Germination Environment

Seed germination is the process of emergence of the root and shoot, leading to the growth of a seedling. The ability to choose and implement appropriate cultural practices to achieve this end demands an understanding of the germination requirements of seeds. Seed germination in the nursery can be divided into two stages, where stage one encompasses the time from seed sowing to radicle emergence, or emergence from the growing medium if seeds are covered. Stage two begins with radicle emergence and lasts until the first true leaf emerges. For a summary of stage one and stage two nursery germination guidelines, see Appendix 5.

Stage 1

Metabolic activity begins with the rapid imbibition of water by the cells of the dry seed. Membrane and organelle systems are reorganized and respiration is initiated to release energy from stored reserves for future needs. Ultimately the seed swells and the seed coat splits along the junction of its two halves.

Goal – Germination Stage 1: Quick and even germination, resulting in uniform crop emergence

Enzyme activity begins quickly after the onset of seed hydration. This activity involves previously stored **enzymes** at the very start of hydration but quickly adds currently synthesized enzymes as germination progresses. Basically, the **metabolic** machinery of the cells is "turned on." Reserves of complex molecules are broken down (**hydrolysis**) into smaller constituents. This releases energy, provides building blocks for use in producing new growth, and serves to increase the **osmotic potential** within cells. The latter triggers further uptake of water which serves to expand or telescope the existing embryo.

The first visible evidence of germination is the emergence of the radicle. It results from the elongation of existing cells and usually occurs within a few days, marking the end of stage one.

Goal – Germination Stage 1: Quick and even germination, resulting in uniform crop emergence.

Stage 2

By this time the vascular system has differentiated and become operational. Fats, proteins, and carbohydrates stored in the megagametophyte and embryo are digested to simpler chemical substances and translocated to the growing points of the embryo (root and shoot apical meristems as well as the **vascular cambium**).

Goal – Germination Stage 2: Maintain uniformity, health, and vigour to facilitate quick and predictable responses to future cultural practices

It is during this stage that the "seedling" is forced to switch from relying on rapidly depleting stored energy reserves to producing its own through photosynthesis. Newly exposed green plant parts must begin to **photosynthesize** and the radicle must begin to draw nutrients from the soil solution. Increase in size involves cell division as well as elongation. It is imperative that once "green" is evident, the 24 hour energy balance be managed so that daytime energy accumulation outweighs night-time respiratory losses and maintenance requirements. Growth requires energy accumulation over and above this break-even point. To facilitate this, photosynthetically active radiation of appropriate intensity must be supplied in addition to managing plant temperature to maintain positive net photosynthesis (see Figure 93).

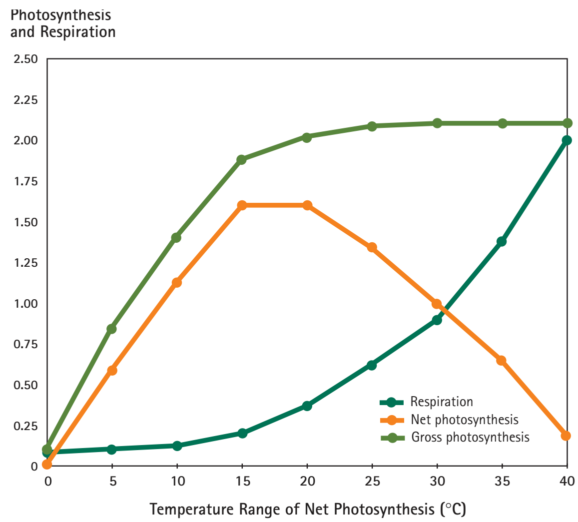

Figure 93 Effects of temperature on photosynthesis, respiration, and net or apparent photosynthesis of Swiss stone pine seedlings (from Tranquiline 1955).

Goal – Germination Stage 2: Maintain uniformity, health, and vigour to facilitate quick and predictable responses to future cultural practices.

Uniformity

Uniformity is a first principle if discussing maximization of forest seedling production efficiency. Growing plants from seeds ensures a certain amount of variability between seeds due to genetic recombination arising from sexual reproduction. In addition, seeds from various parent trees are generally mixed to form a seedlot. Standard (wild) seedlots are normally comprised of seeds from trees of fairly close proximity. Seed orchard seedlots may be comprised of seeds from parents originating from wider geographical areas. The latter can, depending on parent tree selection, be genetically more variable than the former. Using an ingredient with inherent genetic variability (seeds) to produce a product of uniform morphology (seedlings) is a challenge.

