

SECTION 8 SILVICULTURAL PRACTICES AND TREE SEED BIOLOGY

*Some seeds fell by the wayside, ...some fell upon stony places, ...and some fell among thorns;
...but others fell into good ground ...*
(The Bible, Matthew 13:3–8)

8.1 Background

Tree seed studies are often conducted or repeated under field conditions to better understand the significance of seed ecology in forest regeneration. The incentive for much forestry research on seeds is directly related to testing alternative silvicultural treatments that facilitate natural regeneration. This section will briefly review forest practices that affect regeneration by seeds, and offer some suggestions for studying seed dynamics under field conditions.

8.1.1 Principles of forest stand manipulation

In silviculture, the environmental factors discussed in Section 2 are manipulated to enhance the regeneration, establishment, and growth of desired tree crops. Most silvicultural practices are designed to alter either the canopy (the above-ground growing space), or the seedbed (the substrate for seedling establishment and the below-ground growing space).

Promoting forest regeneration from seeds requires a favourable combination of seed supply, seedbed, and environmental conditions (Figure 8.1), so many silvicultural practices are designed specifically to enhance these factors. Silvicultural practices may range from specialized procedures to induce tree seed production to the multipurpose practices of canopy opening and forest floor disturbance. Should these activities be unable to regenerate the desired tree species at target stocking levels, then specific site preparation operations are undertaken to create or improve microsites so they are more suitable for tree seedling establishment.

Regeneration silviculture is based on two important principles of forest ecology:

- Some level of disturbance (natural or artificial) is usually required to free plant growth resources and provide growing space for new trees (Bazzaz 1983; Canham and Marks 1985).
- Seed germination and seedling emergence are crucial steps in the life cycle of many plant species, and only a narrow range of conditions is suitable for seedling establishment (Grubb 1977; Harper 1977; Oswald and Neuenschwander 1993).

Much of the experimentation and monitoring associated with silvicultural research is therefore concerned with assessing the degree of disturbance achieved, or with evaluating the success of young trees in a variety of natural or modified microsites.

8.1.2 Standard silvicultural practices

Forest management activities are implemented over wide areas and long time periods. Timber harvesting, road development, resource zoning, and fire protection policies all affect large areas of land at the forest or landscape scale. However, to researchers studying seed ecology, activities performed at the stand level are more relevant. Typical stand-management activities may include resource inventories, protection from wildfire and pests, timber harvest, and stand renewal. Some activities, such as inventories, have no effect on a stand, while other activities, such as logging or prescribed burning, can be extremely disruptive. The fundamental principles of sustainable resource development and environmental protection assume

that, whatever the type of stand manipulation, all activities should be conducted in a manner that facilitates stand maintenance, rejuvenation, or restoration.

A silvicultural system is a set of stand management treatments for forest tending, harvesting, and replacement. Except for a brief overview, it is beyond the scope of this manual to describe the range of practices that comprise different silvicultural systems (see, for example, Matthews 1989). Each silvicultural system is composed of many individual components, and each component requires testing and modification to be applied effectively in a given forest type. Individual stand management treatments may be prescribed to alleviate some limiting factor, but in practice, numerous treatments usually are enacted as a package.

The amount of mature canopy retained during regeneration of a stand (or the nature of the first

stand entry into the stand for timber harvest) is typically used to describe the entire silvicultural system. In each system, the availability of tree seeds is largely determined by the density and distribution of the residual mature trees left in the stand. Five silvicultural systems used at the Lucille Mountain Project are illustrated in Figure 8.2.

- A clearcut system creates stand openings that are dominated by exposed, full sunlight conditions.
- A seed tree system is similar to a clearcut system in that it creates a microclimate characteristic of open conditions, but a few scattered trees are retained to provide seeds for natural regeneration.
- In shelterwood systems the density of residual trees is greater, so that the retained overstorey provides protection (from sun-scald, frost, etc.) to the regenerating tree crop.

