

J. Derek Bewley • Kent J. Bradford
Henk W.M. Hilhorst • Hiro Nonogaki

Seeds

Physiology of Development, Germination
and Dormancy, 3rd Edition

 Springer

Contents

1	Structure and Composition	1
1.1	Introduction	1
1.2	Seed Structure.....	2
1.2.1	Embryo.....	3
1.2.2	Non-embryonic Storage Tissues	5
1.2.3	Testa (Seed Coat)	6
1.3	Seed Storage Reserves.....	7
1.3.1	Carbohydrates	9
1.3.2	Oils (Neutral Lipids)	14
1.3.3	Proteins.....	16
1.3.4	Phytin	22
1.3.5	Other Constituents.....	23
	Useful Literature References.....	24
2	Development and Maturation	27
2.1	Fertilization	27
2.2	Embryogeny and Storage Tissue Formation	28
2.2.1	Embryonic Tissues	29
2.2.2	Endosperm.....	30
2.2.3	Testa (Seed Coat)	34
2.3	Regulation of Seed Development.....	36
2.3.1	Plant Hormones.....	36
2.3.2	Embryo Polarity and Patterning	38
2.3.3	ABA Content and Sensitivity to ABA During Development	41
2.3.4	Regulation of the Seed Maturation Program.....	43
2.3.5	Epigenetic Control of Endosperm Development	46
2.3.6	Testa Development and Its Interaction with the Endosperm and Embryo.....	48
2.3.7	Somatic Embryogenesis and Apomixis	50

2.4	Germinability During Development.....	52
2.4.1	Ability to Germinate During Development.....	52
2.4.2	Precocious Germination: Vivipary and Preharvest Sprouting	55
2.4.3	Role of Preharvest Drying in Development of Germinability.....	57
2.5	Maturation Drying and the “Switch” to Germination	60
2.5.1	The Acquisition of Desiccation Tolerance.....	60
2.5.2	Protective Mechanisms Associated with Drying	61
2.5.3	Gene Expression Changes Upon Rehydration	67
2.6	Late Maturation Events and Seed Drying	69
2.6.1	Physiological Maturity Versus Harvest Maturity	71
2.6.2	Seed Development and Seed Quality	73
2.6.3	Maturation Drying and Biophysical Aspects of Dry Seeds	75
	Useful Literature References.....	81
3	Synthesis of Storage Reserves	85
3.1	Assimilates for Grain and Seed Filling	85
3.1.1	Sources of Nutrients for Storage Reserve Synthesis	86
3.1.2	Import of Nutrients into the Developing Seed	88
3.1.3	Factors Affecting Seed Production and Quality	92
3.2	Deposition of Reserves Within Storage Tissues.....	96
3.2.1	Starch Synthesis	100
3.2.2	Synthesis of Polymeric Carbohydrates Other than Starch	105
3.2.3	Oil (Triacylglycerol) Synthesis	106
3.2.4	Storage Protein Synthesis.....	114
3.2.5	Phytin Synthesis	125
3.2.6	Modifications of Non-storage Compounds to Improve Nutritional Quality.....	128
	Useful Literature References.....	129
4	Germination.....	133
4.1	Seed Germination: Definition and General Features.....	133
4.2	Measurement of Germination.....	136
4.3	Imbibition	141
4.3.1	Uptake of Water from the Soil	141
4.3.2	Phase I, Imbibition and Imbibitional Damage	143
4.3.3	Phase II, The Lag Phase.....	149
4.3.4	Phase III, Completion of Germination	150
4.3.5	Kinetics of Imbibition	151
4.4	Respiration: Oxygen Consumption and Mitochondrial Development	153
4.4.1	Pathways and Products.....	153
4.4.2	Respiration During Imbibition and Germination	153