Non-uniform or staggered crop emergence results in...lower overall production efficiency

In the nursery the first expression of variability is during germination. To minimize this expression morphologically without losing it genetically, one strives for uniform, rapid crop emergence. This is essential. Non-uniform or staggered crop emergence results in plants that vary in size, nutrient and water uptake requirements, and competitive ability. This reduces the effectiveness of subsequent cultural inputs (nutrients, heat, CO_2, **short-day treatment**) and lowers overall production efficiency in general. For example, one might delay implementation of short-day treatment on a non-uniform (height) crop to allow short individuals to catch up. Consequently, taller individuals may end up over-height, and budset in the whole crop is induced later with less time devoted to hardening. Sowing earlier to compensate for variability just shifts the cost of inefficiency to the beginning of the crop cycle. Sowing earlier when greenhouse heating costs are higher is an expensive option, shifting peak demands on annual cash flow projections. Starting earlier when light conditions are poorer also increases the risks of contracting disease, possibly requiring a greater oversow factor.

In essence, we are dealing with a "miniature forest," where the degree of variability increases with crop age as size differences compound the variability in competitiveness. Smaller plants receive fewer resources such as light/air movement than larger neighbours causing them to grow at progressively slower rates as they drop relatively lower into the understorey. This can result in substantial proportions of a crop falling outside the specification window, increasing grading costs and culling levels.

Bringing non-uniform crops to market often requires much greater inputs of grower attention, technology, and energy. Using extreme measures to keep a crop going at the beginning can result in excessive growth later on, often requiring more extreme shutdown measures.

Once water touches a seed during the pre-stratification soak, the overall seedling crop cycle essentially begins

The uniformity with which required inputs are supplied governs how well the uniformity established thus far is retained. All seeds need to experience the same temperature, oxygen, moisture, seed cover depth, and light conditions. Inherent differences in germination speed between seeds in a seedlot can be compressed to a certain extent by employing higher germination temperatures (25°C fraction as an example in **Figure 94**). To increase crop uniformity of the 15°C fraction (**Figure 94**) one could multiple sow it and thin the late germinants, or raise its germination temperature. If germination speed is high but germination capacity is low (seedlot B in **Figure 95**), crop germination will be uniform but scattered. In this case one would multiple sow and thin the low germination capacity lot, thereby increasing its percent cavity fill.

Once water touches a seed during the pre-stratification soak, the overall seedling crop cycle essentially begins.

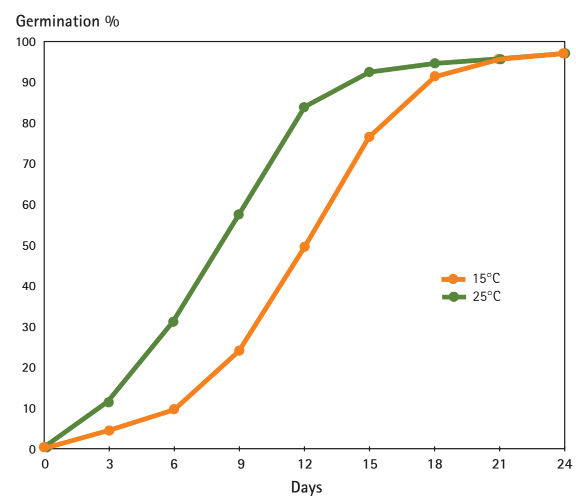

Figure 94 Germination rate comparison of a seedlot at two germination temperatures (25°C and 15°C).

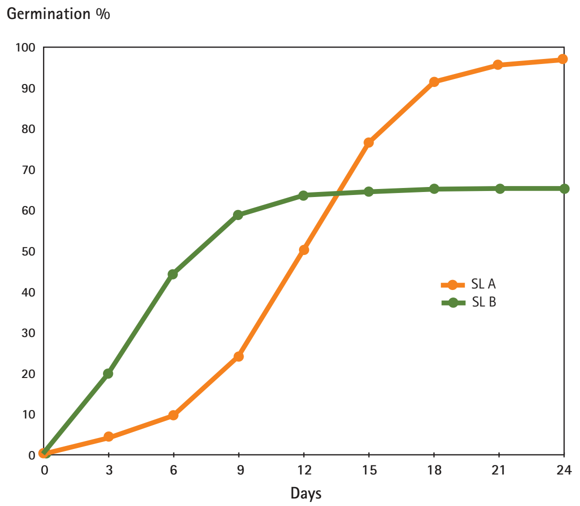

Figure 95 Germination speed vs. total germination (%). Seedlot B will emerge more uniformly even though it yields less viable germinants. Multiple sowing and thinning Seedlot B will increase its percent cavity fill and yield a more uniform crop than single sowing Seedlot A.

