A. Bhattacharya

Physiological Processes in Plants Under Low Temperature Stress

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Preface

Despite increasing average temperature across the years, high temperatures are not the only threat and it is likely that plants, including our field crops, will also experience an increase in more devastating early spring frosts events. It has been reported that there are losses to many economically important crops just from freeze damage. Thus, rather than focusing only on yield gains and quality traits, our crop plants will need to be more flexible in response to changes in their environment so that farmers will get stable yield despite less predictable and more severe weather. To reach this goal, a better understanding on how the whole plant responds to changes in low temperature in the surrounding environment, beginning with how temperature is perceived and how the signal is transferred to nucleus. Plant exposed to a rapid and severe drop in temperature can suffer protoplasmic ice formation resulting in death. In summer, trees and herbaceous plants in northern latitudes cannot withstand freezing, but exposure to chilling temperatures induces hardening through a process called cold acclimation, and acclimated plants can survive winter temperatures far below freezing. Thus, many plants can increase their resistance to various stresses including heat, salt, and drought conditions in response to an elastic strain. The principle focus of this book is on the response of plants to unfavorable low temperatures and to low temperature stress.

Among various environmental stresses, low temperature is one of the important factors limiting the productivity and distribution of plants. It is well established that some of the molecular and physiological changes during cold acclimation are important for plant cold tolerance. The definition of chilling injury has been defined as low temperature damage in the absence of freezing. Freezing injury occurs when the external temperature drops below the freezing point of water. There are many plants, including many of our core agricultural crops that are susceptible to chilling injury and can be killed by their first experience of frost. There are also plants native to cold climates that can survive extremely low temperatures without injury. Crops have basic requirements for temperature to complete a specific phonological phase of growth or the whole life cycle. On the other hand, extremely high and low temperatures can have detrimental effects on the crop growth, development, and yield, particularly at the critical phonological phase. While some of crop plants are morphologically indeterminate, the rate of many phonological processes such as germination, initiation of flower, and development of fruiting bodies is controlled by temperature. The average daily temperature also plays an important role in determining the earliest date of sowing. Crops grown under open environments often pass through periods of abiotic stress during their life cycle. Such stresses many a time overlap so that the crop growth and productivity are adversely affected. Plants pass through a series of morphological, physiological, biochemical, and molecular changes in a quest to mitigate such adversities of the abiotic stresses. Crops experience periods of extreme low temperatures in many regions of the world and are exposed to limited water availability owing to either drought or disturbed water movement and uptake under low ambient temperatures.

Low temperature stress is an inevitable environmental factor that extensively affects plant growth and development. Cold stress is a significant abiotic stress which affects growth and development of crops, leading to loss of strength and lesions on the surface. It is known that temperature affects the main physiological and biochemical processes in plants. The physiological processes most affected are photosynthesis, growth, and respiration when temperatures are above or below the normal ranges of growth. In the same way, biochemical changes such as alterations in the viscosity, permeability, and fluidity of the cell membrane are produced at the enzymatic level. Low temperature stress decreases capacity and efficiency of photosynthesis through changes in gas exchange, pigment content, and chloroplast development and also declines chlorophyll fluorescence. Susceptible plants with cold temperatures have reduced growth, restricted use of precious varieties, and reduced yields. Plants use separate strategies to cope with stressful conditions and integrate a variety of physiological, metabolic, and molecular adaptations. Changes in the structure of proteins and lipid membranes assist to restore homeostasis of metabolites and are regarded as mechanisms by which cells feel cold temperatures. For its metabolic and physical function, the liquid state of the plasma membrane is a structural and functional asset. At low temperatures, the plasma membrane transitions from a liquid state to a stiff gel stage. Low temperature-mediated changes in the physical conformation of the membrane are mainly because of enhanced levels of unsaturated lipids, which increase the fluidity and stability of the membrane, enabling cells to adapt mechanically to cold.

Plant growth and crop yield are majorly affected by low temperature, soil water deficit, salt, and heavy metals. Physiological reactions to stress include wilting of the leaf, abscission of the leaf, decreased leaf region, and decreased water loss through transpiration. Detrimental impacts of stress can be decreased by osmotic modification, which helps with an active accumulation of solutes in the cytoplasm to maintain cell water balance. The use and application of plant growth regulators in agriculture have several practical examples. The plant growth regulators in this context are employed commercially. Commercial uses of auxins include prevention of fruit and leaf drop, promotion of flowering, thinning of fruit, induction of parthenocarpic fruit development, and rooting of cuttings for plant propagation, among others. Considerable success had been obtained in the application of plant growth regulators in some process of plant development such as flowering and fruit development as well as ripening, harvesting, and post-harvesting of fruits and vegetables. Tropical trees are generally induced to flower through environmental cues, whereas floral initiation of temperate deciduous trees is often autonomous. In the tropical evergreen tree, cool temperature is the only factor known to induce flowering, but does not ensure occurrence of floral initiation because there are important interactions with vegetative growth involvement of plant hormones. Those have been characterized in Arabidopsis, including floral initiation through photoperiod and temperature, and regulation by gibberellins and nitrate used

This book is intended to cover major effects of low temperature on various major aspects of physiological processes in plants through review articles. The book has seven review chapters all together. Under low temperature stress, the first issue faced by crop plants is lowering of seed germination percentage, slow growth and developmental processes, and changes in duration of phonological phases. The first review chapter deals with changes in seed **germination, growth, and phenology** under low temperature stress. Following poor germination and slow growth, plant water relations are disturbed under low temperature regime, and the second review chapter deals with **plant water relations** under low temperature stress. With lowering of plant water content and metabolic activities, the most affected physiological process is photosynthesis. The third review chapter deals with effects of low temperature stress on **photosynthesis and its associated processes**. Apart from water relationship and photosynthesis, biological nitrogen fixation, nitrogen uptake, and nitrogen assimilation are also affected by low temperature stress. In the fourth chapter, effects of low temperature stress **nitrogen metabolism** have been reviewed. Changes in photosynthetic and allied processes under low temperature stress causes changes in lipid metabolism in plants and the fifth chapter deals with **changes in lipid metabolism** in plants under low temperature stress. Changes in carbon, nitrogen, and lipid metabolism causes changes in growth and developmental processes due to the effects of plant growth regulators under low temperature condition and the sixth chapter deals with the **role of plant growth regulators** under low temperature conditions. Seventh chapter reviews the effects of low temperature on **dry matter partitioning and seed yield**. These review chapters address how knowledge of the physiological mechanisms of crops can contribute to reaching these goals.

These seven review chapters address knowledge of the physiological mechanisms of crops which can contribute to overcoming the adverse effects of low temperature. Suggestions and advice are most welcome for improvements in the chapters. The author is hopeful that this text will be of use to readers. Suggestions for any future edition from researchers, teachers, and students, who use the book, are welcomed. It is hoped that this book will serve the needs of students, faculty members, and researchers. The author sincerely hopes that the review chapters in this book will meet the requirements of postgraduate students as well as faculty members of plant physiology, and he will be glad to receive constructive criticism and suggestions from faculties.