4.4.3	Mitochondrial Development and Oxidative Phosphorylation	155
4.4.4	Respiration Under Low Oxygen Conditions.....	157
4.5	RNA and Protein Synthesis.....	160
4.5.1	Transcriptomes of Dry and Germinating Seeds.....	161
4.5.2	Proteomes of Germinating Seeds.....	164
4.6	The Completion of Germination.....	166
4.6.1	Embryo Growth Potential Versus Enclosing Tissue Constraints in Radicle Emergence.....	166
4.6.2	DNA Synthesis and Cell Division (Cell Cycle).....	173
4.7	Priming and the Enhancement of Germination.....	175
	Useful Literature References.....	179
5	Mobilization of Stored Reserves.....	183
5.1	Seedling Growth Patterns.....	183
5.2	Mobilization of Stored Reserves.....	185
5.3	Stored Oligosaccharide Catabolism.....	188
5.4	Pathways of Starch Catabolism.....	189
5.4.1	Synthesis of Sucrose.....	191
5.5	Mobilization of Stored Starch in Cereal Grains.....	192
5.5.1	Synthesis and Release of α -Amylase and Other Hydrolases from the Aleurone Layer.....	192
5.5.2	Starch Breakdown and the Fate of the Products of Hydrolysis.....	194
5.5.3	Hormonal Control of Starch Mobilization.....	196
5.5.4	Programmed Cell Death of the Aleurone Layer and Other Tissues.....	202
5.6	Mobilization of Stored Carbohydrate Reserves in Dicots.....	203
5.6.1	Starch-Storing Non-endospermic Legumes.....	203
5.6.2	Hemicellulose-Storing Endospermic Legumes.....	204
5.6.3	Hemicellulose-Containing Seeds Other than Legumes.....	207
5.7	Stored Triacylglycerol Mobilization.....	208
5.7.1	Mobilization of TAGs from Oil Bodies.....	212
5.7.2	Role and Formation of the Glyoxysome.....	213
5.7.3	Utilization of the Products of TAG Catabolism.....	218
5.8	Storage Protein Mobilization.....	218
5.8.1	Protein Mobilization During Germination.....	219
5.8.2	Protein Mobilization Following Germination of Cereals.....	221
5.8.3	Protein Mobilization Following Germination of Dicots.....	224
5.8.4	Protease Inhibitors.....	228
5.8.5	Utilization of Liberated Amino Acids in Dicot Seedlings.....	229
5.9	Phytin Mobilization.....	232
5.10	Control of Reserve Mobilization in Dicots.....	234
5.10.1	Regulation in Endospermic Dicots.....	235
5.10.2	Regulation in Non-endospermic Dicots.....	236
	Useful Literature References.....	244

6 Dormancy and the Control of Germination	247
6.1 Dormancy: Its Biological Role.....	248
6.2 Categories of Dormancy.....	249
6.3 Mechanisms of Dormancy.....	251
6.3.1 Blocks to Germination Within the Embryo.....	251
6.3.2 Blocks to Germination by the Covering Layers.....	254
6.4 Embryonic Inadequacy: The Causes	259
6.4.1 Energy Metabolism of Dormant Seeds	259
6.4.2 Genetic Aspects of Dormancy	261
6.5 The Environment in Dormancy Inception	262
6.6 The Release from Dormancy.....	266
6.6.1 Perception, Signaling, and Role of Hormones with Respect to Dormancy and Germination	266
6.6.2 After-Ripening	276
6.6.3 Low Temperatures (Chilling)	278
6.6.4 Other Effects of Temperature on Dormancy	281
6.6.5 Light	282
6.6.6 Dormancy Release of Seeds with Impermeable Coats	288
6.6.7 Breaking of Dormancy by Chemicals	290
Useful Literature References.....	295
7 Environmental Regulation of Dormancy and Germination.....	299
7.1 Seed Dispersal and Burial	300
7.1.1 The Soil Seed Bank.....	300
7.2 Environmental Control of Germination.....	302
7.2.1 Water	303
7.2.2 Temperature.....	311
7.2.3 Light	317
7.2.4 Nitrate.....	323
7.2.5 Oxygen and Other Gases.....	324
7.2.6 Other Chemicals.....	326
7.3 Secondary Dormancy and Seasonal Variation.....	330
7.3.1 Dormancy Cycling	330
7.3.2 Dormancy Cycling: Mechanisms and Modeling.....	332
7.4 Influences of Plant Life Cycle, Distribution and Origin on Germination	335
7.4.1 Plant Distribution	335
7.4.2 Seasonal and Flowering Interactions Affecting Dormancy.....	336
Useful Literature References.....	338
8 Longevity, Storage, and Deterioration	341
8.1 Ancient Seeds	342

8.2	Longevity of Seeds in Storage.....	346
8.2.1	Patterns of Seed Viability Loss During Storage.....	347
8.2.2	Temperature, Moisture Content, and Seed Longevity.....	351
8.2.3	Other Factors that Affect Seed Viability During Storage	354
8.3	Seed Storage and Conservation.....	356
8.3.1	Short-Term Storage	357
8.3.2	Long-Term Genetic Conservation: Ex Situ Seed Gene Banks.....	358
8.3.3	Long-Term Genetic Conservation: In Situ Centers of Diversity.....	362
8.4	Mechanisms and Consequences of Deterioration in Seeds.....	363
8.4.1	Deterioration Mechanisms in Stored Seeds	364
8.4.2	Consequences of Storage on Germination	367
8.5	Mechanisms of After-Ripening in Dry Seeds	368
8.6	Recalcitrant Seeds	370
	Useful Literature References.....	374
	Glossary of Species Names and their Nomenclature	377
	Index.....	381