Environmental Factors Affecting Germination

Newly sown seeds are placed on top of the growing media, then covered with a thin layer of grit (seed cover). Being in contact with both, seeds are able to lose or gain heat from each of them by conduction. Conventional peat-based growing media and grit are chosen for their high aeration porosity, which can also influence seed moisture content gain or loss. What seeds experience depends on how (forced air, radiant) and from where (above, below) the heat is supplied, and on the moisture conditions of growing media and grit. The argument for under-bench heating generally assumes that seed temperature follows growing media temperature.

It is important to remember that grit is in contact with the seeds and growing media as well. Grit temperature is influenced in large part by above-bench conditions including incoming solar radiation (day), outgoing long wave radiation (night), **convection**, and irrigation water temperature, for example. Depending upon duration and strength of these influences, the conditions the seeds experience may more closely follow grit conditions. Grit forms part of the surface adjacent to which we find the **laminar boundary layer** (LBL) climate. Depending on depth, particle size distribution, and aeration porosity, some grit types may actually be more appropriately assumed to be within the zone termed the LBL.

Laminar Boundary Layer Climate

Factors that interact to determine the boundary layer climate are:

- light intensity, quality, and duration
- humidity
- temperature of the air, growing media, irrigation water
- plant spacing and size
- canopy density
- air movement
- seed cover heat capacity, aeration porosity, colour, and depth.

The LBL is the layer of air in contact and immediately surrounding a surface, in this case the seeds/germinants as illustrated in Figure 96. It is at most several millimetres to 1 cm in depth. The climate within the LBL influences surface condition most directly. Gross greenhouse or compound environments indirectly assert their influence through alteration of the LBL climate. The thickness of the LBL is governed by the turbulence of adjacent air and surface features of the plant part in question. Horizontal airflow fans in greenhouses reduce the thickness of the boundary layer surrounding needles. Epidermal hairs on needles serve to reduce the influence of horizontal airflow fans, thereby retaining boundary layer thickness and its innate buffering capacity. Grit may be seen to perform a similar function for conifer seeds, which do not have epidermal hairs.

Radiation heats surfaces warming the LBL, evaporation and/or transpiration from the surface increases the humidity of the LBL, and gas exchange through stomata alters its gaseous make-up. Gradients of gases, humidity, and temperature exist from the plant/seed surface to the LBL edge. At the edge the gross climate effects changes in the boundary layer climate mainly through convection (mixing). However, any non-radiative transfer across the LBL is by means of molecular diffusion, which is very slow. Therefore, reducing the thickness of the boundary layer is the quickest way to effect changes at the leaf or seed surface since it increases the steepness of the respective gradients. A thin LBL allows removal of unwanted gases faster. It also allows faster removal of transpired water vapour, allowing a plant to more effectively cool itself. In the case of seeds, a thin LBL coupled with a low humidity gross greenhouse climate can result in accelerated evaporation of surface moisture, leading to cooling and subsequent reduction in germination speed, as well as possible drying. During seed germination a thick boundary layer (calm conditions) coupled with a high humidity gross greenhouse climate is desirable. This prevents possible evaporative cooling and drying of seeds, thereby reducing the need for application of irrigation water, which generally performs a further cooling function. Beyond germination a more active climate (lower humidity, horizontal airflow) is more beneficial.

