  |
| Interactions between water and other stressors provide important environmental insights     | 99  |
| Summary   | 100 |
| Further reading   | 101 |
|   |     |

103

140

# Chapter 5 Nitrogen

| Nitrogen assimilated in plants is vital for the production of biomolecules in terrestrial organisms  | 103 |
|--|-----|
| Artificially fixed nitrogen significantly affects the biosphere and atmosphere                       | 104 |
| The concentration of different forms of soil nitrogen varies significantly                           | 107 |
| Plant nitrogen-transporter uptake capacity is<br>tuned to variation in soil nitrogen supply          | 111 |
| Plants integrate nitrogen from different sources by converting it to $NH_3$ for assimilation         | 113 |
| Whole-plant physiological adjustments help to use different patterns of nitrogen supply              | 115 |
| Plants adjust their root morphology in response to shortages of nitrogen                             | 116 |
| Symbioses contribute significantly to plant nitrogen uptake in nitrogen-deficient environments       | 117 |
| Carnivorous plants are mixotrophs that can obtain nitrogen opportunistically from an erratic         |     |
| supply   | 123 |
| Summary  | 126 |
| Further reading  | 127 |
| Chapter 6 Phosphorus   | 129 |
| Phosphorus availability often controls terrestrial biomass production and ecosystem processes        | 129 |
| Current phosphorus fertilizer regimes are unsustainable, inefficient, and often polluting            | 131 |
| Phosphorus homeostasis is a key challenge for plants in terrestrial ecosystems                       | 133 |
| Plants have numerous transporters that regulate uptake and translocation                             | 135 |
| Plants can increase the availability of inorganic phosphorus and the breakdown of organic phosphorus | 136 |

Plants can adjust their root system morphology to optimize phosphorus uptake

| 131 | Chapter 8         | Temperatu          |
|-----|-------------------|--------------------|
|     | Plants are static | poikilotherms, se  |
| 133 | variation in temp | perature is a cons |

| Chapter 8 Temperature   | 175 |
|---|-----|
| Plants are static poikilotherms, so significant<br>variation in temperature is a considerable | 175 |
| Changing global temperature regimes are affecting   | 115 |
| plant growth, development, and distribution   | 177 |
| Plants detect temperature changes via physical changes in numerous biomolecules               | 180 |
| Chilling freezing and heat initiate changes in key  |     |

C 1g, I components of different signaling pathways 183

| Mycorrhizas are major adaptations for phosphorus acquisition in low-phosphorus environments | 142 |
|---|-----|
| Some species use cluster root systems to intensively mine phosphorus from the soil          | 146 |
| Carnivorous plants digest organic phosphorus using phosphatases                             | 150 |
| Summary   | 150 |
| Further reading   | 151 |
|   |     |

| <b>Chapter 7</b> | Essential and                           |  |
|------------------|---|--|
| Beneficial       | Elements                                |  |
| TT               | to see her data as in a the sail for an |  |

153

| Terrestrial plants evolved to mine the soil for an  | otembre |
|---|---------|
| ancient suite of available elements   | 153     |
| The availability of essential nutrients limits biomass production and quality in many         |         |
| ecosystems  | 156     |
| Elemental homeostasis is achieved using both<br>ion-binding compounds and transport proteins  | 157     |
| Plants adjust to a variable supply of micronutrients by overexpressing homeostatic            | 150     |
| components  | 159     |
| Beneficial elements help many plant species to  | 160     |
| cope with a wide range of abiotic stresses  | 100     |
| Sub-optimal sulfur availability can inhibit the   |         |
| compounds   | 162     |
| Potassium can limit ecosystem production, but   |         |
| its use in fertilizer has a moderate environmental impact                                     | 164     |
| Calcium deficiency can occur in a variety of<br>plants, and magnesium deficiency in a variety |         |
| of crops  | 166     |
| Adaptations of root anatomy and morphology  |         |
| deficiency  | 168     |
| Many plants use symbioses with fungi and  |         |
| changes in rhizosphere microflora to aid nutrient   |         |
| uptake  | 170     |
| Ionomics  | 171     |
| Summary   | 173     |
| Further reading   | 174     |
|   |         |
| Chapter 8 Temperature   | 175     |
| Plants are static poikilotherms, so significant variation in temperature is a considerable    |         |

