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Chapter 1

Challenges Facing the Forest Industry in Relation to Seed Dormancy and Seed Quality

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Abstract

Artificial regeneration of forests through planting requires high quantities of quality seeds for growing vigorous seedlings. These seedlings are raised in nurseries, where germination capacity (GC) and speed are the most important germination parameters. Germination performance is enhanced by prescribing species-specific dormancy-breaking treatments to individual seedlots in bare-root and container nurseries. For most conifer species in British Columbia, the dormancy-breaking treatments and germination conditions have been worked out, but fine-tuning and optimization could improve germination capacity and speed of germination. Implications of inter- and intra-species variations in germination behaviour and seed quality and their influence on the development of unintentional directional selection of specific genotypes are discussed. The potential of molecular and genomics approaches to understand the underlying biology of seed germination-related problems is also discussed.

Key words: Nursery, Stratification, Germination capacity, Germination speed, Climate change, Dormancy

1. Introduction

Seeds of any plant species are produced to ensure the establishment and survival of future generations. In forestry, seeds are needed for natural regeneration after natural disturbances or harvesting, and seedlings are grown in nurseries for artificial regeneration and afforestation. Seed genetic quality and physiological attributes, such as vigour, viability, and germination behaviour, are important for artificial regeneration through the production of healthy seedlings. Seedling production failure is often associated with economic losses. Therefore, it is desirable to maximize seed utilization efficiency by converting every seed sown to a seedling.

The literature is vast in the area of general seed biology, and several books are available with detailed information on basic

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aspects of seed physiology and the biology of seed dormancy and germination (1–5). We also refer the reader to several other books that are more specific to tree seeds and their ecology (6–8).

In this chapter, we outline the implications of seed biology attributes, such as germination behaviour and dormancy, in particular, on seedling production in the forest nursery industry and highlight the challenges caused by these biological constraints. In British Columbia (BC), Canada, the nursery industry produces, on average, over 200 million seedlings yearly for reforestation programmes on Crown and private forest land (9). The BC regeneration programme has a large economic impact, considering the intensive cascading activities that must follow seedling production, such as planting, tending, and the maintenance of a competition-free environment until the legislated "free-to-grow" state is reached and seedlings attain the required 3-m height. On average, roughly 50% of the raised seedlings originate from natural stand seed collections while the remaining are grown from orchard seed with various levels of genetic gain, depending on the species and breeding zone (10).

Most of the trees grown in British Columbia for reforestation are conifers. Therefore, we emphasize the seed characteristics of conifers. We describe the different types of seed dormancy and how these affect nursery operations, highlighting the evolutionary mechanisms leading to seed dormancy. Further, seed quality, as represented by the proportion of seeds that germinate after dormancy-breaking treatments, has a direct impact on maximum germination capacity (GC). Also important is the ability of the germinated seeds to undergo vigorous early post-germinative growth leading to emergence. Germination and early growth capacity are probably the most important characteristics of a seedlot for nursery operations, and they have a strong economic impact on the profit margin of a nursery; however, germination promptness (known as lag time) is also important since it is associated with crop uniformity and the amount of energy used to maintain a favourable germination environment. As most conifers are very heterogeneous and often show high levels of genetic variation in most seed traits, dormancy and germination are no exception (6). The observed genetic variation in seed attributes of conifers, in turn, places even more complications on nurseries in order to account for and accommodate these differences in seed germination behaviour. We describe the magnitude of these effects and illustrate how the nursery industry copes with these added challenges. At the conclusion of the chapter, we outline how molecular biology and its present and emerging tools can be used to address some of the problems that the forest nursery industry is facing in light of challenges associated with seed dormancy and seed quality.

2. Seed Pretreatments

In some provinces in Canada, seed extraction, processing, sanitation treatment, testing, storage, and even dormancy-breaking treatments are carried out by provincial seed centres while in others, this responsibility falls to licensees responsible for reforestation or individual tree nurseries (B. Wang, pers. comm.). To prevent seed or seedling losses, damaging seed-borne pathogens must be eliminated. These pretreatments represent a sound preventative measure and are particularly important prior to exposing the seeds to a warm and moist environment. Kolotelo et al. (11) review the current knowledge and practices of seed sanitation.