The laminar boundary layer is the layer of air in contact and immediately surrounding a surface

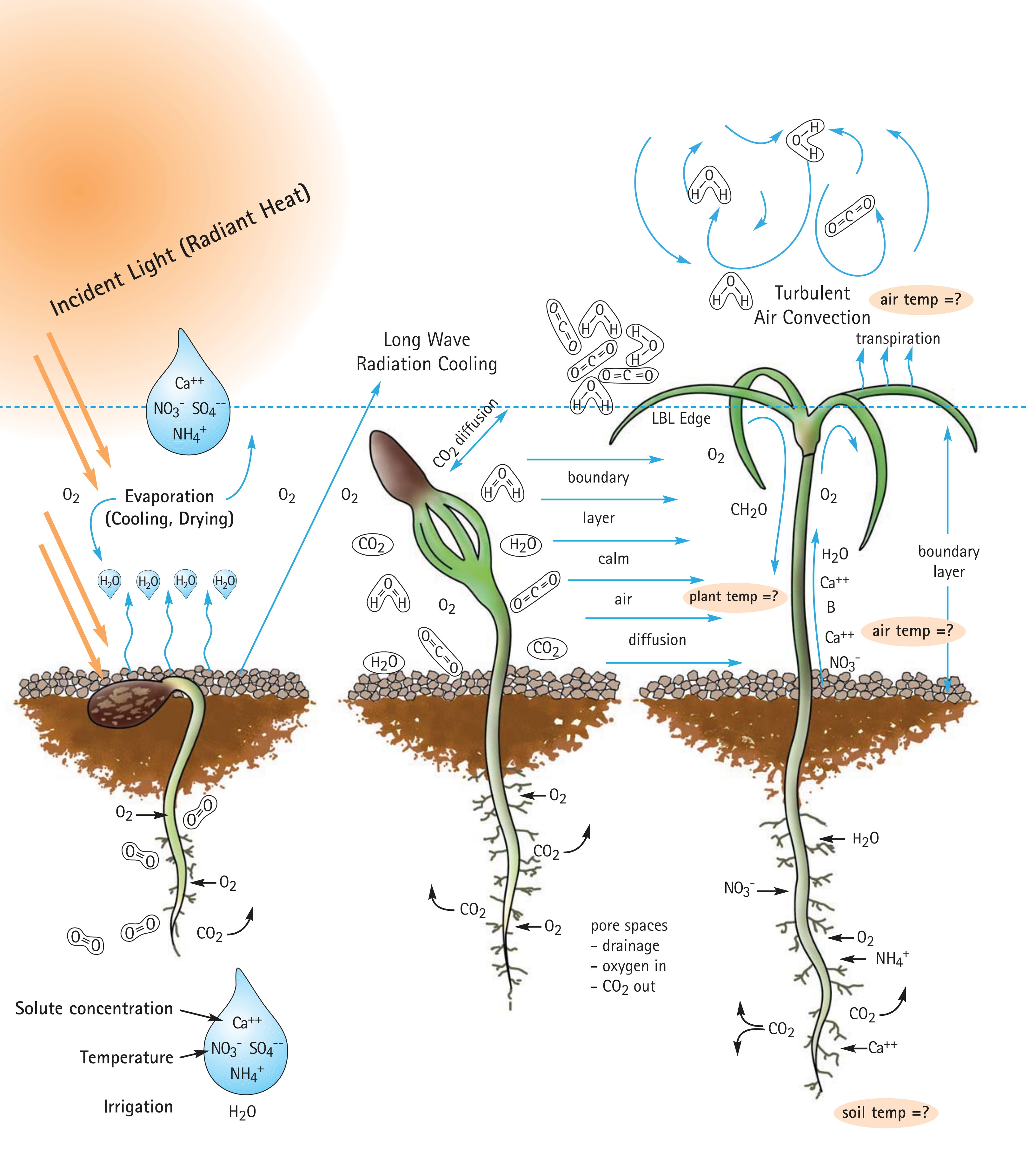

Figure 96
The laminar boundary layer (LBL) in a forest nursery setting.

Moisture

Water is essential for all life processes, and is one of the primary driving forces of germination. Successful stratification is dependent on specific moisture contents. After stratification, germination relies on unimpeded access to water. Water is key to imbibition, activation of the metabolic machinery, and radicle emergence.

Water potential is a measure of how "free" or easily extractable water is. It is measured in units of pressure (Mega-Pascals). Pure water has a defined water potential of zero (0.00 MPa), making it the easiest to extract or obtain. Adding **solutes** (dissolved substances such as fertilizer salts, for example) lowers the water potential below zero, effectively making water less "free" or more difficult to extract.

As water is preferentially extracted from the soil/growing media by transpiring plants and/or surface evaporation, the solute concentration rises, reducing water potential or the ease with which it can be extracted. For this reason it is important to monitor water quality during the growing cycle so that it can be replenished or replaced prior to becoming unavailable.