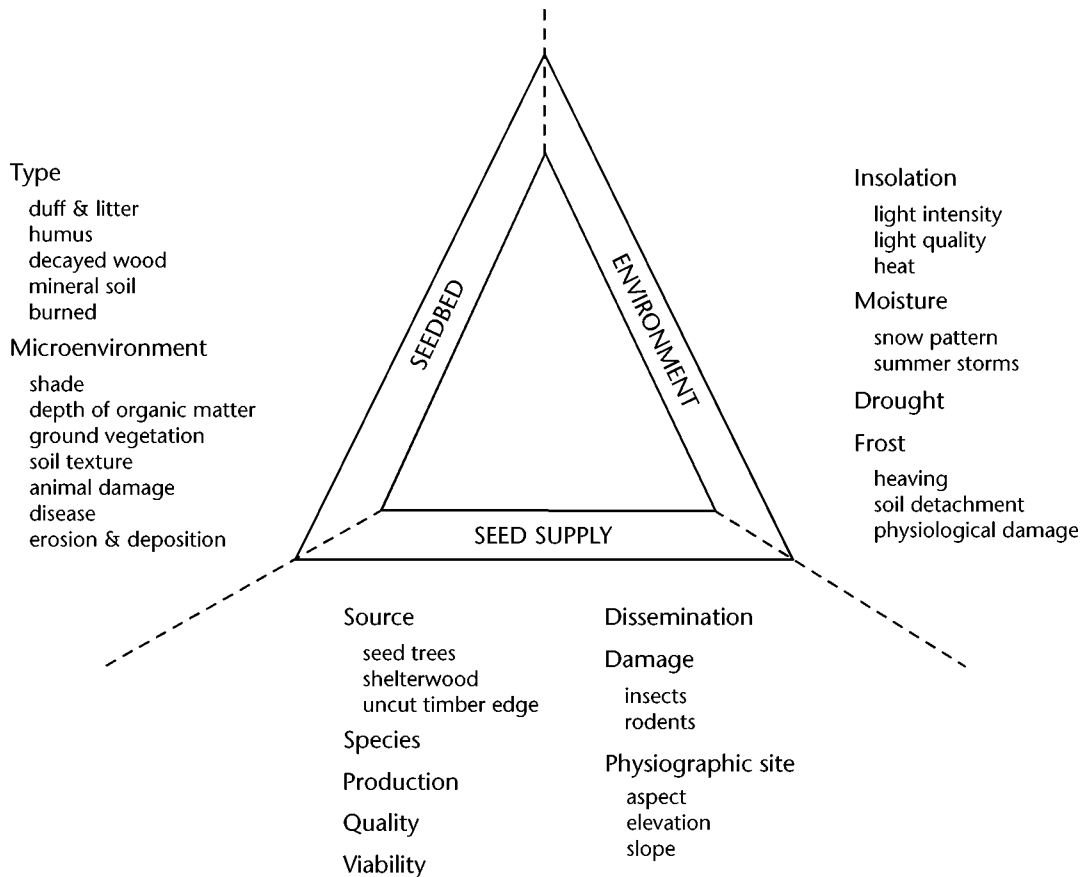


FIGURE 8.1 Effective natural regeneration depends on an adequate seed supply, a suitable seedbed, and an appropriate environment. All sides of this "natural regeneration triangle" must be adequate to achieve successful natural regeneration (from Roe et al. 1970).

- Clearcut, seed tree, and shelterwood systems regenerate even-aged stands. In selection systems, single trees or small groups of trees are harvested to regenerate the forest in smaller canopy gaps, maintaining continuous forest cover and an uneven-aged structure to the tree population.

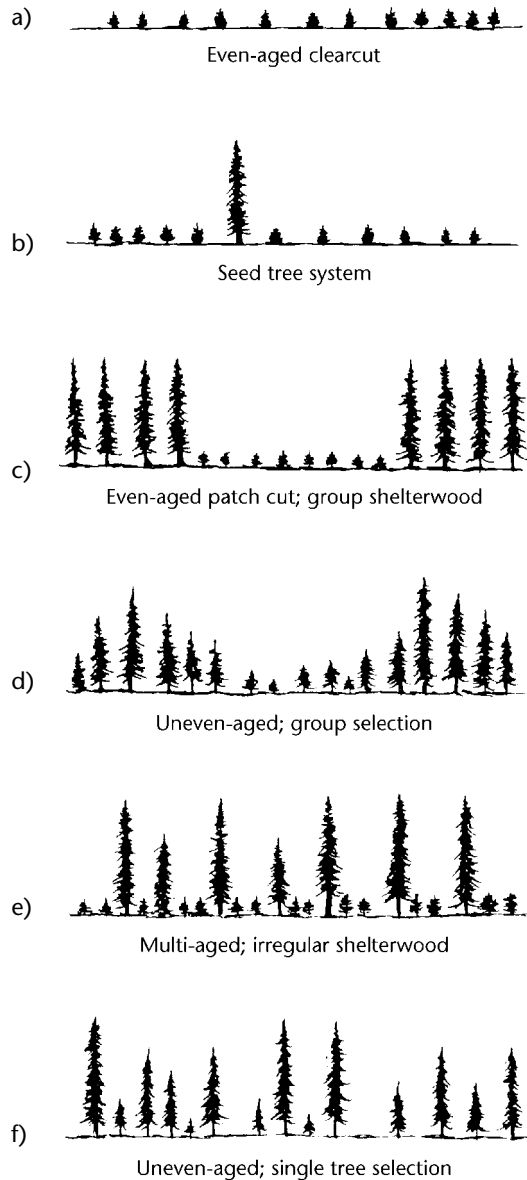


FIGURE 8.2 Illustration of stand structure resulting from different silvicultural systems used in the Lucille Mountain Project in the Engelmann Spruce–Subalpine Fir (ESSF) biogeoclimatic zone, Prince George Forest Region, British Columbia (adapted from Jull et al. 1996).