Of equal importance to seed sanitation is the application of proper dormancy-breaking treatments, which are effective for multiple seedlots. Again, in many cases, this falls into the responsibility of individual nurseries and special care must be taken to ensure that these treatments are followed as prescribed (see below). A fact requiring special attention is that seeds that are ready to be germinated may be more susceptible to damage during handling or storage, and inadvertent desiccation of seeds prior to sowing must be avoided. Using sound sanitation management and appropriate dormancy-breaking treatments ensures that seeds reach their potential germination capacity given a favourable germination environment.

3. Seed Dormancy

Dormancy is the inability of a viable and healthy seed to germinate under otherwise suitable conditions. These conditions include sufficient water and oxygen, and suitable temperature and light quality or intensity. Generally, there are two types of dormancy recognized: endogenous and exogenous (5). These have also been referred to as embryo dormancy and coat-enhanced dormancy, respectively (4). In endogenous dormancy, conditions within the embryo prevent germination; in exogenous dormancy, structures "outside" of the embryo, such as the megagametophyte or seed coat, prevent the emergence of the radicle, in some cases, by imposing mechanical restraint. There are many classes and subclasses of dormancy (for complete coverage, see Baskin and Baskin (5)), but for the purpose of this chapter, the details of dormancy and how it may be overcome are relevant to many if not most conifers of the temperate and boreal zones. Seeds of some conifer species, such as the true firs (*Abies* spp.), yellow-cedar, and western white pine, are deeply dormant at maturity. For yellow-cedar (*Callitropsis nootkatensis*

(D. Don) Oerst.) (formerly known as *Chamaecyparis nootkatensis* ([D.Don] Spach)), the megagametophyte is the major seed tissue that imposes dormancy (12). For seeds of western white pine (*P. monticola* Dougl. ex D. Don.), both the testa and the megagametophyte contribute to the inhibition of germination of mature dormant seeds (13, 14). Nonetheless, factors within the embryo appear to contribute to some extent in seeds of both conifer species. Regardless of the general category of seed dormancy, there are several mechanistic factors that impose and maintain dormancy of conifer seeds. For yellow-cedar, mechanical restraint of the megagametophyte and the biosynthesis/action of inhibitors (particularly ABA) in the embryo and seed tissues appear to be the predominant factors. In seeds of western white pine, ABA also plays a pivotal role. Here, a change in ABA flux, i.e. in the relative capacity of seeds to affect ABA biosynthesis versus ABA catabolism, is a key controller of the dormancy-to-germination transition.

Conifers that require dormancy-breaking treatment refinements to fine-tune and optimize germination behaviour include the deeply dormant true firs (*Abies* spp.) and whitebark pine (*Pinus albicaulis* Engelm.) (Kolotelo, pers. comm.).

4. Dormancy-Breaking Treatments

There is an adaptive significance of seed dormancy in tree species that must survive winter and cold temperatures. This is related to ensuring that a seed does not germinate unless an extended period of favourable growth conditions are met (15). Most seeds of northern hemisphere conifers mature in the early fall and if germination occurs soon thereafter, this would be potentially fatal for the newly sprouted seedling. To avoid this survival bottleneck, an evolutionary safety mechanism, such as the need for a prolonged period of moist chilling (to mimic cold, wet conditions), has evolved. However, it is paramount that following dormancy-breaking treatments, favourable conditions for germination must be met so that germination occurs successfully and is synchronous within the population. Applying a uniform dormancy-breaking treatment across a seedlot enhances the chances for higher and prompt germination.

Recommended times of the moist-chilling or “stratification” treatments (from the original placement of seeds between layers or strata of moist materials, such as cloth, sand, or peat (11)) vary in length (ranging from 0 to 150 days) for most northern conifer species. Generally, imbibed seeds are placed at temperatures around 5°C for the prescribed period for each species. However, within-species variation is evident in germination behaviour due to genetic variation in levels of dormancy and germination parameters (16–18) (see also Farmer (6) for a more complete review). Genetic variation

Table 1
Moist chilling requirements for seeds of British Columbia trees and other boreal, north-temperate trees