Kanpur, Uttar Pradesh, India Amitav Bhattacharya

Contents

1 Effect of Low-Temperature Stress on Germination, Growth, and Phenology of Plants: A Review 1
1.1 Low-Temperature Stress 2
1.1.1 Chilling Injury 5
1.1.2 Freezing and Frost Injury 6
1.1.3 Physiological and Molecular Changes Under Low Temperature 7
1.2 Low Temperature and Seed Germination 10
1.2.1 Seed Priming and Germination Under Low Temperature 15
1.3 Seedling Growth Under Low Temperature 19
1.4 Root Development Under Low Temperature 23
1.5 Constraints of Environmental Temperature 26
1.5.1 Low Temperature 27
1.6 Growth and Development Under Low Temperature 30
1.6.1 Vegetative Growth 33
1.6.2 Temperature Effects on Aboveground Growth and Biomass Production 37
1.6.3 Reproductive Growth 37
1.6.4 Yield and Yield-Related Attributes 41
1.6.5 Temperature Sensitivity of Different Growth Phases 42
1.7 Response of Perennial Crops to Low-Temperature Stress 43
1.8 Mechanisms of Acclimation to Low Non-freezing Temperatures 44
1.8.1 The Role of Carbohydrates 45
1.8.2 The Role of Osmolytes 45
1.8.3 The Role of Plant Growth Hormones 47
1.8.4 Modifications to Plant Cell Membranes 48
1.8.5 The Role of Reactive Oxygen Species 49
1.8.6 Interaction(s) of Genes 50
1.8.7 Alteration of Meiotic Recombination and Somatic Mutation 54

1.9 Phenological Development 55
1.10 Temperature and Flower Induction 57
1.10.1 Effect of Temperature During Flower Maturation and Shoot Development 58
1.11 Molecular/Genetic Aspects of Flowering Response to Climate Change 64
1.12 Simulation of Phenology for Future Climate 66
References 67

2 Low Temperature Stress and Plant-Water Relationship: A Review 107
2.1 Plant and Water 108
2.2 Soil and Water 111
2.2.1 Soil Moisture Constants 111
2.2.2 Soil Temperature 114
2.2.3 Soil Water Storage and Availability to Plants 115
2.2.4 Water Transmission Characteristics 116
2.2.5 Crop Rooting Behavior and Soil Water Retention 116
2.3 Plant-Water Relations 117
2.3.1 Concept of Water Potential 121
2.3.2 Components of Water Potential 122
2.4 Water Uptake by Roots 126
2.4.1 Root Water Uptake Concepts 128
2.4.2 Water Absorption by the Roots 129
2.4.3 Root Water Uptake under Low-Temperature Conditions 130
2.4.4 Transpiration 132
2.4.5 Ascension of Water Through the Plant: Vascular System 133
2.4.6 Disruption of Water Movement 135
2.4.7 Signal Controlling Root Water Uptake Under Stress Condition 135
2.5 Plant-Water Relationship under Low-Temperature Stress 137
2.5.1 Transpiration and Transpiration Efficiency 142
2.5.2 Water-Use Efficiency 144
2.5.3 Induction of Tolerance 148
2.5.4 Low-Temperature Tolerance of Woody Plants 154
2.5.5 Approaches for Induction of Low-Temperature Stress Tolerance 155
2.5.6 Nutrient Management to Alleviate the Low-Temperature Stresses 156
2.6 Mechanism of Water Status Regulation 159
2.6.1 Morphological and Anatomical Characteristics and Water Control 160
2.6.2 Stomata Metabolism 161

2.6.3 Redox Signaling 161
2.6.4 Sugar Signaling 162
2.6.5 Control of Oxidative Stress 163
2.6.6 Control on Lipid Changes 165
2.6.7 Hormonal and Molecular Responses at Different Levels of Water Stress 165
2.6.8 Osmotic Regulation 167
2.7 Acclimation to Cold Stress 169
References 171

3 Effect of Low Temperature Stress on Photosynthesis and Allied Traits: A Review 199
3.1 Plant Metabolic Activities Under Change in Global Temperature 200
3.2 Photosynthesis Under Low Temperature 204
3.2.1 Low Temperature Stress and Chloroplast Membrane Integrity 212
3.2.2 Low Temperature Stress and Pigment System 214
3.2.3 Effect of Low Temperature on Stomata 215
3.3 Impact of Suboptimal Temperature on Photosynthesis 220
3.3.1 Photosynthesis in C4 Plants 228
3.3.2 Control of Photosynthetic Processes in C4 Plants 231
3.3.3 Thermal Acclimation of C4 Photosynthesis 233
3.4 Cellular Mechanisms Against Chilling Damage and Oxidative Stress 235
3.5 Effect of Low Temperature Stress on CO_2 Fixation 237
3.6 Effect of Low Temperature on Respiration and ATP Generation 240
3.7 Low Temperature and Photorespiratory Process 242
3.8 Cold Acclimation and Its Role in Providing Freeze Tolerance . . . 245
3.9 Low Temperature Stress-Induced Changes 248
3.9.1 Effects on Photosynthetic Pigments 248
3.9.2 Effects on Photosystems 249
3.9.3 Effects on Gas-Exchange Characteristics 251
3.9.4 Effects on Activities of Key Photosynthetic Enzymes 252
3.10 Improving Photosynthetic Capacity Through Photosynthetic Related Genes or Transcription Factors 253
3.10.1 Transfer of C4 Genes/Traits to C3 Plants 254
3.10.2 Role of Mitogen-Activated Protein Kinases (MAPKs) in Photosynthesis 255
3.11 Strategies to Ameliorate Cold Stress and Improve Photosynthesis 256
3.12 Management Strategies Against Low Temperature Stress 257
3.12.1 Selection and Breeding Strategies 257

3.12.2 Agronomic and Physiological Measures 259
3.13 Conclusion and Future Prospects 262
References 263

4 Low-Temperature Stress and Nitrogen Metabolism in Plants: A Review 299
4.1 Low-Temperature Stress and Metabolic Response in Plants 300
4.2 Nitrogen Cycle 304
4.2.1 Nitrogen Fixation 305
4.2.2 Decomposition 306
4.2.3 Nitrification 306
4.2.4 Denitrification 307
4.2.5 Biogeochemical Linkage of Nitrogen and Carbon 308
4.2.6 Soil Organic Matter 309
4.2.7 Perturbations and Nitrogen and Carbon Biogeochemistry 310
4.2.8 Organic Nitrogen 311
4.2.9 Mineralization 312
4.2.10 Biological Nitrogen Fixation 312
4.2.11 Nitrogen Fixation in Nonleguminous Plants 315
4.3 Factors Influencing Biological Nitrogen Fixation in Legumes . . . 317
4.3.1 Temperature 317
4.3.2 Soil Water Status 318
4.3.3 Nitrogen Concentration in the Root Zone 320
4.3.4 Carbon Demand for Fixation 321
4.3.5 Seasonal Regulation of Biological Nitrogen Fixation 322
4.3.6 Changes in Nitrogen Fixation with Plant Growth Stage 322
4.3.7 Influence of Nitrate on Nodulation 322
4.3.8 Influence of Nitrate on Nitrogenase Activity 323
4.4 Nitrogen Assimilation 323
4.4.1 Nitrate Reduction 324
4.4.2 Ammonia Assimilation 332
4.5 Cold Acclimation and Tolerance to Freezing Stress 335
4.5.1 Cold Acclimation 335
4.5.2 Physiological and Metabolic Responses to Low Temperature 337
4.5.3 Inducible Response 342
4.5.4 Nitrogen and Amino Acid Metabolism 343
4.5.5 Protein Metabolism 344
4.5.6 Free Amino Acids 345
4.5.7 Role of γ-Aminobutyric Acid in Cold and Frost Tolerance 348

4.5.8 Exogenous Application of Amino Acid Under Temperature Stress 349
4.5.9 Enzyme Variation 351
4.5.10 Protein Content 352
4.5.11 Genetic Analysis of Cold Acclimation 352
4.6 Protein Synthesis 353
4.6.1 Types of Proteins 353
4.6.2 Protein Synthesis 359
4.7 Chilling Stress and Potential Management Opportunities 363
4.7.1 Plant Responses to Chilling and Drought Stresses 363
4.7.2 Molecular Responses 365
4.7.3 Management Strategies 367
4.7.4 Exogenous Diethyl Aminoethyl Hexanoate Ameliorates Low-Temperature Stress 371
References 372