CONTENTS

| In some plants, chilling temperatures can induce<br>an acclimation response based on the CBF regulon             | 184 |
|--|-----|
| Adaptation to non-optimal temperature<br>necessitates maintaining membranes in the<br>liquid-crystal state       | 186 |
| Freezing-tolerant plants produce cryoprotectants<br>and osmoprotectants  | 188 |
| Heat-tolerant plants have protein curation<br>mechanisms adapted to increase the rate of<br>protein repair       | 191 |
| Anatomical and morphological adaptations of<br>leaves aid plant tolerance of prolonged cold<br>and heat          | 194 |
| Temperature-induced physiological changes trigger developmental and phenological responses                       | 198 |
| Summary  | 199 |
| Further reading  | 199 |
| Chapter 9 Salinity   | 201 |
| Terrestrial plants are descended from freshwater algae, so saline water is generally toxic to them               | 201 |
| Plant responses to salinity are important in<br>irrigated agriculture and in salt marshes and<br>mangrove swamps | 204 |
| Exposure to salt induces osmotic and ionic stresses in plants  | 208 |
| Sodium can enter plants via symplastic and<br>apoplastic pathways, but can be removed from<br>the cytoplasm      | 211 |
| Salt-tolerant plants compartmentalize sodium,<br>and halophytes also control potassium:sodium<br>ratios          | 213 |
| At high salinity, halophytes synthesize<br>specialized metabolites in order to adapt to<br>especial challenges   | 215 |
| Salt tolerance in crops has been increased by manipulating biochemical and physiological                         | 210 |
| traits   | 217 |
| Halophytes that face severe osmotic stresses have morphological and physiological adaptations                    | 219 |
| Some halophytes use specialized organs to excrete sodium chloride from their leaves                              | 221 |
| Mangrove and salt-marsh plants tolerate<br>waterlogging and salinity   | 223 |
| Summary  | 224 |
| Further reading  | 225 |
| Chapter 10 Soil pH   | 227 |

Soil pH affects the growth of both wild and domesticated plants

227

229

Soil pH is operationally defined and human activities are affecting it on a global scale

Plant cells have multiple mechanisms for buffering cytosolic pH 233 Acid soils contain high solution concentrations of ions that are toxic to plant cells 234 Some plants resist the effects of moderate soil acidity by excluding aluminum from the cytoplasm 237 For many plants on acid soils, mycorrhizal associations increase aluminum resistance 240 On very acidic soils, some plants take up and 241 compartmentalize aluminum Basic soils are low in important nutrients and 243 induce characteristic symptoms in plants Some plants have adapted to scavenge iron, zinc, and manganese from basic soils 246 Nicotianamine aids iron homeostasis, and in 247 grasses evolved into root exudates that chelate iron Ecologically important iron and zinc deficiency responses are finding important agricultural uses 249 250 Summary Further reading 251

#### Chapter 11 Flooding

| Flooding is a significant variable in both<br>unmanaged and managed terrestrial ecosystems        | 253 |
|---|-----|
| Human activity is adversely affecting wetlands and increasing the incidence of flooding           | 255 |
| Waterlogged soils are low in oxygen and some nutrients, but high in toxins                        | 255 |
| Soil waterlogging rapidly induces hypoxia, cellular acidosis, and decreased water uptake          | 258 |
| Physiological adjustments enable some plants to withstand soil waterlogging for short periods     | 259 |
| Ethylene signaling is central to plant responses to excess water                                  | 261 |
| In many plants, waterlogging-induced hypoxia induces changes in root anatomy                      | 262 |
| Wetland plants form extensive constitutive<br>aerenchyma and adapt morphologically to<br>flooding | 266 |
| In some flooded soils, pneumatophores help<br>woody plants to aerate their roots                  | 268 |
| The adaptations of wetland plants often produce oxidized rhizospheres                             | 269 |
| Some plants can adapt to submergence of their shoots  | 271 |
| Emergent aquatic macrophytes can force oxygen<br>down through organs buried deep in anoxic mud    | 273 |
| Some aquatic macrophytes are adapted to living permanently submerged                              | 275 |
| Summary   | 275 |
| Further reading   | 276 |