Species	Soak period (h)	Moist chilling (d)	Germination temperature[a] (°C)	Additional comments	References
Pseudotsuga menziesii	24	21	30–20		(11)
Larix occidentalis	24	21	30–20		(11)
L. laricina		30–60	30–20		(5)
Pinus contorta, *P. ponderosa*	24	28	30–20		(11)
P. monticola	336	98	30–20		(5)
P. albicaulis		90–120	30–20		
P. banksiana		0–7	30–20		(5)
Tsuga heterophylla, *T. mertensiana*	24	28	20–20		(11)
Abies grandis	48	28	30–20		(11)
A. amabilis, *A. grandis*, *A. lasciocarpa*	48	56	30–20		(11)
A. balsamea		28	30–20		(5)
Chamaecyparis nootkatensis	48	84	30–20	Footnote[b]	(11)
Thuja plicata	0	0	30–20		(11)
Picea spp. (*P. glauca and glauca × engelmannii hybrids*, *P. sitchensis*)	24	0	30–20		(11)
P. mariana		24	20–10		(5)
Betula papyrifera		14	25–25		(5)
Alnus spp.		0	30–20		(5)
Populus spp.		0	30–20 or 5–25		(5)

[a] Eight hours at the higher temperature and 16 h at the lower temperature

[b] Twenty eight days at 20°C followed by 56 days at 2–5°C. *Chamaecyparis nootkatensis* is now known as *Callitropsis nootkatensis*

in germination parameters and dormancy places an added level of complexity causing non-uniform germination patterns in the nursery that can lead to unintentional selection of certain families especially at the time of thinning seedlings in containerized nursery operations (19, 20). Moist-chilling conditions for British Columbia's conifers are listed in Kolotelo et al. (11) and for other boreal and north-temperate tree species in Baskin and Baskin (5) and are summarized in Table 1.

In natural regeneration methods, where successful seedling establishment relies on the natural seed *rain*, dormancy is the safety mechanism that prevents "premature" germination of seedlings in the fall. The moist-chilling periods required to break dormancy are such that seeds germinate only when the conditions (usually determined by temperature, and likely also photoperiod) are favourable during the following spring. This enhances the chances for successful seedling emergence and survival; however, unpredictable environmental contingencies often occur causing reduced recruitment or in some cases total recruitment failure. Hence, artificial regeneration is often favoured.

5. Germination in the Nursery

5.1. Containerized Nursery

Germination conditions and dormancy-breaking treatments are usually explored and tested in the laboratory under closely controlled conditions with respect to temperature, light levels, and other necessary requirements, depending on the specific requirements of the species. Recently, El-Kassaby and co-workers (21) demonstrated the utility of the non-linear four-parameter Hill function (4-PHF) to estimate and biologically interpret the four parameters with respect to germination. After fitting germination data (cumulative germination percent over time), the lag or onset of germination, time of maximum germination rate, instantaneous rate of germination, and final germination percentage (germination capacity) can easily be calculated given the four parameters describing the shape of the curve of the Hill function. The ability to express the course of germination mathematically allowed the application of the integration approach of Richter and Switzer (22) to quantitatively estimate the degree of dormancy (see El-Kassaby et al. (21)). In this approach, the level of dormancy was quantified as the area between a seedlot's germination curves under stratification (moist chilling) and control (unstratified) conditions (Fig. 1). With this information, the extent of dormancy and the efficacy of dormancy-breaking treatments, as well as differences among test entries, such as provenances, families, or orchard clones, can be assessed. Other non-linear functions also allow the estimation of some of these characteristics (23–25). However, it is prudent to point out that often laboratory germination tests do not reflect greenhouse results (5) and testing under "unfavourable" conditions has been advocated to reflect the true potential of treated seed (26).

Appropriate and species-specific dormancy-breaking treatments lead to greater uniformity and greater speed of germination (see also Chapter 4). According to Kolotelo (pers. comm.), the greatest cost in greenhouse seedling production is heating