Silvicultural systems were originally designed to facilitate natural regeneration, usually by seeds. However, if natural regeneration proves unsuccessful or too unpredictable, dependence on natural seed availability can be bypassed through artificial regeneration, which introduces seeds or seedlings for stand renewal. Direct seeding can be undertaken in a broadcast manner (often from aircraft), but it is more effective if efforts are focused in spots or strips that have been prepared to favour germination and establishment (Mitchell et al. 1990). By planting seedlings, germination and early growth occur in the generally more favourable environment of forest seedling nurseries. Coppice systems count on the vegetative sprouting of stumps or roots (e.g., the profuse suckering of trembling aspen after harvest), which also bypasses the greater risks of reproduction and establishment of hardwoods from seeds.

Successful seedling establishment is a good indicator of the degree of canopy opening and forest floor disturbance that can be tolerated without degrading the ecosystem. For experimental purposes, some silvicultural practices may be performed and monitored on a relatively small scale—on research plots rather than on the entire stand. Treatments might include mounds made by hand or burning slash and forest floor with a propane torch. However, care should be taken when extrapolating the effects of microscale treatments to the probable effects of macroscale disturbance. The disturbance created by large equipment on soil properties, for example, is not equivalent to the effects created by hand equipment. Many treatments only produce reliable results if they are implemented with large machines over several hectares.

8.2 Effects of Canopy Manipulation

A complex of irradiance, temperature, humidity, wind, and other microclimate factors are associated with the shading and sheltering influence of forest canopies. These factors change in proportion to the degree of canopy opening in silvicultural systems. Indeed, silvicultural systems are classified in large part according to the degree they open the canopy in the first, or regeneration, cutting (Matthews 1989; Klinka et al. 1994).

The removal of part or all of the tree canopy releases light, water, and nutritional resources for seeds and seedlings, but it also often results in development of ground and shrub canopies that impose more restrictions than the original overstorey. Some interactions with other canopy-related factors may be difficult to anticipate, for example, the effects of one canopy layer on another layer, or the effects of different vegetation layers on the same microsite.

8.2.1 Light

The most immediate and dramatic effect of tree harvesting is increased light levels in the understory (Figure 8.3). Ecosystems vary in the degree to which increased light levels stimulate the growth of understory (shrub and herb) vegetation, and such growth may negate in a few years the effects of canopy opening on the forest floor. The increased amount of light caused by total canopy removal may stimulate the rate of germination of species such as pines (Li et al. 1994). For other species, partial canopy removal may be more favourable to germination and early survival because retaining partial canopy cover helps moderate the moisture and temperature of the seedbed. Protected microsites that maintain higher-than-ambient levels of humidity may not support optimal seedling growth, but still are important for seed germination and emergence (Frenzen and Franklin 1985; Battaglia and Reid 1993). Partial

canopy cover provides protection from sun scalding, photoinhibition, desiccation, and radiation frosts that might critically affect the survival of young, unignified seedlings.

8.2.2 Temperature

Canopy removal may have a greater influence on the temperature than on the light properties of microsites (Figure 8.4). Total forest canopy removal results in higher (and potentially lethal) soil temperatures and more extreme temperature fluctuations (Hungerford and Babbitt 1987; Stathers and Spittlehouse 1990), both of which can negatively affect seed germination and seedling survival. On the other hand, complete canopy removal and some forest floor disturbance are often beneficial at high elevations, high latitudes, or on northern exposures where soil temperatures may be too cold for germination (Bonan 1992; Balisky and Burton 1995).

8.2.3 Moisture

The most usual immediate effect of canopy removal is a rise in the water table; the loss of tree cover reduces transpiration and increases moisture in the root zone. However, the removal of a tree canopy exposes the soil surface to direct sun, to high surface temperatures, and to increased wind speed, and this can result in rapid drying of the surface layers that constitute the seedbed. These conditions often arise

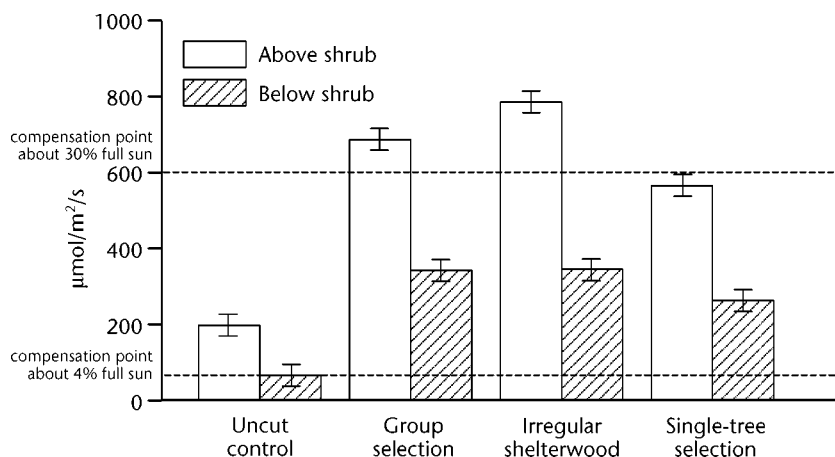


FIGURE 8.3 Measured levels of photosynthetic active radiation (PAR) available to seedlings above and below the shrub layer in various partial cut systems at the Lucille Mountain Project, Prince George Forest Region, British Columbia (Jull et al. 1996). Results are shown for treatments illustrated in Figure 8.2d, e, and f.