5 Lipid Metabolism in Plants Under Low-Temperature Stress: A Review 409
5.1 Biological Role of Lipids in Plants 410
5.2 Lipids in Plants 412
5.3 Importance of Lipid Metabolism to Cold Stress 416
5.3.1 Role of Cytosolic Lipid Droplets in Stress Response 419
5.3.2 Role of Triacylglycerol in Stress Response 420
5.3.3 Lipid Antioxidant and Galactolipid Remodeling Under Low Temperature 421
5.3.4 Low-Temperature Stress and Free Fatty Acids 422
5.4 Effect of Low-Temperature Stress on Different Plants 423
5.4.1 General Effects of Chilling Temperature (Between 20 and 0 °C) on Plant Physiology 424
5.4.2 General Effects of Freezing Temperature (Below 0 °C) on Plant Physiology 424
5.4.3 Rapeseed (*Brassica napus*) 425
5.4.4 Potato (*Solanum tuberosum*) 427
5.4.5 Wheat (*Triticum aestivum*) 428
5.4.6 Rice (*Oryza sativa*) 428
5.4.7 Sorghum (*Sorghum bicolor*) 429
5.4.8 Soybean (*Glycine max*) 429
5.4.9 Food Legumes 430
5.4.10 Adzuki Beans (*Vigna angularis*) 431
5.4.11 Strawberry (*Fragaria virginiana*) 431
5.4.12 Sugarcane (*Saccharum officinarum*) 432
5.4.13 Tobacco (*Nicotiana tabacum*) 433
5.4.14 Coffee (*Coffea arabica*) 433
5.4.15 Cucumber (*Cucumis sativa*) and Fig Leaf Gourd (*Cucurbita ficifolia*) 435

5.4.16 Zoysiagrass . . . 435
5.5 Roles of Lipid Signaling in Stress Responses . . . 436
5.5.1 Role of Lipid as Signaling Molecule During Stress Response . . . 437
5.5.2 Role of Phosphatidic Acid in Signaling . . . 438
5.5.3 Role of Free Fatty Acid in Signaling . . . 439
5.5.4 Role of Sphingolipids in Signaling . . . 439
5.5.5 The Signal Transduction of Membrane Lipids Under Cold Stress . . . 440
5.6 Role of Lipid in Mitigating the Low-Temperature Stress . . . 442
5.6.1 Effects of Cold Stress on Membrane Permeability . . . 443
5.6.2 Effects of Cold Stress on Membrane Lipid Peroxidation . . . 444
5.6.3 Effects of Cold Stress on Membrane Lipid Component . . . 444
5.6.4 Effect of Cold Stress on Membrane Remodeling . . . 445
5.6.5 Effects of Cold Stress on Membrane Lipid Unsaturation . . . 446
5.7 Mechanism of Temperature Adaptation . . . 447
5.7.1 *cis*-Unsaturated Fatty Acids and Membrane Fluidity . . . 450
5.7.2 Low-Temperature Effect on Lipids of Cyanobacteria . . . 451
5.7.3 Low-Temperature Effects on Lipids of Higher Plants . . . 452
5.7.4 Low-Temperature Stress in Field and Forage Production . . . 453
5.7.5 How Low Temperature Is Perceived? . . . 454
5.8 Cold Stress: Symptoms, Sensing, and Strategy . . . 455
5.8.1 Lipid Profiling Under Cold Stress . . . 458
5.8.2 Role of Unsaturated Fatty Acids to Low-Temperature Stress . . . 459
5.8.3 Lipid Metabolism of Horticultural Products . . . 460
5.8.4 Characterization of Cold Stress Responses . . . 463
5.9 Metabolic Changes During Cold Stress and Cold Acclimation . . . 464
5.9.1 Role of Triacylglycerol in Plant Stress Response . . . 468
5.9.2 Effect of Exogenous Lipids on Cold Acclimation and Fatty Composition . . . 472
5.10 Lipid Biosynthesis Under Low-Temperature Stress in Plants . . . 473
5.10.1 Temperature-Induced Lipid Pathway Adjustments in Plants . . . 475
5.10.2 Glycerolipid Response to Cold and Freezing Temperature . . . 478
5.10.3 Triacylglycerol Biosynthesis . . . 479
5.11 Lipid Hydrolysis Under Low-Temperature Stress . . . 481
References . . . 484

6 Plant Growth Hormones in Plants under Low-Temperature Stress: A Review . . . 517
6.1 Plant Growth Hormones . . . 518
6.2 Classes of Plant Growth Hormones . . . 521
6.2.1 Abscisic Acid . . . 522
6.2.2 Auxins . . . 523
6.2.3 Gibberellins . . . 524
6.2.4 Cytokinins . . . 525
6.2.5 Ethylene . . . 526
6.2.6 Brassinosteroid . . . 526
6.2.7 Jasmonates . . . 527
6.2.8 Salicylic Acid . . . 528
6.2.9 Strigolactones . . . 528
6.2.10 Polyamines . . . 529
6.3 Importance and Use of Plant Growth Hormones . . . 530
6.3.1 In Vitro Plant Tissue Culture . . . 534
6.4 Physiological Responses in Plants to Low Temperature . . . 535
6.4.1 Classification of Plants under Low Temperature . . . 541
6.5 Role of Different Growth Hormones on Growth and Yield . . . 543
6.6 Effect of Low Temperature on the Activity of Plant Growth Hormone . . . 549
6.6.1 Abscisic Acid and Low-Temperature Stress . . . 550
6.6.2 Role of Auxins under Cold Stress . . . 551
6.6.3 Brassinosteroids and Low-Temperature Stress . . . 552
6.6.4 Salicylic Acid and Low Temperature . . . 552
6.6.5 Gibberellic Acids and Low Temperature . . . 554
6.6.6 Cytokinins and Low-Temperature Stress . . . 555
6.6.7 Jasmonic Acid and Low-Temperature Stress . . . 556
6.6.8 Thiourea and Low-Temperature Stress . . . 556
6.7 Role of Growth Hormones in Plants under Low Temperature . . . 557
6.7.1 Effect on Plant Architecture . . . 558
6.8 Mechanism of Cold Tolerance and Role of Growth Hormones . . . 559
6.9 Metabolic Effects of Growth Hormones for Abiotic Stress Tolerance . . . 566
6.9.1 Abscisic Acid . . . 567
6.9.2 Auxins . . . 568
6.9.3 Cytokinins . . . 568
6.9.4 Ethylene . . . 570
6.9.5 Gibberellins . . . 571
6.9.6 Brassinosteroids . . . 572
6.9.7 Jasmonates . . . 573
6.9.8 Salicylic Acid . . . 574
6.9.9 Strigolactones . . . 576
6.9.10 Polyamines . . . 577

6.10 Strategies for Crop Improvement through Growth Hormones under Low-Temperature Stress 578
6.10.1 Compatible Organic Solutes 579
6.10.2 Plant Growth Regulators 582
6.10.3 Exogenous Use of Organic Compounds 583
6.10.4 Agronomic Management 585
1-Naphthaleneacetic Acid 586
References 587