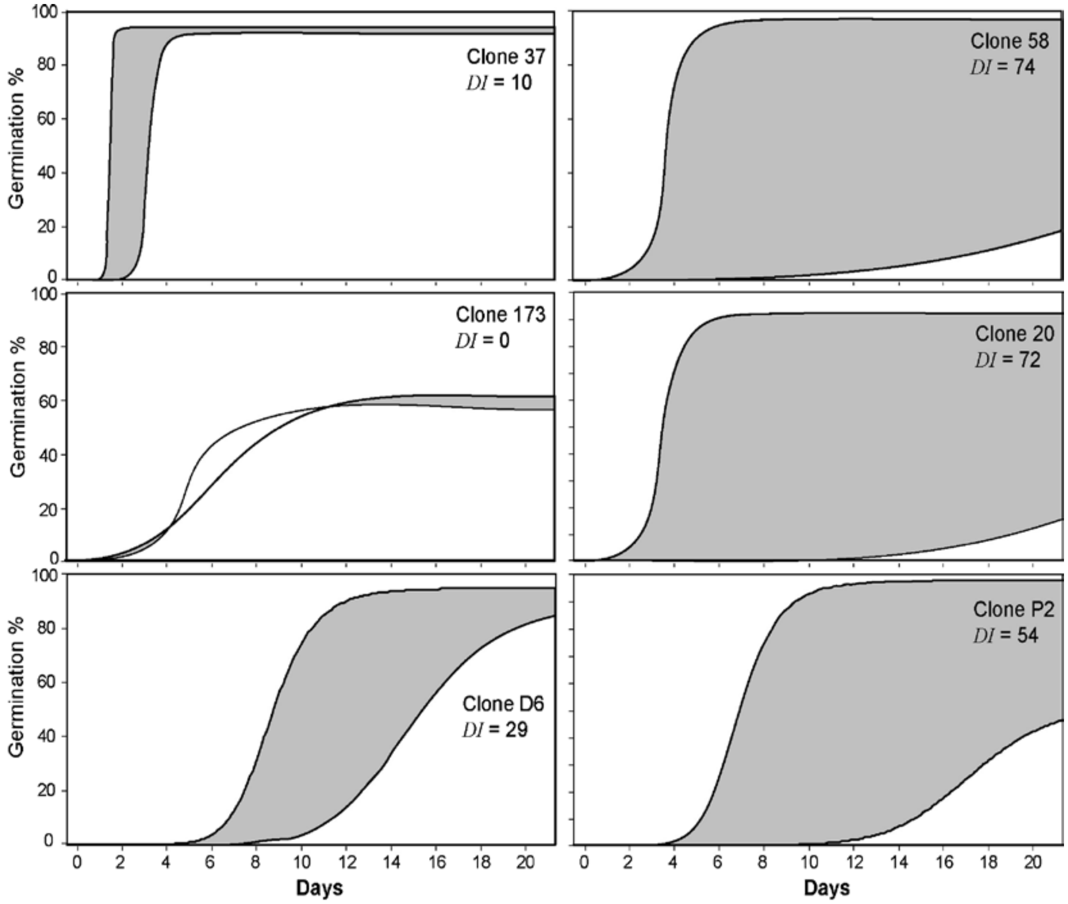

Fig. 1. A quantitative illustration of dormancy (DI) as determined by the area between germination courses of moist-chilled seeds (*upper line*) and untreated (non-moist-chilled seeds (*lower line*)) showing the range of variation among seed orchard clones of lodgepole pine (*upper panel*), white spruce (*middle panel*), and Douglas-fir (*lower panel*).

during germination. This is especially a consideration in northern climates, where greenhouse germination mostly takes place during early spring when outdoor temperatures are often below 0°C. Therefore, treatments that cause an increase in germination speed (and a decrease in the lag) have cost benefits for nurseries.

Due to the scaling up of the size of seed populations to be germinated when transitioning from the laboratory to the greenhouse, germination results may not be the same. The increase in space, number of seedlots, and species often results in environmental conditions being fairly heterogeneous; as a consequence, germination results often fall short of what was assumed based on laboratory germination testing. However, even under tight environmental control and following generally accepted standards, laboratory germination tests show that seedlot performance still can vary. For example, based on 3,173 germination tests, 1,798 seedlots of which were lodgepole pine, the average germination capacity was 92% (27). Compounded by the much wider amplitude in environmental conditions in the nursery growing environment, such as soil medium, potential moisture gradient in the soil mixture, temperature differences in different locations within a greenhouse, and varying light intensity levels, the variation in germination parameters may be much larger than expected as compared to those based on laboratory tests. Furthermore, the seeding window in any nursery is much more prolonged or delayed due to operational constraints resulting in potentially more variation, especially in large seedlots. Finally, in the laboratory, a seed is scored as "germinated" when the radicle is four times the length of the seed; in the nursery, the assessment of germination is usually done much later (for example, when the cotyledons shed the seed coat) (11), adding another temporal component to the differences between laboratory and nursery measures of germination. Despite these contributing factors promoting the incongruence between laboratory and nursery results, in cases where this has been assessed, the differences between nursery and laboratory GC are small and account for only 2.5% across 17 tree species and 978 seedlots (28).