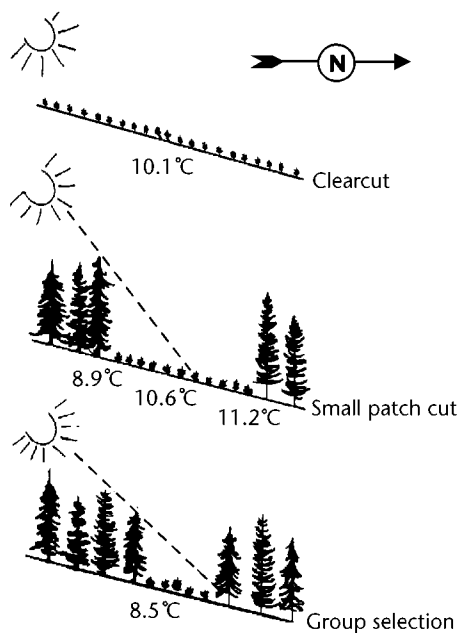


FIGURE 8.4 Growing-season soil temperatures (at 10 cm depth, 4-year means) on a north-facing slope in clearcut, small patch cut, and group selection treatments (Jull et al. 1996). Results are shown for treatments illustrated in Figure 8.2 a, c, and d.

after canopy removal in clearcuts, and historically, have been the major reason to develop silvicultural systems that provide better protection to seedbeds and to newly established seedlings.

8.2.4 Suggested questions and approaches

Monitoring of tree seed germination and early seedling population dynamics is often part of evaluating the effectiveness of silvicultural systems in promoting forest regeneration. Much of the incentive for choosing one silvicultural system over another is the expectation that one method is more effective in producing seeds or creating better conditions for germination and early seedling survival. In some stands, trees are retained to provide seeds or to protect young seedlings (such as seed tree, shelterwood, strip cut, and some patch-retention systems). Questions that might be asked in regeneration silviculture field trials include the following:

- Is cone production per tree greater in partially girdled trees than in untreated trees?

- Is seed rain density significantly greater under a shelterwood system than a seed tree system?
- Is tree seed germination more successful with or without some canopy cover? Does this vary by species and latitude?
- What is the seed-to-seedling ratio under alternative stand treatments?
- Can a given stand or stand treatment meet a desired level of stocking through natural regeneration?
- What level of canopy retention significantly reduces (or increases) early seedling survival?
- Does one tree species germinate and/or establish better than another under a particular canopy treatment (e.g., a shelterwood cut removing 50% basal area)?
- Do canopy effects on germination depend on seedbed conditions? For example, is shade better for germination on all substrates, or just for seeds germinating in the duff layer?
- What is the relation between canopy reduction, understory development, and the light and resource levels of the seedbed?

The objective of many studies is to correlate indicators of successful natural regeneration with various canopy openings. For example, tree seedling establishment has been correlated with canopy density, subcanopy irradiance levels (e.g., Burton and Mueller-Dombois 1984; Stewart 1988; Canham et al. 1990; Denslow and Hartshorn 1994), specific environmental variables (Geier-Hayes 1987; Oswald and Neuenschwander 1993; Denslow and Hartshorn 1994), or site variables. Seedling establishment is usually enhanced in forest gaps or disturbances (Platt and Strong 1989; Coates and Burton [1998]), but under extreme environmental conditions better establishment may be found in protected, shaded microsites (Frenzen and Franklin 1985). Evaluating the success or failure of silvicultural treatments may depend on when the assessment is made (i.e., after one growing season or after 5 years). Successful establishment of seedlings may depend more on the ability of germinants to survive on a particular site than on the number of seeds that initially germinate (Burton 1997). Optimal conditions for seed germination are not necessarily optimal for plant survival and growth of the same species (Parrish and Bazzaz 1985; Oswald and Neuenschwander 1993; Schupp 1995).

Once relationships are noted, more detailed experiments may be undertaken to verify initial study results. This may be accomplished, for example, by studying the effects of canopy shading on tree seed germination in glasshouses or slathouses where shade levels can be controlled (e.g., Minore 1972; Alexander 1986). In this regard, note that “neutral shade” treatments created in slathouses are sometimes considered unrealistic because they do not mimic the spectral shift normally found under plant canopies. In neutral shade treatments, light passes through a filter with no change in the relative proportions of various wavelengths. Under plant canopies, the light spectrum has proportionately less light in the red and blue wavelengths and more in the green wavelengths (see Section 2.3.3. and Figure 2.4). Nevertheless, neutral shade is a useful experimental tool because it allows researchers to vary the quantity of light while maintaining constant light quality.