7 Effect of Low Temperature on Dry Matter, Partitioning, and Seed Yield: A Review 629
7.1 Dry Matter Partitioning 630
7.2 Dry Matter Partitioning and Yield in Cereals 633
7.3 Dry Matter Partitioning and Yield in Grain Legumes 635
7.4 Dry Matter Partitioning and Yield in Grain Oilseed Crops 637
7.5 Carbon Partitioning and Acclimation to Environmental Stress . . . 640
7.6 Factors Affecting Dry Matter Partitioning 641
7.6.1 Energy Investment in Seeds, Fruits, and Storage Organs 642
7.6.2 Breeding 643
7.6.3 Determinacy 644
7.6.4 Effects of Pests and Diseases 645
7.6.5 Temperature Extremes During Flowering and Grain Filling 645
7.6.6 Pre-/Post-anthesis Water Use 646
7.6.7 Water Use, Soil Mineral Nitrogen, and Harvest Index 648
7.6.8 Hormonal Control of Photosynthate Partitioning 649
7.6.9 Plant Growth and Carbon Partitioning 650
7.6.10 Effects of Nitrogen Partitioning 651
7.7 Exploring G × E Interaction for Increasing Harvest Index in Crops 652
7.8 Management Techniques to Increase Harvest Index 655
7.9 Carbon Partitioning in Different Plant Parts 657
7.10 Temperature Effects on Dry Matter Partitioning 659
7.10.1 Low temperature (Chilling) Stress 661
7.10.2 Low Root Temperature and Dry Matter Production . . . 661
7.11 Dry Matter, Grain Yield, and Harvest Index Values for Crops . . . 663
7.11.1 Wheat 664
7.11.2 Barley 664
7.11.3 Sorghum 664
7.11.4 Rice 664
7.11.5 Maize 665
7.11.6 Chickpea 665
7.11.7 Field Pea 665

7.11.8 Faba Bean 666
7.11.9 Lentil 666
7.11.10 Lupin 666
7.11.11 *Brassica* Crops 667
7.11.12 Sunflower 668
7.12 Seed Yield 668
7.13 Low Temperature and Seed Yield 670
7.14 Factors for Yield Gaps 671
7.15 Physiological Traits Associated with Improvement in Seed Yield 672
7.15.1 Time to Flower and Plant Height 673
7.15.2 Dry Matter Production and Its Partitioning 674
7.15.3 Main Yield Components 676
7.15.4 Associations Between Yield Attributes 677
7.15.5 Yield Potential Versus Stress Adaptation: GE Interaction 678
7.16 Changing Climate and Seed Yield 679
7.17 Effect of Temperature Stress on Seed Yield 685
7.18 Physiological Avenues for Increasing Yield Potential 688
7.18.1 Increasing Radiation-Use Efficiency 688
7.18.2 Biomass Increase 691
7.18.3 Phenological Adjustment 691
7.18.4 Plant Responses to Low Temperature 692
7.18.5 Reproductive Development Under Low Temperature 692
7.18.6 Yield Components and Yield Under Low Temperature 693
7.18.7 Traits for Tolerance to Abiotic Stress 693
7.18.8 Combination of Stress 694
7.19 Engineering for Cold Stress Tolerance in Crop Plants 695
7.19.1 Role of Proteomics in Crop Stress Management 697
7.19.2 Chilling Acclimation 699
References 700

About the Author

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Effect of Low-Temperature Stress on Germination, Growth, and Phenology of Plants: A Review

1

Abstract

Climatic models indicated that in this century, both average temperatures and extreme events frequency will increase in the Mediterranean basin. These changes are expected to have a great impact on agriculture in general and on crop phenology in particular. Great progress has been made in understanding the responses of plants to abiotic stress. There are inherent physical, morphological, and molecular limitations to the plant's ability to respond to stress. Plant responses to abiotic stress are dynamic and complex. Among the various abiotic stresses, low temperature adversely affects germination, normal plant growth, development, and phonological events. Consistent with the increasing temperatures, crop development is expected to be faster; thus, phenological stages will be reached early, and the length of the growth period of crops with determinate cycle (i.e., cereals, grapevine, etc.) will be shorter. These impacts, together with the higher risk to have extreme climate events during sensitive phonological phases, may have strong negative effects on final yield and on yield quality. The actual impact of phonological change needs to be assessed for specific crop environment combinations, providing the basis to formulate feasible adaptation options to climate change. In other terms, the simulated changes in phenology cannot be interpreted without considering the environmental context in which a species lives. For winter crops, the effect of predicted prolonged summer drought periods and heat weaves for the next decades may be smoothed or prevented due to the faster development that will allow escaping these and then avoiding reduction in final yields. In contrast, crops, whose growing cycle takes place in summer time, are likely to experience a severe reduction of final yield as the result of increased frequency of extreme climatic events and a reduced time for biomass accumulation to yield.

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Keywords

Chilling and freezing injury · Seed germination and seedling growth under low temperature · Root development in low temperature · Growth and development under low temperature · Perinea crops and low temperature · Mechanism of low-temperature acclimation · Low-temperature and phonological development · Temperature and flower initiation · Molecular and genetic aspect of flowering during climate change

1.1 Low-Temperature Stress

Temperature is one of the major environment variables affecting the growth, development, and yields of crops, especially the rate of development (Luo 2011). Crops have basic requirements for temperature to complete a specific temperature phenophase or the whole life cycle. On the other hand, extremely high and low temperatures can have detrimental effects on crop growth, development, and yield, particularly at the critical phenophase. While some of the crop plants are morphologically indeterminate, the rate of many phenological processes such as germination, floral initiation, and development of fruiting bodies is controlled by temperature (Hearn and Constable 1984). Average daily temperature also plays an important role in determining the earliest date of sowing; defining season length, which can influence both yield potential and yield quality (Bange et al. 2008; Bauer et al. 2000; Dong et al. 2006a); and determining where a particular crop can be produced sustainably. Luo et al. (2014a), working with cotton phenology under temperature regimes and using general circulation model, pointed out that there will be less impact of cold temperatures on earlier growth and potentially a longer growing season that can improve crop yield. However, there will be more incidences of hot days impacting growth and more rapid crop development in late phonological stages.

Among various environmental stresses, low temperature is one of the most important factors limiting the productivity and distribution of plants. Low temperatures, defined as low but not freezing temperatures (0–15 °C), are common in nature and can damage many plant species. In order to cope with such conditions, several plant species have the ability to increase their degree of freezing tolerance in response to low, non-freezing temperatures, a phenomenon known as cold acclimation. It is well established that some of the molecular and physiological changes that occur during cold acclimation are important for plant cold tolerance (Zhu et al. 2007). Low temperature or cold stress is another major environmental factor that often affects plant growth and crop productivity and leads to substantial crop losses (Xin and Browse 2000; Sanghera et al. 2011). Chilling stress results from temperatures cool enough to produce injury without forming ice crystals in plant tissues, whereas freezing stress results in ice formation within plant tissues. Plants differ in their tolerance to chilling (0–15 °C) and freezing (<0 °C) temperatures. Both chilling and freezing stresses are together termed low temperature or cold stress: the damage due to cold stress can range from chilling injury and freezing injury to suffocation and heaving. In general, plants from temperate climatic regions are considered to be chilling-tolerant to variable degrees, and their freezing tolerance can be increased by exposing to cold, but non-freezing, temperatures; this process is known as cold acclimation. However, generally, the plants of tropical and subtropical origins are sensitive to chilling stress and lack this mechanism of cold acclimation (Sanghera et al. 2011). Low temperature may affect several aspects of crop growth, viz., survival, cell division, photosynthesis, water transport, growth, and finally crop yield.