ix

253

CONTENTS x

| Chapter 12                              | Inorganic Toxins  | 279        | Summary   |  |
|---|---|------------|---|--|
| A few reactive eler<br>and many non-ess | nents are essential, but they<br>sential elements can also    |            | Further reading   |  |
| be toxic                                |   | 279        | Chapter 14 Air Pol  |  |
| Human activity is                       | significantly increasing the                                  |            | Chapter 14 All Pol  |  |
| concentrations of<br>ecosystems         | inorganic toxins in the Earth's                               | 281        | that interacts with the atmosp                                    |  |
| Homeostatic mecl<br>translocation of re | nanisms control the uptake and active elements in plants      | 284        | Adverse effects of air pollution important in the twenty-first of |  |
| Exposure to inorga and reproduction     | anic toxins decreases growth<br>via physiological and genetic | 000        | The deposition of air pollutan<br>on the properties of plants an  |  |
| Amplified homeou                        | tatis mashenisms in the roots                                 | 200        | Plants can assimilate some su                                     |  |
| of some species p                       | roduce a metal-tolerant                                       |            | capacity  |  |
| physiology                              | mese from basic soils   | 292        | Direct uptake of gaseous reac                                     |  |
| Some plants have                        | the capacity to minimize the                                  |            | can affect plant growth and ed                                    |  |
| uptake of toxins fr                     | om high external concentrations                               | 295        | Semi-volatile and volatile orga<br>can be absorbed by and release |  |
| Some plants can h                       | yperaccumulate inorganic                                      |            |   |  |
| toxins in their sho                     | ots   | 296        | Chronic effects of ozone on te                                    |  |
| Chronic exposure                        | to toxins in metalliferous                                    |            | will be significant in the twen                                   |  |
| ecosystems provid                       | les some unique biological                                    | 300        | Particulates filtered by plants                                   |  |
| Control of soil to                      | plant transfer of inorganic                                   | 500        | atmosphere can affect their gi                                    |  |
| toxins is useful in                     | agriculture and   |            | Plants can be used to monitor                                     |  |
| phytoremediation                        |   | 301        | quanty  |  |
| Summary                                 |   | 303        | Summary   |  |
| Further reading                         |   | 303        | Further reading   |  |
|   |   |            |   |  |
| Chapter 13                              | Organic Toyins  | 205        | Chapter 15 Synop:   |  |
| Chapter 15                              | organic toxins  | 305        | Plant-environment interaction                                     |  |
| functional groups                       | the reactivity of many organic                                | 305        | role in determining the bound<br>effects in Earth systems         |  |
| Synthetic organic                       | compounds underpin modern                                     |            | The understanding of plant st                                     |  |
| life but can have a                     | significant environmental                                     | 000        | mechanisms can be extended  |  |
| impact                                  | ionality of a contract to bland theory                        | 308        | with other organisms  |  |
| The entry of organ                      | chemical properties   | 300        | Our understanding of the imp                                      |  |
| Organic toxine olic                     | it reactive and perhaps also                                  | 309        | variation in plant-environmen                                     |  |
| proactive stress res                    | sponses in plants   | 313        | and scale of variation  |  |
| In plant cells, man                     | y organic toxins can be                                       |            | Understanding how plant stre                                      |  |
| transformed enzym                       | natically   | 315        | will provide insights about the                                   |  |
| In some plants, or                      | ganic toxins and their  |            | interface   |  |
| transformation pro                      | oducts can be deactivated by                                  | u segos a  | Understanding plant-environ                                       |  |
| conjugation                             |   | 317        | helps us to confront global cha                                   |  |
| In some plants, co.                     | njugated organic toxins can be                                | 210        | Further reading   |  |
| Non target site he                      | rbicido registen eo con evolvo                                | 519        |   |  |
| from xenobiotic de                      | etoxification mechanisms                                      | 320        | Abbreviations list  |  |
| Target-site resistar                    | ce helps plants to adapt to                                   | Iddgborn B | Cleaning alabai terminentari                                      |  |
| catastrophic expos                      | sure to herbicides  | 323        | Glossary  |  |
| Plants enhance the                      | e bioremediation of water and                                 |            | Index   |  |
| soils contaminated                      | l with organic xenobiotics                                    | 324        |   |  |
| Manipulation of pl                      | ant tolerance of organic toxins                               | Summary    |   |  |
| is of increasing imp                    | portance  | 327        | Contraction of the second and here                                |  |