Water potentials also govern seed moisture uptake, and although dry seeds can muster very low water potentials (-100 MPa) with which to draw moisture and **start** imbibition, equilibrium can occur readily if water becomes more difficult to acquire. This can slow water uptake to the point of preventing complete imbibition and disrupting germination. So while we may want water with moderate solute levels with which to prime seeds, once seeds are at the "germination starting gate" and we want germination to proceed, water should be more "free" (closer to 0.00 MPa water potential).

...seeds are like sponges, competing for H_2O with solutes in the water

In summary, seeds are like sponges, competing for H_2O with solutes in the water, which behave like many little sponges. If there are too many solute particles present, seeds are unable to compete and obtain enough water with which to commence or continue the germination process (**Figure 97**).

Some ways in which water stress can be imposed on the embryo/germinant are through incomplete initial imbibition, dry media, high solute levels in the applied water, high evaporative demand causing drying, and pelleting. The coating used for pelletizing seeds competes very effectively for moisture with the seed coat itself when water becomes limiting. These conditions cause slow, non-uniform germination and reduce total GC.

Oxygen

Oxygen availability is extremely important because it is necessary for respiration, which provides the energy required for maintaining metabolic processes of seeds during stratification and germination.

Respiration = $C_6H_{12}O_6 + 6O_2$ >>> $6CO_2 + 6H_2O$ + energy

Good gas exchange between the germinating medium and the embryo is essential. If oxygen concentration falls substantially below 21% (concentration in ambient air), germination of most seeds is inhibited (Khademi et al. 1992). Thus O_2 supply to and CO_2 dissipation away from the embryo are essential. Both are limited by physical properties of growing media, grit, water management practices, type of seed coat or pellet if pelletized, and sowing depth. Excess moisture hinders gas exchange between a seed and the external environment with possible negative impacts on respiration rate. Oxygen diffusion rate is ~10,000 times faster in air than water. This is why seeds can literally drown! Low oxygen environments are also conducive to root diseases.

Oxygen diffusion rate is ~10,000 times faster in air than water

Some common causes of poor oxygen/CO_2 diffusion rates are over-watering (frequency and/or duration), very fine or compacted growing media, excessive sowing depth, fine packing grit cover, and algae forming impermeable layers on growing media/grit surfaces.

Vigour is the ability to deal with unfavourable conditions and varies between species and seedlots. However, it also varies between seeds within a seedlot. During unfavourable conditions, such as low O_2 or temperature, it may be expressed as reduced crop uniformity (e.g., seedlot portion grown at 15°C in **Figure 94**).

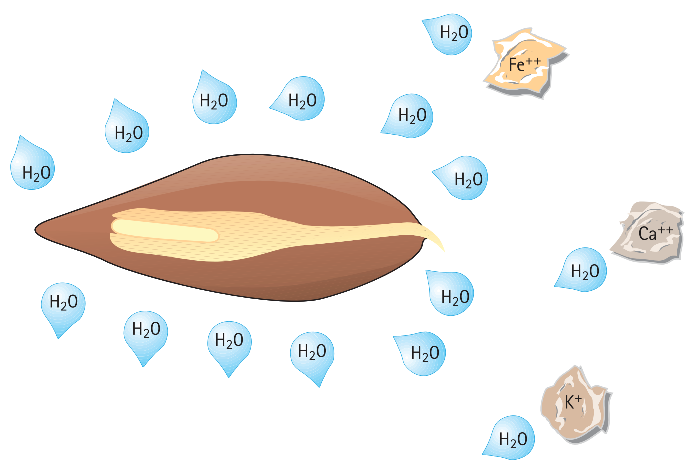

Figure 97 Seed vs. solute – the battle for water.

Under optimum conditions most seeds germinate quickly. A low O_2 environment impacts those seeds having a higher energy requirement most—they will be slower to germinate (germination rate) or they may run out of energy and die (affecting germination %).

Oxygen availability can thus affect:

- germination rate
- germination capacity
- seed/embryo viability
- germinant viability.

Temperature

Assuming dormancy is overcome and moisture, oxygen, and carbohydrate reserves are not limiting, the rate at which biochemical processes proceed within a seed depends on seed temperature. The function that describes how the rate of a biochemical reaction changes with changing temperature is called the "Q_{10} factor" (Keeton 1972; Lehninger 1977). Over a specified range, it describes how the rate of a chemical reaction changes per 10°C change in temperature.