Temperature is the main factor that determines the geographic distribution of organisms, in the context of both latitudinal and altitudinal gradients of thermal niche occupation (Hochachka and Somero 2002). The thermal range of the biosphere is broad and varies from +400 °C of the hydrothermal winds operating at the bottom of the oceans (Jupp and Schultz 2000) to −94.3 °C of the surface air of the Dome Argus, Antarctica (Scambos 2017). No organism has the capacity to withstand the full range of biosphere temperatures. Thus, life is limited to a much narrower temperature range, from −20 to +122 °C (Deming 2002; Fitter and Hay 2002). Specifically, the existence of plants is limited to an approximate thermal range of −10 to +60 °C, defined by the freezing point of intracellular water and the temperature of protein denaturation (Fitter and Hay 2002; Źróbek-Sokolnik 2012; Taiz and Zeiger 2015). This survival range can be exemplified by the woody trees of regions, such as Alaska, northern Canada, Europe, and Asia, which are highly adapted to intracellular water freezing (Taiz and Zeiger 2015), and by plants from arid regions such as cacti and agaves, which tolerate high diurnal temperatures that exceed 60 °C (Nobel 2003). The importance of temperature as a physical factor on the distribution of organisms is a consequence of its direct influence on molecular (DNA, proteins) or supramolecular (membranes, chromosomes) structures, which results from merely a thermodynamic effect (Ruelland and Zachowski 2010; Knight and Knight 2012). These changes are usually fast; therefore, changes in the ambient temperature can be quickly detected by cell organelles, triggering specific pathways of biochemical and molecular responses in each of these cell compartments and making up an integrated cell response to temperature changes (Ruelland and Zachowski 2010).

Minimum survival temperatures vary according to the natural environment, acclimation state, and growth form of the plant and, in many cases, may vary among different organs and tissues within the plant (Larcher 2003). Tissues of chilling-intolerant lowland tropical plants that never experience subfreezing temperatures can be killed at temperatures between 0 and 10 °C, while tissues that can survive these temperatures but not freezing temperatures are referred to as chilling-tolerant. Plants from regions with episodic or persistent seasonal temperatures below 0 °C are usually described using pairs of the words *frost*, *freezing*, or *cold* and *tolerant*, *hardy*, or *resistant*, with the terms *tolerance*, *hardiness*, and *resistance* used to describe the phenomenon of survival at low temperature. Low-temperature tolerance can be classified as follows:

- Moderate low temperature, −20 to –40 °C
- Intermediate low temperature, −40 to –60 °C
- Extreme low temperature, <–60 °C

More systematic exploration of low-temperature tolerance requires quantitative estimates of minimum survival temperatures for whole plants or plant tissues. These can be assessed by a wide variety of methods. Typically, whole plants or plant parts are exposed to a range of subfreezing temperatures in a temperature-controlled chamber, although some studies have applied low-temperature treatments to intact plants in the field (Taschler et al. 2004). Low-temperature stress results in various observable or measurable symptoms of injury, including death of whole plants, visible necrosis of specific tissues and organs, or less obvious cellular symptoms that can be detected by vital staining, osmotic responsiveness, chlorophyll fluorescence, or measurement of relative electrolyte leakage in affected tissues. The latter gives a useful measure of injury because a general symptom of cellular injury is a loss of semipermeability of the plasma membrane, which then results in the release of intracellular electrolytes (Steponkus 1984). These kinds of measurements are often used to determine a minimum survival temperature or construct temperature response curves and interpolate the temperature, resulting in 50% plant or tissue death, LT_{50}. Under natural conditions, trees may be subject to more complex environmental conditions than those imposed in laboratory tests, such as prolonged low temperature, repeated freezing and thawing, solar warming followed by rapid cooling, or light stress, so that laboratory estimates may not correspond to minimum survival temperatures in the field. In general, laboratory estimates of LT_{50} or minimum survival temperature are somewhat to well below the minimum temperatures encountered in the sampling location or natural range of the species in question. When different methods are directly compared, they often give generally similar estimates of LT_{50} (Burr et al. 1990), and LT_{50} values based on the same or similar methods can be compared among different tissues and species or track relative changes in low-temperature tolerance over time.

Low- and high-temperature stress are becoming the major researchable issues for agricultural scientists worldwide due to the challenges imposed by changing climate (Shah et al. 2011). Based on the ability to occupy thermal niches, organisms can be classified into psychrophiles, which live and reproduce at temperatures below +15 °C, some of which maintain metabolic activities at temperatures up to −20 °C; mesophiles, which live comfortably between +15 and +40 °C; and thermophiles, which have their best performance from +50 to +60 °C (moderate thermophiles). The term *hyperthermophiles* (or extreme thermophiles) has been used for organisms with optimal growth rates above +80 °C (Counts et al. 2017; Dalmaso et al. 2015; Pikuta et al. 2007). This classification is based mainly on studies of microorganisms that live in environments with extremely low and high temperatures (e.g., Antarctica and geothermal regions, respectively). Therefore, the thermal limits of each class may vary according to the temperatures that different groups of organisms can tolerate (Nievola et al. 2017).

Crops grown under open environments often pass through periods of abiotic stress during their life cycle. Such stresses many a time overlap, so crop growth and productivity is adversely affected. Plants pass through a series of morphological, physiological, biochemical, and molecular changes in a quest to mitigate such adversities of the abiotic stresses (Hussain et al. 2018). A lot of work reports the adaptive responses of crop plants to different abiotic stresses, wherein emphasis has been laid on individual stress factors (Jongdee et al. 2002; Chinnusamy et al. 2007; Nejad et al. 2010; Basu et al. 2016; Wang et al. 2016; Anjum et al. 2017). Crops experience periods of extreme low temperatures in many regions of the world (Ruelland et al. 2009; Wang et al. 2016) and are exposed to limited water availability owing to either drought or disturbed water movement and uptake under low ambient temperatures (Shinozaki et al. 2003; Zhang et al. 2004; Beck et al. 2007). Studies show that primarily chilling and drought pose a similar impact on stomatal development and leaf growth; nevertheless, the mechanisms of drought-induced changes in some physiological processes are quite different than those induced by chilling (Deng et al. 2012). Plants may exhibit common molecular and physiological responses on exposure chilling and drought (shared response); others may be specific to a given stress factor (Atkinson et al. 2013; Sewelam et al. 2014). In general, chilling stress thermodynamically declines the kinetics of several physiological as well as metabolic processes occurring in plants (Ruelland et al. 2009; Hussain et al. 2016). It severely reduces the rate and uniformity of germination, hampers seedling vigor, and delays ontogenetic plant development (Cruz and Milach 2004; Oliver et al. 2007), resulting in severe crop yield losses (Ruelland et al. 2009).

1.1.1 Chilling Injury

Chilling injury occurs when chilling-sensitive plant species are stored at temperatures above the freezing point of tissues but lower than 15 °C. Chilling-sensitive plants are those that are sensitive to chilling and suffer damage when exposed to it. Chilling temperatures effects on plants in temperate climates lead to a reduction or complete crop failure due to either direct damage or delayed maturation (Lukatkin et al. 2012). Even a small drop in temperature can cause visible damage to chilling-sensitive plants. The most noticeable visual symptoms of chilling injury in herbaceous plants are leaf and hypocotyl wilting (Frenkel and Erez 1996), which often precedes the appearance of infiltration (water-saturated areas) (McMahon et al. 1994); the appearance of surface pits and large cavities (Cabrera et al. 1992; Frenkel and Erez 1996); discoloration of leaves and internal tissues (Yoshida et al. 1996a; Tsuda et al. 2003); accelerated aging and rupture of chilled tissues; slow, incomplete, or uneven ripening (Dodds and Ludford 1990); deterioration of the structure and flavor (Ventura and Mendlinger 1999); increased susceptibility to decay (Cabrera et al. 1992); and, in the case of prolonged chilling, leaf necrosis and plant death (Frenkel and Erez 1996). Potential symptoms of chilling injury are surface lesions; water-soaking of tissues; water loss; desiccation or shrivelling; internal discoloration; tissue breakdown; failure of fruit to ripen, or uneven or slow ripening; accelerated senescence and ethylene production; shortened storage or shelf life; compositional changes; loss of growth or sprouting capability; and wilting and increased decay due to leakage of plant metabolites, which encourage growth of microorganisms, especially fungi (Lukatkin et al. 2012). Seeds of chilling-sensitive plants do not germinate at temperatures below 10–15 °C (Ismail et al. 1997) and by this parameter can be divided into two main groups (Markowski 1988). The seeds of the first group (representatives, Solanaceae and pumpkin) are not damaged during imbibitions at chilling temperatures. With temperature increase they grow normally, but initiation of root growth leads to underdeveloped root tip tissue, tissue necrosis after the root tip, and damage to the cortex or stele (Jennings and Saltveit 1994). The second group includes plants whose seeds are particularly sensitive to low temperatures during imbibitions and may not germinate at low temperatures: beans, soybeans, chickpeas, corn, and cotton (Zemetra and Cuany 1991). A characteristic effect of chilling temperatures on chilling-sensitive plants is growth slowing, more pronounced in susceptible species and varieties in comparison with the tolerant species (Venema et al. 1999a). In addition, there is a delayed development and lengthening of the growing season (Skrudlik and Kościelniak 1996). At the same time, flowering rate and fruit and seed filling are reduced (Skrudlik and Kościelniak 1996; Lejeune and Bernier 1996).