Often, the next step after conducting controlled studies is to introduce pre-counted seeds into field plots. Section 7.3 outlines some methods for how to study germination under field conditions. Treatments may consist of canopies comprising different species (Burton and Bazzaz 1991) or different degrees of canopy opening to test, for example, the effects of full shade, partial shade, and full sun on direct seeding spots (Smith and Clark 1960; Burton 1997). Canopy cover effects can be measured within a stand, or at different distances from a stand edge (Burton 1996; Coates and Burton [1998]). These two conditions evaluate slightly different aspects of the influence of light and shade; different canopy thinning levels alter the size and duration of sunflecks, while plots placed at different distances from a stand edge differ primarily in the daily duration of uninterrupted direct sunlight.

When studying canopy treatment effects on seed production, seed rain density, or seed dispersal, differences in the seed supply are of greater importance than differences in the amount or quality of light. Seed trap arrays, either randomly distributed under different canopy treatments or in transects away from a stand edge, are one of the most common methods for monitoring the influence of forest canopies on seed supply (Figure 4.5 and Section 4.4).

8.3 Effects of Seedbed Manipulation

The success of natural regeneration or direct seeding depends, in part, on how well seedbed environments meet the requirements for seed germination and seedling establishment. The suitability of seedbeds is determined by many factors, including their thickness, water-holding capacity, hydraulic continuity, thermal properties, and chemistry. These factors are so inextricably linked that ecological and silvicultural researchers have found it useful to characterize the seedbed as a single (though complex) environmental factor or metafactor, which is usually described as a categorical variable.

8.3.1 Seedbed preferences

Microsites are sometimes evaluated as a way to compare the suitability of seedbeds. In the following discussion, the term *seedbed* could include many different types of microsites for seed germination, such as different elevations or aspects of a mound or berm, or different degrees of mixing of the forest floor with the mineral soil.

Typical seedbeds encountered in managed forests include mineral soil (compacted or not compacted), forest floor (possibly divided into undecomposed litter and decomposed humus layers), logs or rotting wood, and mats of mosses or lichens. Other substrates, such as bare rock, standing water, or undecomposed logging slash, are never considered as potential seedbeds. Combinations of materials are sometimes recognized, such as moss on rotting wood versus moss on mineral soil, or different (measured) thicknesses of forest floor over mineral soil or rock. Most of these materials are considered to be distinct when consumed or scorched by fire.

Because of wide differences in physical characteristics, temperatures, and the availability of water and mineral nutrients, seedling establishment varies greatly in different natural seedbeds (see Table 8.1 and example in Section 8.3.4). Mineral soil is a good seedbed because of its high infiltration capacity, adequate aeration, and close contact between soil particles and seeds (Kramer and Kozlowski 1979). Although mineral soils warm earlier and attain higher temperatures in the spring, in bright sunlight the surface

TABLE 8.1 Comparative seedbed suitability of some northwestern tree species (from Minore 1979). Species in the upper groups are better suited to the seedbed than those in lower groups. Data are insufficient for species comparisons within the groups.

Organic seedbeds		Mineral soil seedbeds		Burned seedbeds
Coastal	Interior	Coastal	Interior	
<i>Tsuga heterophylla</i>	<i>Picea glauca</i> ,	<i>Alnus rubra</i>	<i>Larix occidentalis</i> ,	<i>Pseudotsuga menziesii</i> , <i>Abies grandis</i> , <i>Pinus ponderosa</i> <i>Tsuga heterophylla</i> , <i>Larix occidentalis</i> , <i>Picea engelmannii</i> , <i>Pinus contorta</i> <i>Thuja plicata</i> , <i>Pinus monticola</i> , <i>Abies lasiocarpa</i>
<i>Thuja plicata</i>	<i>Pseudotsuga menziesii</i>	<i>Picea sitchensis</i>	<i>Picea engelmannii</i>	
<i>Picea sitchensis</i>	<i>Abies lasiocarpa</i> ,	<i>Thuja plicata</i>	<i>Pinus contorta</i> ,	
<i>Alnus rubra</i>	<i>Pinus contorta</i>	<i>Tsuga heterophylla</i>	<i>Abies lasiocarpa</i>	
	<i>Larix occidentalis</i> ,		<i>Pseudotsuga menziesii</i> ,	
	<i>Picea engelmannii</i>		<i>Picea glauca</i>	

temperature of mineral soils and burned materials can become so high as to be lethal to germinating seeds. However, when moisture is adequate, most native British Columbia hardwoods and conifers germinate best on mineral soil seedbeds.

Litter and duff are less suitable than mineral soil because they warm slowly, inhibit root penetration, prevent good seed–mineral soil contact, dry rapidly, and shade small seedlings. Sphagnum moss often is a suitable seedbed because of its high water-holding capacity, but it may subsequently smother young seedlings. Decayed wood is also an excellent natural seedbed for seeds of forest trees, probably because of its capacity for water retention (Knapp and Smith 1982; Harmon et al. 1989). However, although forest floor (or duff) and moss layers may be suitably moist during the spring, they often dry out faster than mineral soil and rotting wood. Therefore, organic materials usually form better seedbeds when they are under partial shade.