Between 5°C and 35°C for biochmical reactions in plants, the Q_{10} factor is approximately 2. This is an exponential relationship. This means that over the specified temperature range, a 10°C increase produces a doubling of the respiration rate (**Figure 98**).

Respiration of stored seed reserves fuels germination. Respiration rate thus approximates germination speed, governed by temperature. Practically speaking, each 1°C rise in seed temperature effects a 10% increase in respiration rate or germination speed. Going from 5 to 15°C, 10°C to 20, or 15 to 25°C doubles respiration rate, hence going from 5 to 25°C quadruples it! When balancing heating cost against the benefits of germinating at higher temperatures this exponential function becomes important. Because respiration/germination rates are higher at elevated temperatures, a 10% increase in respiration/germination rate effected by a 1°C temperature rise is much larger and potentially more beneficial when starting from a higher instead of lower initial temperature.

...each 1°C rise in seed temperature effects a 10% increase in respiration rate or germination speed

Raising germination temperatures into the 20 to 25°C range can provide substantial gains in terms of reduced crop cycle growing time and gains in crop uniformity and disease escape. However, does it pay, especially at high per unit energy costs?

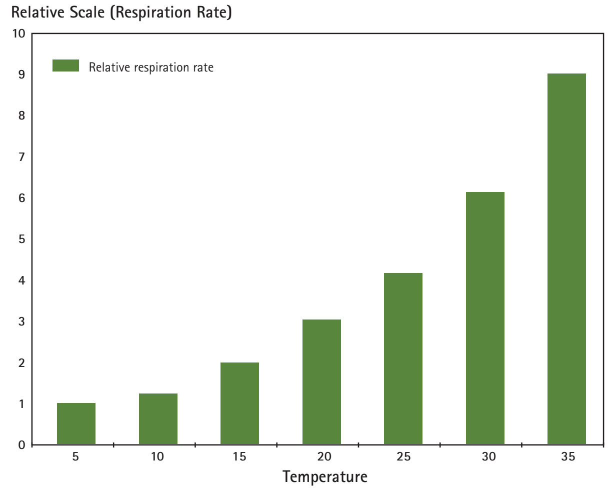

Figure 98 Plant respiration increases exponentially with temperature, having a Q_{10} of 2 between 5 and 35°C.

The cost of raising growing facility temperature is a function of the area of the structure, heat loss value of the covering, air exchanges per unit time, and outside temperature/ wind/precipitation conditions. Generally speaking, greenhouse heating is a linear function between temperature and heating cost (**Figure 99**). This suggests that the heating cost of a 1°C rise in greenhouse temperature is approximately the same regardless of the starting point.

Combining Figures 98 and 99 gives the following (**Figure 100**).

Figure 100 demonstrates that with each successive increase in greenhouse temperature, the return on the heating investment increases (in terms of increased germination speed). In the above scenario (6 mm single poly at -10°C outside temperature), the first unit of heating energy is consumed to achieve a greenhouse temperature of 5°C. Relative respiration (germination) rate is at 1. Adding a second unit of heating

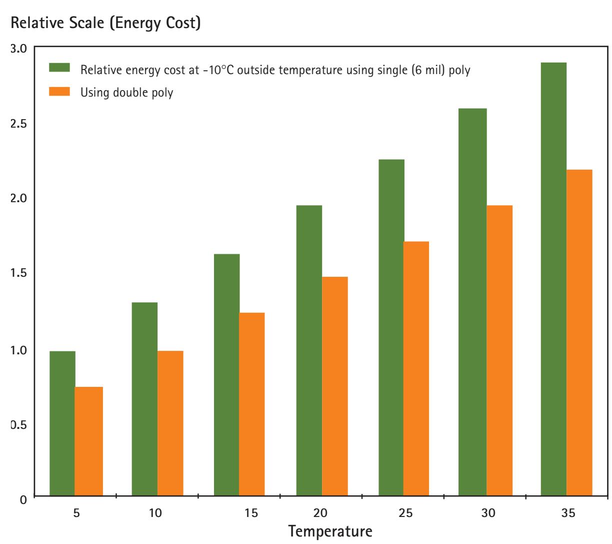

Figure 99 The relative greenhouse heating costs using single and double polyethylene roofing material.