Chilling injuries occur above the freezing point (0 °C), and plants of tropical and subtropical origin are most susceptible. Injured foliage appears purple or reddish and sometimes wilted. Chilling injury can be obvious or invisible. Chilling can delay crop blooming, cause direct damage, or reduce plant vigor. Chilling injury happens often in tropical and subtropical plants grown in subtropical areas but can happen in native, temperate forest plants as well, depending on critical temperatures, duration of low temperature, temperature changes, age, hydration status of plants, and time of year. Plants can drop damaged leaves, become wilted, produce misshapen new growth, display discolored foliage, or even have whole or portions of the plants dying. The damage may also be unseen by the naked eye but manifest later as delayed blooming or stunted growth.

1.1.2 Freezing and Frost Injury

Freezing and frost injuries occur at or below the freezing point (0 °C). Freeze damage happens during an advection freeze when an air mass with temperatures below freezing moves into an area and displaces warmer air, causing the temperature of plants to become low enough for ice crystals to form inside their cells. Frost damage happens during a radiation freeze. This occurs on clear nights without wind when plants radiate more heat to the atmosphere than they received. This creates a temperature inversion where cold air close to the ground gets trapped by moist, warmer air above it. When the air temperature at ground level nears or drops below freezing, the plant's temperature becomes colder than the surrounding air temperature, causing ice crystals to form on the surface of the foliage, stems, and flowers. During both frost and freeze injury, ice crystals form in plant tissues, dehydrating cells and disrupting/rupturing plant membranes. This causes physical damage as expanding rigid ice crystals puncture cellular membranes and dehydration damage as all water within plant tissues freezes, rendering it inaccessible for photosynthesis. Once physical damage has occurred, it manifests itself as brown to yellow necrosis, often leading to portions of the plant or the entire plant dying. Cold hardy species are less susceptible to freezing and frost injury.

1.1.3 Physiological and Molecular Changes Under Low Temperature

Plants respond and survive under stress conditions by bringing changes at the molecular and cellular levels as well as at the biochemical and physiological levels (Xin and Browse 2000). Low-temperature stress inhibits seedling establishment, effecting early growth stages of rice and resulting in poor crop maturation. In order to gain stable rice production, cold tolerance at the seedling stage is an important character. One of the most effective ways to avoid the low-temperature damage is to develop cold-tolerant genotype (Lou et al. 2007). Mineral nutrition acquisition and assimilation are strongly influenced by both high- and low-temperature stress in plants (Rivero et al. 2006). Some essential nutrients such as nitrogen, sulfur, phosphorus, magnesium, and calcium are structurally important for the proteins, nucleic acids, chlorophylls, certain secondary metabolites, and defense-related micro- and macromolecules, while others have both structural and functional roles (Epstein and Bloom 2005; Taiz and Zeiger 2006).

As a result of exposure to low temperatures, many physiological and biochemical cell functions have been correlated with visible symptoms (wilting, chlorosis, or necrosis). Often these adverse effects are accompanied by changes in cell membrane structure and lipid composition (Matteucci et al. 2011), cellular leakage of electrolytes and amino acids, a diversion of electron flow to alternate pathways (Seo et al. 2010), alterations in protoplasmic streaming, and redistribution of intracellular calcium ions (Knight et al. 1998). It also involves changes in protein content and enzyme activities (Ruelland and Zachowski 2010) as well as ultrastructural changes in a wide range of cell components, including plastids, thylakoid membranes and the phosphorylation of thylakoid proteins, and mitochondria (Zhang et al. 2011a, b). Brief exposures to low temperatures may only cause transitory changes, and plants generally survive. However, prolonged exposure to stress causes plant necrosis or death. To overcome stresses generated by exposure to low non-freezing temperatures, plants can trigger a cascade of events that cause changes in gene expression and thus induce biochemical and physiological modifications that enhance their tolerance (Zhu et al. 2007). This phenomenon is known as chilling or cold acclimation.

In addition to reduced plant growth and productivity (Tommasini et al. 2008), the nutrient uptake behavior of plants is also impaired under chilling temperature (Xu and Huang 2006) and soil water-deficit stress (Hu et al. 2007). Temperature affects the physiochemical and microbial processes in soils, which may modify the plant-nutrient relationships (Yan et al. 2012). Poor root system of plants under chilling stress reduces the uptake of several nutrients, including nitrogen, phosphorus, and potassium (Domisch et al. 2002; Yan et al. 2012). Under chilling stress, shoot growth of maize seedlings was reduced by the direct effect of low temperature on shoot meristems and by restricted supply of nutrients via roots (Hund et al. 2007). Farooq et al. (2009b) concluded that reduced root length, low hydraulic conductance, poor root branching, and thicker root axis under chilling stress lead to reduced mineral nutrient uptake in plants. However, the variations in such effects may arise based on plant species, stress period, physiological plant growth stage, or the frequency of changing the nutrient solutions.

Low temperatures have an effect on mineral nutrition of plants. Absorption of ions by roots is difficult, as well as their movement in the aboveground parts of plants. The distribution of nutrients between the plant organs is disrupted, with general decrease in nutrient content in the plant. Chilling of plants leads to a decrease in the activity of nitrate reductase, reduction in the nitrogen incorporation in the amino acids and proteins, and a drop in the proportion of organic phosphorus and an increase in inorganic phosphorus content (Zia et al. 1994), which is a consequence of a breach of phosphorylation and enhanced decomposition of organic phosphorus compounds. Mechanisms to reduce the absorption of nutrients by chilling temperatures include depression of respiration and/or oxidative phosphorylation, impaired enzymatic transport systems associated with conformational protein changes in membranes, changes in membrane potential, reduction of supply of ATP to H^+-transporting ATPase, as well as lowering the permeability coefficients for ions.

Chilling injury is thought to be caused by loss of membrane fluidity, detected as membrane phase changes below the critical temperatures in sensitive taxa. Biochemical consequences include altered reaction rate of membrane-bound enzymes, ion leakage, and loss of compartmentalization. The resulting metabolic imbalances lead to cellular injury. Chilling may produce lesions in the thylakoid membranes of the leaf chloroplasts and result in lowered photosynthesis. Most tropical plants are susceptible to chilling injury, whereas temperate zone plants are less often affected. The economic losses caused by chilling injury to temperate-zone horticultural crops are difficult to estimate, but are not thought to be great. Fruit of some horticultural crops, e.g., apples, tomatoes, and cucumber, suffer breakdown disorders in or following low-temperature storage that are attributed to chilling injury. Some vegetable transplants are also believed to be prone to chilling injury at low temperature if not properly hardened when transplanted from the greenhouse. Freezing injury, which affects survival and production of many plants, is of great economic importance to temperate zone horticulture and will be dealt with exclusively in the remainder of this review. Various types of freezing injury result from untimely frosts in the spring and autumn or from extremely low temperatures in midwinter. Some susceptible plants, such as corn and beans, are killed the moment they freeze (1–4 °C), whereas some hardy woody perennials can tolerate temperatures as low as –60 °C when they are fully acclimated. Most horticultural crops are damaged at temperatures between these extremes. The hardiness level varies with taxa, plant organ, and season.