| Chapter 14 Air Pollutants  | 331 |
|--|-----|
| Plants are dependent on an extensive surface area that interacts with the atmosphere                         | 331 |
| Adverse effects of air pollution on plants will be important in the twenty-first century                     | 334 |
| The deposition of air pollutants on plants depends<br>on the properties of plants and pollutants             | 336 |
| Plants can assimilate some sulfur dioxide, but<br>anthropogenic deposition rates can exceed this<br>capacity | 337 |
| Direct uptake of gaseous reactive nitrogen species can affect plant growth and ecosystem dynamics            | 339 |
| Semi-volatile and volatile organic compounds can be absorbed by and released from vegetation                 | 342 |
| Chronic effects of ozone on terrestrial plants<br>will be significant in the twenty-first century            | 345 |
| Particulates filtered by plants from the atmosphere can affect their growth                                  | 348 |
| Plants can be used to monitor and manage air quality   | 350 |
| Summary  | 351 |
| Further reading  | 352 |

329 329

# sis and Outlook 355

| effects in Earth systems355The understanding of plant stress response<br>mechanisms can be extended by comparisons<br>with other organisms356Our understanding of the importance of<br>variation in plant-environment interactions can<br>be extended by modeling that includes the pattern<br>and scale of variation358Understanding how plant stress responses evolved<br>will provide insights about the plant-environment<br>interface359Understanding plant-environment interactions<br>helps us to confront global challenges361Further reading362Abbreviations list363Glossary365Index378   | Pla                  | ant-environment interactions play a significant<br>le in determining the boundaries of non-linear   |     |
|--|----------------------|---|-----|
| The understanding of plant stress response<br>mechanisms can be extended by comparisons<br>with other organisms356Our understanding of the importance of<br>variation in plant-environment interactions can<br>  | eff                  | fects in Earth systems  | 355 |
| Our understanding of the importance of<br>variation in plant-environment interactions can<br>be extended by modeling that includes the pattern<br>and scale of variation358Understanding how plant stress responses evolved<br>will provide insights about the plant-environment<br>interface359Understanding plant-environment interactions<br>helps us to confront global challenges361Further reading362Abbreviations list363Glossary365Index378  | Th<br>me<br>wi       | ne understanding of plant stress response<br>echanisms can be extended by comparisons<br>ith other organisms  | 356 |
| Understanding how plant stress responses evolved<br>will provide insights about the plant-environment<br>interface359Understanding plant-environment interactions<br>helps us to confront global challenges361Further reading362Abbreviations list363Glossary365Index378   | Ou<br>va<br>be<br>an | ur understanding of the importance of<br>riation in plant–environment interactions can<br>e extended by modeling that includes the pattern<br>ad scale of variation | 358 |
| Understanding plant-environment interactions<br>helps us to confront global challenges361Further reading362Abbreviations list363Glossary365Index378  | Un<br>wi<br>int      | nderstanding how plant stress responses evolved<br>Il provide insights about the plant–environment<br>terface   | 359 |
| Further reading362Abbreviations list363Glossary365Index378   | Un<br>he             | nderstanding plant-environment interactions<br>Plps us to confront global challenges  | 361 |
| Abbreviations list363Glossary365Index378   | Fu                   | urther reading  | 362 |
| Glossary 365<br>Index 378  | At                   | bbreviations list   | 363 |
| Index 378  | GI                   | lossary   | 365 |
|  | In                   | dex   | 378 |
| in off is operationally before and build build and a subset and the Second and the second sec |                      | ing, freeding, and and find the berthely significant  |     |