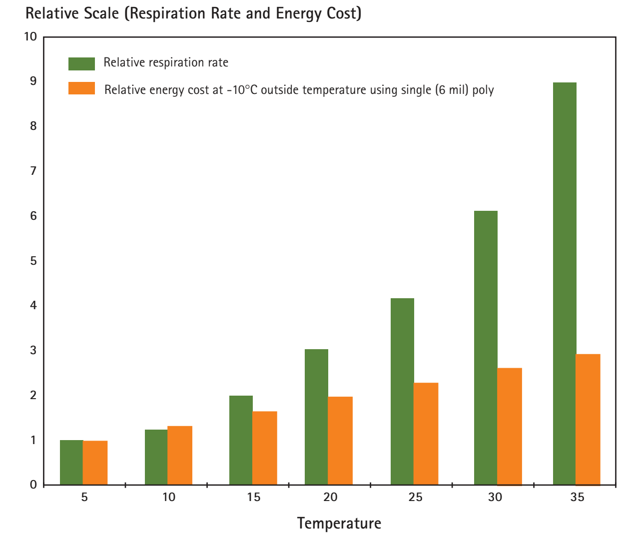

Figure 100 A comparson of the gains in respiration rate (approximating germination speed) and energy costs with changes in germination temperature.

energy brings greenhouse temperature to 20°C and effects a respiration rate of 3. Adding a third unit of heating energy brings greenhouse temperature to 35°C and raises respiration/germination rate to 9!

To summarize the above, it pays to increase temperature because of gains made in uniformity, germination speed and disease escape. In addition, because increased germination speed allows for a reduction in crop cycle time and total heating time, the higher the per unit energy cost the more it pays to increase germination temperature.

To increase fuel efficiency in poorly insulated buildings such as greenhouses, it makes sense to modify temperature management strategies depending on the prevailing weather. Since total heat sum appears to govern germination speed (Edwards and Leadem 2000), it is possible to make up for cool periods with warm ones. For example, during very windy weather consider using a lower heating setpoint, then make up for it during calm periods with higher temperatures (less heat loss due to convection). Those able to employ black-out screens as **energy curtains** may find the night a cheaper time to heat, allowing maintenance of a higher average germination temperature at a lower cost (less long wave radiative heat loss, smaller volume of air to heat, gain an insulating air layer). Remember that greenhouse air temperature does not necessarily equate to seed temperature. On sunny days grit temperatures can be substantially higher than air temperature, possibly warranting irrigation to cool the germinating seed. On clear nights, in a polyethylene house without an energy curtain, long wave radiative heat loss can easily drop growing media temperature 3 to 5°C below air temperature. Sensors should be installed in the growing media close to the seeds to estimate seed temperature. Monitoring seeds along with greenhouse air temperature on a continuous basis allows determination of the optimum heating strategy for a particular germination facility. It will also instill an appreciation of the impact of irrigation/misting cycles on seed temperature, mainly cooling, which may warrant more careful attention to humidity and water management strategies.

...total heat sum governs germination speed

A positive day/night differential of up to 10°C is recommended by some but found unnecessary by others. The theory is that it is an evolutionary trait developed to prevent deeply buried seeds from germinating. Only surface soil temperatures experience a significant day/night differential during spring, signalling the ability to make it to the surface should germination be attempted.

It can be said that root and shoot growth is an extension of germination, hence temperatures that promote good growth generally promote good germination. However, for many plants optimum germination temperatures are somewhat higher than optimum growing temperatures. This may be due to the fact that energy requirements for germination are generated from respiring storage reserves and germination-type growth involves primarily a reactivation and "unfolding" of previously developed systems and structures. Photosynthesizing organs have maintenance energy requirements that increase exponentially with temperature. The latter leads to the concept of "net growth" which equals photosynthetic production minus respiratory maintenance requirements (Figure 93).

..."net growth" equals photosynthetic production minus respiratory maintenance requirements

To facilitate rapid germination, low to mid 20°C seed temperatures are recommended. This allows the germinant to be transferred from a *germinating* environment to a *growing* environment sooner. A germinating environment employs continuous warm, low light, low to zero nutrient, low **vapour pressure deficit** (high **relative humidity**), and high soil moisture conditions. Maintaining these conditions after germination increases the risk of contracting fungal diseases, and leads to extremely soft plants, incapable of resisting stress in general.