The major adverse effect of cold stress in plants has been seen in terms of plasma membrane damage. This has been documented due to cold stress-induced dehydration (Steponkus et al. 1993). The plasma membrane is made up of lipids and proteins. Lipids in the plasma membrane are made up of two kinds of fatty acids: unsaturated and saturated fatty acids. Unsaturated fatty acids have one or more double bonds between two carbon atoms, whereas saturated fatty acids are fully saturated with hydrogen atoms. Lipids containing more saturated fatty acids solidify faster and at temperatures higher than those containing unsaturated fatty acids. Therefore, the relative proportion of these two types of fatty acids in the lipids of the plasma membrane determines the fluidity of the membrane (Steponkus et al. 1993). At the transition temperature, a membrane changes from a semi-fluid state into a semicrystalline state. Cold-sensitive plants usually have a higher proportion of saturated fatty acids in their plasma membrane. Therefore, cold-sensitive plants have a higher transition temperature. On the contrary, cold-resistant plants have a higher proportion of unsaturated fatty acids and hence a lower transition temperature. The agricultural crops which can withstand even during the freezing temperatures of late spring or early fall frost can be used more successfully for cultivation during cold stress. Therefore, selection of low-temperature-tolerant crops is very important for the sustainability of agriculture.

It has been noticed that cold-induced ice formation is the real cause of plant damage. Ice formation in plant tissues during cold stress leads to dehydration. Ice is formed in the apoplastic space of a plant tissue because that has relatively lower solute concentration. It is known that the vapor pressure of ice is much lower than water at any given temperature. Therefore, ice formation in the apoplast establishes a vapor pressure gradient between the apoplast and surrounding cells. As a result of this gradient, the cytoplasmic water migrates down the gradient from the cell cytosol to the apoplastic space. This adds to existing ice crystals in the apoplastic space and causes a mechanical strain on the cell wall and plasma membrane, leading to cell rupture (Olien and Smith 1977; Uemura and Steponkus 1997). In addition to the well-established harmful effect of cold stress alterations in lipid composition of the biomembranes, affecting their fluidity (Welti et al. 2002), certain additional factors may also contribute to damage induced by cold stress. This includes synthesis and accumulation of compatible solutes, synthesis of cold acclimation-induced proteins (Shinozaki and Yamaguchi-Shinozaki 2000), changes in the carbohydrate metabolism (Frankow-Lindberg 2001), and the boosting of the radical scavenging potential of the cells (Hernández-Nistal et al. 2002; Baek and Skinner 2003). Taken together, cold stress results in loss of membrane integrity, leading to solute leakage. Further, cold stress disrupts the integrity of intracellular organelles, leading to the loss of compartmentalization. Exposure of plants to cold stress also causes reduction and impairing of photosynthesis, protein assembly, and general metabolic processes. Recently, attempts have also been directed toward analyzing the effect of cold stress on the whole plant metabolome. Metabolic profiling of *Arabidopsis* plants revealed that cold acclimation increases 75% of the 434 analyzed metabolites (Cook et al.

2004; Kaplan et al. 2004). However, metabolite profiles in *Arabidopsis* do not appear to correlate with cold acclimation capacity (Hannah et al. 2006). The role of such metabolites in plants has been known as osmoprotectants. In addition to their role as osmoprotectants and osmolytes, certain metabolites induced during cold acclimation might act as signals for reconfiguring gene expression (Yadav 2010). For example, cold stress induces the accumulation of proline, a well-known osmoprotectant. Cold stress affects virtually all aspects of cellular function in plants. One of the major influences of cold stress-induced dehydration is membrane disintegration. Such changes caused by cold stress adversely affect the growth and development of plants.

Oxidative stress is crucial in relation to chilling-induced injuries in plants (Srivalli et al. 2003; Hussain et al. 2016). Chilling stress exacerbates reactive oxygen species production in plants' cell. Excess production and the accumulation of reactive oxygen species causes oxidative damage at cellular level, disrupts cellular membranes, and leads to enzyme inactivation, protein degradation, and ionic imbalance in plants (Baier et al. 2005; Tarchoune et al. 2010). The reactive oxygen species disturb the cellular macromolecules, including DNA, and hence may cause deletion of bases due to alkylation and oxidation, which are linked with various physiological and biochemical disorders in plants (Tuteja and Tuteja 2001). Plants possess a highly efficient and sophisticated antioxidative defense system to control the overproduction of reactive oxygen species (Hussain et al. 2016). The reactive oxygen species-induced damages and disruption of cellular homeostasis are alleviated by the action of different enzymatic (e.g., catalase, superoxide dismutase, peroxidase, glutathione reductase, glutathione peroxidase) and nonenzymatic (e.g., ascorbic acid, carotenoids, α-tocopherol, and glutathione content) antioxidants (Gill and Tuteja 2010; Chen et al. 2016; Hussain et al. 2016). In plants, the levels of reactive oxygen species are regulated by their production rate as well as the extent of their detoxification by enzymatic and/or nonenzymatic antioxidant systems. Mechanism of reactive oxygen species production and its scavenging by high antioxidative capacity has been associated with tolerance of plants to abiotic stresses (Gill and Tuteja 2010).

1.2 Low Temperature and Seed Germination

Germination is the process by which a plant grows from a seed. Germination can be thought of in a general sense as anything expanding into greater being from a small existence or germ, a method that is commonly used by many seed germination projects. Germination is the growth of a plant contained within a seed; it results in the formation of the seedling. The seed of a vascular plant is a small package produced in a fruit or cone after the union of male and female sex cells. All fully developed seeds contain an embryo and, in most plant species, some store of food reserves, wrapped in a seed coat. Some plants produce varying numbers of seeds that lack embryos; these are called empty seeds, which never germinate. Dormant seeds are ripe seeds that do not germinate because they are subject to external environmental conditions that prevent the initiation of metabolic processes and cell growth.

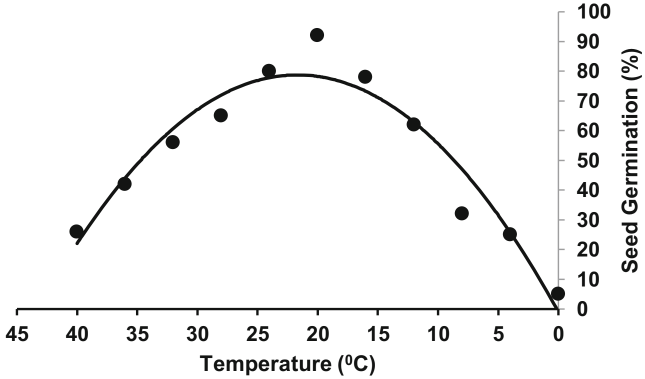

Fig. 1.1 Effect of temperature on seed germination

Since seed germination is one of the most critical stages in the life cycle of plants, the differences in germination time have important effects on plant growth, competitiveness, and reproduction, particularly for annuals in arid areas (Kos and Poschlod 2010; Akiyama and Agren 2013; Lu et al. 2016).