Duff seedbeds are better tolerated by large-seeded species because these species can use their stored reserves to subsidize radicle penetration to the mineral soil. Thus, in boreal and subalpine forests, an organic forest floor is an acceptable substrate for true fir (*Abies* spp.) seeds (Alexander et al. 1984), but would not be suitable for the smaller seeds of spruce (*Picea* spp.) (Noble and Ronco 1978; Klein et al. 1991). Some

species can establish on both mineral soil and on moss and duff. If sufficient moisture is present, amabilis fir, subalpine fir, tamarack, Engelmann spruce, black spruce, Sitka spruce, Douglas-fir, western hemlock, and mountain hemlock have been found to germinate well on organic and inorganic substrates (Fowells [compiler] 1965; McCaughey 1993).

For some species, the properties of organic substrates preclude seedling establishment. Western redcedar, because of its small seeds, germinates poorly on duff (Fowells [compiler] 1965). Similarly, mineral soil and rotten logs are best for the germination and initial establishment of the very small seeds of paper birch. Newly germinated seedlings are extremely fragile; a paper birch seed that germinates on a fallen hardwood leaf cannot push its radicle through to the moist soil, and if it germinates under a leaf, the tiny seedling is almost always cut off from the light (Hutnik 1954).

The relatively large seeds of bigleaf maple and Garry oak have little problem penetrating leaf litter and organic substrates. Under field conditions, bigleaf maple germination often occurs on relatively undisturbed seedbeds in association with leaf litter and other organic substrates (Tappeiner and Zasada 1993). The best natural seedbed for Garry oak is moist soil covered with 2 cm or more of leaf litter. After

germination, the radicle quickly penetrates deep into the moist mineral soil (Fowells [compiler] 1965). In undisturbed forest, white spruce and western hemlock seedlings often are found on decayed wood, which has several advantages over most other natural seedbeds. For these small seeds, decayed wood usually provides more moisture, less chance of smothering conditions, and freedom from damping-off (Fowells [compiler] 1965).

Very wet conditions are required by western white pine and ponderosa pine seeds for germination and seedling survival, and they are thus restricted more by water availability than by a specific substrate (Fowells [compiler] 1965). Delayed germination and the inability of Rocky Mountain juniper to establish on dry sites probably account for its generally sparse natural regeneration. Juniper seedlings are found most often in the moist soil of rocky crevices and in canyons near perennial water (Fowells [compiler] 1965). Under natural conditions, poplar and willow seeds require a steady supply of water during germination and early seedling development. Seeds of both species can germinate while floating in water or when fully submerged (Wyckoff and Zasada [1998]; Zasada et al. [1998]). The high water requirements of these species is primarily due to their unique pattern of epigeal germination (Figure 7.5). In both poplars and willows, the radicle does not emerge immediately, but instead, a ring of fine hypocotyl hairs (the coronet) performs the dual function of water absorption and initial attachment of seeds to the substrate. Seedlings often fail to survive because the root hairs dry too quickly or fail to securely attach seeds to the soil.

Seedbeds can be manipulated to favour establishment by certain species. The rapid growth of hardwoods may pose serious competition problems for conifers. Red alder, which establishes quickly in full sunlight on exposed mineral soil, is an aggressive pioneer of avalanche paths, road cuts, log landings, skid trails, or other areas where mineral soil has been freshly exposed to seedfall. To exclude red alder, some forest managers try to reduce alder seed supplies by removing seed trees in the vicinity, and by disturbing the site as little as possible to avoid creating favourable seedbed conditions for red alder (Lousier and Bancroft 1990).

8.3.2 Site preparation

Mechanical site preparation equipment was first used to expose mineral soil for natural regeneration, not for planting (Smith 1986). Mechanical site preparation not only modifies the relative abundance of seedbed materials by increasing the exposure of mineral soil, but also creates new microsites with raised or depressed elevations or changes in aspect. Site preparation operations may remove, mix, or invert the organic layer and upper soil horizon to create suitable microsites for seedling establishment (often called planting spots) (McMinn and Hedin 1990). Some seedbed scarification methods, such as dragging anchor chains or shark-fin barrels, remain common means to enhance natural regeneration of lodgepole pine and western larch.

Prescribed burning is detrimental to natural regeneration of conifers because conifer seeds are generally on or close to the surface of the forest floor, and are therefore vulnerable to even a low-severity fire. However, fire creates seedbeds with better heat-holding capacity and seed-substrate contact, and if some residual cover and seed trees remain in the surrounding area, seeds dispersed after a fire are more likely to establish greater numbers of seedlings. Prescribed burning releases nutrients more rapidly than through usual biological degradation processes; however, depending on site factors, these may or may not be available to seedlings (Chapter 22 in Pritchett 1979).

8.3.3 Suggested questions for seedbed studies

Field seedbed research generally focuses on comparing different seedbed attributes (type, amount, or response to manipulation) and how they affect tree establishment. Substrate manipulation does not usually affect seed availability on the ground, because natural seedfall is primarily related to the overstorey. Seed banks and seed predators could, however, be influenced by site preparation. Site preparation can influence the microtopography of the seedbed and, for very small seeds such as willows and poplars, this can be critical. A heterogeneous seedbed comprised of particles of litter or soil prominences can strand these seeds on rapidly drying surfaces where either seeds do not germinate, or root hair growth is insufficient to make firm contact with the water-supplying substrate (McDonough 1985).