5.2. Bare-Root Nursery

The environmental conditions in bare-root nursery beds are not nearly as "controlled" as in greenhouses, and germination results are expected to vary considerably. With the exception of watering, the nursery manager cannot manipulate much of the outdoor environment to enhance germination. However, as it is not as crucial to have anticipated germination rates as predicted by laboratory tests, this may not present problems. However, it should be pointed out that the seed-to-seedling ratio in bare-root nurseries is expected to be much lower than that of their container counterparts. In a container nursery, every empty cavity affects the operation profit margin, since this space is heated, irrigated, and fertilized without any return on investment (see below). In a bare-root nursery, the practice of over-sowing to account for these short falls is more prevalent leading to the unwise use of seed which can be fairly serious, especially if high-quality seed, such as orchard seed, is used. Despite this, as noted below, container nurseries are not immune from this practice too. However, it has been shown that prolonged moist chilling renders seeds competent to germinate at (lower) temperatures than those that are more commonly encountered in uncovered nursery beds (29, 30).

6. Sowing to Maximize Germination Capacity

In container nurseries, the "space currency" is determined by the number of blocks used and the number of cavities per block. Thus, it is very important that each cavity within every block results in the production of one seedling and this is more evident when blocks with larger cavities are used as relatively more space is allocated to each cavity (11). To counteract any fall-downs in the number of filled cavities, "over-sow" is commonly practiced. The amount of over-sowing is called the sowing factor and is precisely determined given the expected germination capacity of a seedlot (31). Of course, knowing the GC of a seedlot becomes crucial for achieving the objective of close to 100% cavity occupancy. This practice forces nursery managers to use a greater number of seeds per cavity as compared to the "ideal" one seed per cavity (which requires 100% germination capacity), and often leads to a waste of seeds.

The effects of improving germination capacity on the cost of nursery operations are illustrated here. The number of seeds required to produce one healthy and acceptable seedling at a germination capacity of 91% is 2.33. In comparison, at a GC of 98%, the number of seeds required drops to 1.87 (11). For a crop of 1 m^2 plantable seedlings, at a cost of 5 cents/seed, the difference is $23,000. Clearly, attempts to improve seed quality and germination percent have immediate pay-offs.

Multiple sowing usually results in the presence of multiple germinants per cavity, which is commonly followed by thinning after a certain period when germination is assumed to be complete. This practice not only wastes seeds, but can also have some undesired consequences as demonstrated by El-Kassaby and Thomson (19) and El-Kassaby (20). Since germination parameters (including dormancy, speed, and germination capacity) are under strong genetic control (maternal), it is expected that seeds from different seed donors (families) should manifest this genetic variation in their germination behaviour. Thus, certain families are preferentially thinned at an early stage if a greater proportion of their seeds are either affected by slow germination or deep dormancy. The resulting unintentional selection causes some families to be under-represented in the final seedling crop and in the most severe case, this practice could lead to the deployment of seedling crops with reduced genetic variability. If there is reduced genetic variability of orchards' seedlots and nursery crops, this may in turn lead to their diminished capacity to deal with unpredictable environmental contingencies during their long lifespan.

In bare-root nurseries, this unintentional selection may also take place but unless sowing is done in family blocks (i.e. using seeds from individual seed donors), there are no other remedies to counteract this negative selection effect. However, processing individual family seedlots may put too much strain on seed processing and seed storage facilities to be of a practical solution.

7. Seed Quality

To a large extent, the level of dormancy and the successful pretreatment to break it affect the onset (lag) and speed of germination. Seed quality on the other hand is the driving force governing germination capacity or maximum germination percent of a seedlot. In industrial settings, this is the most important attribute of a seedlot and strongly affects a multitude of cascading actions starting from the over-sow determination and ending with the expected size of seedling crops recovered at the end of the growing season. Of course, the role of dormancy cannot be overemphasized since standard seed pretreatments are insufficient to overcome deep dormancy and a seedlot's true germination capacity can be underestimated.

The proportion of non-viable seeds in a seedlot strongly affects the average seed quality and, as a result, the average germination capacity of a population. Because of this, it is most important to be able to reliably separate filled and viable seeds from non-viable and/or empty seeds (see separation procedures in ref. (11)). Seed production and mating dynamics should be investigated if the proportion of non-viable seeds is consistently from the same seed donor (for example, from a seed orchard). Causes for empty seeds could be high selfing rates, lack of pollen availability at the time of ovule receptivity, and insect predation.