Low temperature is one of the main abiotic stresses affecting the growth, development, and spatial distribution of plants (Sun and Huang 2011) and tends to reduce and delay the germination rate of seeds and even causes germination failure (Wang et al. 2008). However, most desert plants such as *Salsola affinis* (Wei et al. 2007; Luo et al. 2014b), *Salsola korshinskyi* (Li et al. 2012), *Lepidium perfoliatum* (Yang et al. 2015), *Haloxylon ammodendron* (Tian 2014), *Anabasis elatior* (Han et al. 2011), and *Anabasis aphylla* (Peng et al. 2018) are highly adaptable to cold environments and can thus germinate under such conditions. Seed germination is sensitive to environmental condition. Seed germination can occur only in response to specific combinations of environmental cues present in the field such as temperature regime, precipitation, or light (Donohue et al. 2010), although after dormancy is fully broken, seeds of many species can germinate over a wide range of conditions (Yi et al. 2019). Temperature requirement for dormancy break and germination have been the focus of much seed ecology research (Baskin and Baskin 2014; Finch-Savage and Leubner-Metzger 2006). Under proper conditions, the seed begins to germinate, and the embryonic tissues resume growth, developing toward a seedling. Seed germination depends on both internal and external conditions. The most important external factors include temperature, water, oxygen, and sometimes light or darkness (Raven et al. 2005). Various plants require different variables for successful seed germination. Often this depends on the individual seed variety and is closely linked to the ecological conditions of a plant's natural habitat. For some seeds, their future germination response is affected by environmental conditions during seed formation; most often these responses are types of seed dormancy.

Cold stress generally results in poor germination (Fig. 1.1), stunted seedlings, yellowing of leaves, withering, and reduced tillering. The effects of cold stress at the reproductive stage of plants delay heading and result in pollen sterility, which is

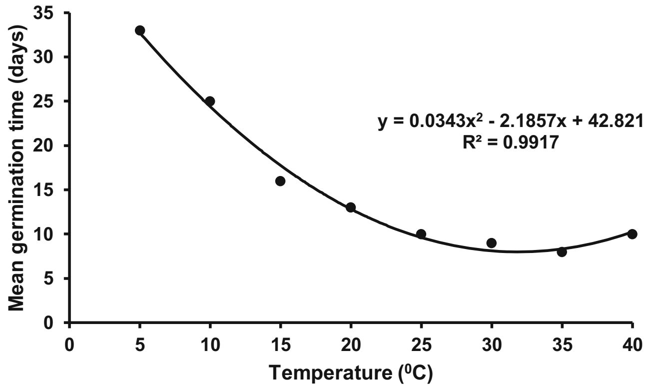

Fig. 1.2 Effect of temperature on the time of germination

thought to be one of the key factors responsible for the reduction in grain yield of crops (Suzuki et al. 2008). Appropriate time for sowing wheat will change in accordance to environmental as well as soil temperature (Rashed Mohassel and Koochaki 2000). Wheat seeds germinate well in temperatures above 4 °C and budding occurs sooner. Minimum temperature for the bud production was about 2 °C and near 0 °C in mid-winter wheat, with the best and most suitable temperatures ranging from 8 to 10 °C and the maximum temperature ranging from 20 to 22 °C (Khodabandeh 2003). Germination stage is sensitive to soil temperature because the absorption seed needs water by enzymatic activity or is breathing (Voorhees et al. 1981). Germination and growth before emergence normally is controlled by soil temperature (Hegarty 1973). According to Macduff and Wild (1986), 3–9 °C is the optimum temperature for turnip root growth in terms of length and number. Barley root length increased with increasing temperature in the thermal range of 3–25 °C after 20 days of germination (Zabihi-e-Mahmoodabad et al. 2011). Abbasal-Ani and Hay (1983) reported that root systems of seedlings of barley, oats, rye, and wheat are shorter at low temperatures (5 °C) than at high temperatures (15 and 25 °C) and the rate of growth is also fast. Davidson (1969) has reported that temperature has an effect on the growth allocation between shoots and roots. Chilling injury is a serious problem during germination and early seedling growth in many plant species. The optimum temperature range for germination of rice seed lies between 20 and 35 °C, with 10 °C being the minimum critical value below which rice does not germinate (Yoshida 1981). There are many reports on positive correlation between germination at low temperature and root development at an early stage and between the germination and seedling establishment (Nahar et al. 2012). Angadi et al. (2000a, b) observed that the number of days to 50% germination in *Brassica napus* was only 3 days at 8 °C, which was nearly 13 days at 2 °C. It has been demonstrated that under low-temperature regimes, the rate of seed germination is low, or, in other words, the number of days taken for seed germination is higher under low temperature as compared to normal temperature (Fig. 1.2). There have been reports about the low rate of germination. This low-temperature effect was more pronounced in *Brassica rapa*, because at 2 °C, emergence was less than 50%, even after 20 days of sowing (Angadi et al. 2000a, b). Buriro et al. (2011) reported that the increase in temperature significantly enhanced germination and related traits in wheat cultivars. All the wheat varieties germinated well (80–97%) sown at 10–30 °C. The maximum seed germination vigor index occurred at 20–30 °C, and these temperature regimes were identified as optimum for wheat seed germination. The delay in germination percentage and the reduced germination percentages were observed in *Gossypium hirsutum* at low temperature below 20 °C (Krzyzanowski and Delouche 2011). In *Triticum aestivum*, the germination is drastically hampered at temperature below 8–10 °C (Zabihi-e-Mahmoodabad et al. 2011). The optimum germination temperature differs by species. Seed germination of *Hosta sieboldiana* occurs over a range of temperature, from 10 to 30 °C, but the germination rate is most rapid at 25–30 °C (Kanazawa et al. 2015). The optimum germination temperature of *Hosta plantaginea* is 25 °C, but the germination percentage is very low (<25%, Oh et al. 2003).

Rice seed germination and some physiological parameters during seed germination are affected by low temperature (Xiaochuang et al. 2017; Kuk et al. 2003; Wang et al. 2018). Low temperature (19–20 °C) results in a reduction in photosynthetic parameters and affects antioxidant enzyme activity and membrane lipid peroxidation (Rao et al. 2019). A previous study suggested that the difference in high air temperature and soil temperature could affect carbohydrate metabolism in plants (Xu and Huang 2000). Increasing the root-zone temperature has a positive effect on plant development (Beauchamp and Lathwell 1967). Root growth is affected by various soil temperatures (McMichael and Burke 1998), and root temperature significantly affects root growth and function (Arai-Sanoh et al. 2010). Additionally, soil temperature significantly affects root vigor, root proline content, and malondialdehyde concentration (Bai et al. 2017). Soil temperature also affects photosynthesis (Wu et al. 2012). Thus, high or low temperature during the day or at night in the air or in the soil as well as high- or low-temperature irrigated water for rice plants could result in different growth responses in rice plants (Li et al. 2019).

In chickpea (*Cicer arietinum* L.), cold temperature (<15 °C) at emergence reduces seed germination with low vigor. In sensitive genotypes, cold temperature causes whole plant necrosis and plant death (Devasirvatham et al. 2015). Genotypic differences in chickpea was identified in Australia, and field screening for cold tolerance during the late vegetative stage was done by exposing them to −7.4 °C for 3 weeks (Malhotra and Singh 1991), and cold-tolerant genotypes were identified, which showed improved establishment under low temperatures (Wery et al. 1994). Seeds from different species and even seeds from the same plant germinate over a wide range of temperatures. Seeds often have temperature range within which they will germinate, and they will not do so above or below this range. Many seeds germinate at temperatures slightly above 16–24 °C, while others germinate just above freezing, and still others germinate only in response to alternations in temperature between warm and cool. Some seeds germinate when the soil is cool (between −2 and 4 °C), and some when the soil is warm (24–32 °C). Some seeds require