Typical research questions associated with seedbed manipulation include the following:

- Which seedbed type is best for conifer or hardwood germination and establishment?
- Is there a critical thickness of forest floor material above which germination or early seedling survival is inhibited?
- Does site preparation (e.g., broadcast slash burning, mechanical site preparation) stimulate or inhibit germination—from the seed bank? —of fresh seeds deposited on the ground surface?
- Is seedling recruitment density significantly greater with or without seedbed scarification (e.g., dragging anchor chains)?
- Is tree seed germination more successful on untreated forest floor or in scarified patches with exposed mineral soil?
- What is the seed-to-seedling ratio under alternative site preparation treatments?
- Will seedbeds suffer greater predation in forested or in open conditions?
- Does one tree species germinate and/or establish better than another under a particular site preparation treatment (e.g., a broadcast slashburn)?
- Does the influence of seedbeds on tree seed germination depend on canopy conditions? For example, is mineral soil significantly better than organic substrates for germination under all canopy conditions, or just in open areas?
- How quickly do seedbeds “deteriorate” and how does this affect seed-to-seedling ratios?
- Can seedbeds be manipulated to enhance (or reduce) hardwood regeneration relative to that of conifers?

8.3.4 Methods for seedbed research

Some seedbed studies have used sieved materials in pots placed in growth chambers or greenhouses (Minore 1972; Ahlgren and Ahlgren 1981). Such studies may be used to demonstrate allelopathic effects (such as Brown 1967; Yoder-Williams and Parker 1987), but do not replicate the thermal and moisture dynamics affecting seed germination in forest seedbeds. Pots or trays containing experimental seedbeds, even when used in the field (though less so if buried in the ground), dry more rapidly along the edges,

or retain moisture at the base. Seedbed trials are best conducted within frames (cylindrical or rectangular) that allow full hydraulic contact of the test material with the underlying soil. At the very least, containers should be placed flush with the ground surface.

Another approach is to use removable germination containers filled with intact substrate from the study site. Haeussler et al. (1995) constructed cylinders (8 cm diameter, 5 cm high) from PVC pipe and glued fine nylon mesh to the base. A core of forest floor or mineral soil was removed from the plot and placed intact into a container. The container was replaced into the core hole with its upper rim protruding 1 cm. Seeds were sown into each container, and a protective cage to exclude predators (60 mm plastic mesh measuring 8 × 8 cm, 6 cm high) was staked over each germination container.

The establishment of tree seedlings on a variety of substrates has been investigated for many ecosystems (Fisher 1935; Minore 1972). While controlled and replicated experimental treatments are preferable, the same information can be inferred from sample surveys comparing the observed abundance of seedlings found on different seedbeds with the expected abundance of seedlings on those seedbeds (Christy and Mack 1984; Geier-Hayes 1987). Only young or small seedlings (less than 5 years old) should be counted because the seedbeds from which they are derived can deteriorate over time. This approach is discussed in the following example and in Table 8.2a and Table 8.2b.

EXAMPLE

(P. Burton and N. Daintith, unpublished data)

Objective. To determine whether naturally regenerated subalpine fir, interior spruce, and Douglas-fir seedlings exhibit any association with different seedbeds within a partially cut Douglas-fir stand.

Hypothesis. If there is no difference between substrates for germination and establishment of tree seedlings, then the abundance of seedlings found on each substrate will be proportional to the abundance of that substrate.

Method. Seedbed abundance in an interior Douglas-fir stand northeast of Williams Lake, B.C., was measured by estimating percent cover along line transects spaced at regular intervals (Table 8.2a). All

TABLE 8.2(a) *The relative abundance of seedbed substrates in an interior Douglas-fir stand (P. Burton and N. Daintith 1994, unpublished data)*

	Mineral soil	Disturbed duff/moss	Undisturbed duff/moss	Rotten wood
seedbed as % of total area	2.74	11.88	66.73	18.65

TABLE 8.2(b) *Expected and observed seedling association with four forest floor substrates in an interior Douglas-fir stand*

	Mineral soil		Disturbed duff/moss		Undisturbed duff/moss		Rotten wood		Total observed seedlings	Chi-square value ^a
	Exp	Ob	Exp	Ob	Exp	Ob	Exp	Ob		
Subalpine fir	1.2056	0	5.2272	2	29.3612	22	8.2060	20	44	21.99
Interior spruce	0.5206	0	2.2572	1	12.6787	5	3.5435	13	19	31.11
Douglas-fir	3.7264	0	16.1568	1	90.7528	42	25.3640	93	136	224.49

Exp = expected number of seedlings (null hypothesis);

Ob = observed number of seedlings (survey data).

^a See chi-square calculations below.