The most reliable way to test for seed quality is to carry out a germination test under standard conditions using generally accepted protocols after recommended and prescribed dormancy-breaking treatments are applied. This testing procedure follows International Seed Testing Association (ISTA: http://www.seedtest.org) or Association of Official Seed Analysts (AOSA: http://www.aosaseed.com) rules which are designed for uniformity in testing standards and procedures. However, it should be pointed out that in several instances, the prescribed methods need further refinements (32, 33).

8. What Will the Future Hold?

Global warming and its associated climate changes are generally accepted in the scientific and forestry community. The extent of the impacts on forest communities and anticipated responses of forests are much more controversial and uncertain. One counteracting measure against the anticipated changes is a general trend to diversify the forests and possibly promote the use of hardwoods (broad-leaf trees) and southern conifers seed sources. Experience in the nursery industry is not advanced in growing broad-leaf trees as the bulk of the seedlings for regeneration in Canada is (still) conifers. This implies that more research and testing are needed to develop suitable protocols and procedures to successfully grow poplars, alders, willows, birches, and maples on large commercial scales economically in forest nurseries as some species of these genera may present seed biology challenges (34). Additionally, the seed pretreatment of southern conifers seed sources might require some adjustments for attaining maximum seed use efficiency.

Finally, seeds from species with deep dormancy may not receive the required moist chilling at low temperatures if winters become warmer, shortening the time of chilling so that seeds may not germinate even under otherwise favourable germination conditions (35). However, Johnson et al. (36) have speculated that the "after-effect" phenomenon observed in Norway spruce (*Picea abies* L.) and other conifer species (37–40) is a regulating mechanism that affects adaptive plasticity rendering seedlings less susceptible to the potentially harmful effects of a rapidly changing environment. These types of studies point to an epigenetic mechanism (the precise nature of which is not yet known) that contributes to a rapid response to systemic changes in temperature (41). This mechanism operates during embryo development and adjusts the timing of bud set in accordance with the temperature conditions in which the mother tree lives. More specifically, the timing of dehardening and bud burst in the spring, leader shoot growth cessation in the summer, and bud set and cold acclimation in the fall are processes that are advanced or delayed according to the temperature during female sexual reproduction. Thus, seedlings (both normal seedlings and seedlings derived through somatic embryogenesis) "remember" the temperatures and photoperiod prevailing during embryogenesis and seed maturation. The epigenetic changes that potentially underlie this phenomenon clearly affect adaptive traits in Norway spruce and in other conifer species (40). More research is needed to understand the molecular basis of these phenomena, particularly events that underlie this type of "cellular memory" in plants.

Recently, genetic conservation efforts have increased and one aspect of conservation is ex situ conservation mainly in the form of seed collections stored in safe storage facilities. This conservation strategy relies on knowledge of optimal conditions during long-term seed storage, storability potential for each species, and known deterioration rates of seedlots (11).

9. Role of Molecular Biology and Genomics

Successful dormancy-breaking treatments and germination protocols have been worked out for most temperate forest species as demonstrated by the large number of seedlings produced and planted annually. However, there are recalcitrant species, where more basic research is needed to elucidate the bottlenecks to achieve successful propagation at high germination capacity. Yellow cedar and some of the true firs (*Abies* spp.) present some challenges with respect to more complicated dormancy-breaking requirements and lower germination capacity (see Chapter 4). The work by Kermode and co-workers (e.g. (42); see also Chapter 4) is an example of how basic research is contributing directly to operational procedures.

The recent advances in gene expression research and genomics/ functional genomics initiatives have created an opportunity for understanding the underlying biological basis of seed germination and dormancy. It is anticipated that the molecular studies on the most studied species, such as spruces and pines, will lead the way and provide a wealth of resources to further this area (e.g. through vast EST libraries and micro-arrays). Furthermore, QTL analysis (Chapter 11) further enhances our understanding of the genetic control over germination parameters.

Molecular studies may also contribute to elucidating the basis of the responses of conifers to changing climates. How do trees cope with stresses associated with seed production in an environment to which they are not adapted? Furthermore, as noted earlier, the molecular basis of the after-effects (cellular memory) should be studied, especially as it may become relevant to triggering adaptation mechanisms in a changing climate. Finding ways to increase the storability and reduce the aging process in stored seeds would also contribute to our management of seed, especially for the purpose of ex situ conservation.

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