Light

Some conifer seeds require light to germinate, but the seeds must be fully imbibed and the required intensity is low, 1–5 lux (equivalent to bright moonlight) (Leadem 1996). The red light (660 nm) portion of the spectrum stimulates germination and the far-red portion (730 nm) inhibits germination. Growers in BC have used this strategy with some success when incompletely stratified seeds have had to be sown in an emergency. Basically it involves applying the seed cover (grit) several days to a week after sowing the seeds, thereby allowing light to help initiate the germination process. The red/far-red ratio impacts on various plant growth characteristics, hence may be worth investigating with respect to germination rate and capacity.

The recommended photoperiod is a 20-hour extended day to help reduce **etiolation** (stretching) of the **hypocotyl** after germination and prevent premature budset in northern seedlots. Etiolation increases with a reduction in the red/far-red ratio. During the winter months, when light intensity, quality, and natural photoperiod are lowest, etiolation can be excessive, resulting in very weak, spindly plants.

Sunlight warms surfaces it can reach, altering the boundary layer climates associated with them. This is beneficial in most cases but will induce horizontal temperature gradients between shaded and non-shaded sections in the propagation area. Exposed plant parts will warm and growth rates increase relative to shaded parts or other plants, something to keep in mind when considering uniformity. Artificial light generates heat as well but the degree to which it warms surfaces depends on its intensity, spectral distribution, and distance from the object in question. When targeting 8 to 10 foot-candles (~80 to 100 lux) for photoperiod extension this contribution is generally not significant. However, seedlings growing directly under individual lights may display enhanced growth, especially if lights are installed close to the crop.

Seedlots with low vigour have been known to benefit from reduced grit depth. Part of this response may be due to increased light and oxygen penetration through to the seeds, or increased seed temperature if the intensity of light is high enough. Mostly it is attributed to reduced physical resistance to "emergence" above the seeds.

Relative Humidity

Assuming complete imbibition (*and moist/wet growing media*), the relative humidity near a seed (laminar boundary layer) during stage 1 needs to be as close to 100% as possible. Free water on seeds should be limited to a film, which will act as insurance against loss of moisture from within the seeds while not limiting gas exchange. Under no circumstances should seeds be submersed or "floating" for extended periods of time. During germination stage 1 seeds only take water up for various metabolic and physical processes. No transpiration is taking place, required, or even possible, hence any substantial vapour pressure deficit near seeds will only cause them to dry.

During stage 2 the radicle has emerged and cotyledons are turning green and unfolding, signalling the presence of chlorophyll and the ability to activate the photosynthetic process upon exposure to light. Transpiration of water vapour quickly increases in importance as the seedling needs to begin taking up water and nutrients from the soil solution, evaporatively cool itself, and maintain stomatal function. As soon as this stage is evident in the majority of the crop it is imperative that relative humidity levels are dropped (slightly) to allow transpiration to commence. Maintaining a stage 1 environment to allow late germinants to catch up can compromise early germinants. A judgement call eventually has to be made. Below ground the radicle needs to encounter an environment conducive to growth as well. Access to oxygen, mineral nutrients and water is imperative. Maintenance of gas exchange and temperature requires careful attention to irrigation management.

Evaporating water is one of the most effective cooling mechanisms... and can reduce the speed of germination

Relative humidity can influence the temperature of a moist surface and its LBL through the process of evaporative cooling. Evaporation occurs when there is a vapour pressure gradient between a moist surface and its surroundings—in this case the seeds, grit or media surface, and the surrounding air mass. Evaporating water is one of the most effective cooling mechanisms (e.g., goose bumps after climbing out of the lake on a hot summer day!). If relative humidity is low during stage 1, evaporation will occur from the seeds, grit, and media surface, thereby cooling them and the laminar boundary layer. This will reduce the speed of germination (respiration/growth rate) and may lead to reduced uniformity. Boundary layers and surfaces have been found to be as much as 5°C cooler than the adjacent air mass.

Besides cooling, any drying can effect a water stress, slowing or stopping the germination process. This would need to be overcome with extra misting or watering, resulting in additional cooling, and possibly a reduction in gas exchange for a period of time. Extreme desiccation will damage the emerging radicle or cause death of the germinant.

As the young seedling continues to grow, only a portion of it remains in the horizontal LBL above the container or growing media surface. If the boundary layer is much cooler than the media, adjacent air, or both, condensation can form on lower plant parts, encouraging disease organisms. Cooler plant parts function slower than warm plant parts, hence a bottleneck effect can occur in the stem (or roots) with respect to plant fluid flow. This can seriously compromise current and future seedling growth rate and function (e.g., early blossom-end rot of tomatoes).