Calculations to determine the goodness-of-fit for different seedling and seedbed associations

Subalpine fir:

$$\begin{aligned}
 \text{Chi-square} &= \sum (\text{observed} - \text{expected})^2 / \text{expected} \\
 &= (0-1.2056)^2 / 1.2056 + (2-5.2272)^2 / 5.2272 + (22-29.3612)^2 / 29.3612 + (20-8.2060)^2 / 8.2060 \\
 &= 1.2056 + 1.9924 + 1.8455 + 16.9508 \\
 &= 21.99 \text{ (exceeds the critical value 7.815)}
 \end{aligned}$$

Interior spruce:

$$\begin{aligned}
 \text{Chi-square} &= \sum (\text{observed} - \text{expected})^2 / \text{expected} \\
 &= (0-0.5206)^2 / 0.5206 + (1-2.2572)^2 / 2.2572 + (5-12.6787)^2 / 12.6787 + (13-3.5435)^2 / 3.5435 \\
 &= 0.5206 + 0.7002 + 4.6505 + 25.2365 \\
 &= 31.11 \text{ (exceeds the critical value 7.815)}
 \end{aligned}$$

Douglas-fir:

$$\begin{aligned}
 \text{Chi-square} &= \sum (\text{observed} - \text{expected})^2 / \text{expected} \\
 &= (0-3.7264)^2 / 3.7264 + (1-16.1568)^2 / 16.1568 + (42-90.7528)^2 / 90.7528 + (93-25.3640)^2 / 25.3640 \\
 &= 3.7264 + 14.2187 + 26.1902 + 180.3591 \\
 &= 224.4944 \text{ (exceeds the critical value 7.815)}
 \end{aligned}$$

the seedlings encountered in separate regeneration survey plots were classified according to the seedbed in which they were found (*observed values*, Table 8.2b). The *expected value* in each cell (seedbed/species category) is derived from the percentage of the seedbed area multiplied by the total number of seedlings of the species encountered (e.g., 2.74% mineral soil \times 44 subalpine fir seedlings = 1.2056).

Chi-square values are calculated separately for each species based upon *observed* and *expected* values, as shown below. Values are calculated for each seedling and seedbed association, then summed to create a chi-square test statistic for the species.

If the chi-square test statistic for a species exceeds the critical value (determined from published tables of the chi-square distribution), then seedbeds—in general—have a significant effect on seedling establishment. In addition, if one value of the sum exceeds the critical value, then that individual value is significantly different.

Null hypothesis. In Table 8.2a, the null hypothesis of random association of seedlings and seedbeds is rejected for $\alpha = 0.05$ and degrees of freedom = 3 (number of seedbed categories, minus one).

Results:

1. The calculated chi-square test statistic exceeded the critical value (7.815) for each species, indicating that the observed seedling/seedbed associations were non-random.
2. A comparison of chi-square test statistics for different seedbeds shows that values contributed by rotten wood exceeded the critical value (7.815) for all three species: subalpine fir (16.9508), interior spruce (25.2365), Douglas-fir (180.3591).
3. In addition, for Douglas-fir, the calculated chi-square test statistic exceeded the critical value (7.815) for disturbed duff/moss (14.2187) and for undisturbed duff/moss (26.1902). Therefore, the lack of seedling establishment on those seedbeds could not be attributed merely to chance.

Conclusions:

Calculated chi-square test statistics for all three tree species confirmed that different seedbeds within a partially cut interior Douglas-fir stand significantly affected seedling establishment.

Comparisons of expected and observed seedling and seedbed associations indicate that seedlings of all three species were found more frequently on rotten wood, and that Douglas-fir seedlings did not establish well on duff/moss substrates. It is not known whether Douglas-fir seeds were unable to germinate on moss/duff substrates, or whether the seedlings emerged, but did not survive.

Cautions on use of the chi-square statistic:

The use of the chi-square test statistic is conditional upon achieving expected values greater than 5.0. An expected value greater than 5.0 must be obtained for the test statistic to be chi-square distributed (Lesperance 1996). In this example, all of the expected values for mineral substrates were less than 5.0, as were the expected values for interior spruce on disturbed duff/moss and rotten wood.

If this situation occurs, there are several alternatives to employ:

1. Increase the sample size. To calculate the sample size required, divide the expected value needed (5.0) by the percentage of the least abundant substrate. In this example, mineral soil represents 2.74% of the total seedbed area. Thus, the minimum number of seedlings required for each species would be $5.0 \div 0.0274 = 182.48$ seedlings.
2. Combine the data in different columns. Observations for mineral soil could be combined with the observations for disturbed duff/moss or rotten wood. In this case, combining data is probably not a viable option because mineral soil is very different from the other substrates.
3. Rather than assume the chi-square distribution, use a random procedure to determine the empirical distribution. Refer to Manly (1997) for further information on this topic.

Inferring substrate suitability from a one-time survey (as in the example above) may be adequate for some purposes, but understanding the actual constraints to natural regeneration requires establishing controlled treatment plots and evaluating tree seedling emergence and survival over time. In this way, the effects of seed rain, seed predation, seed germination, and germinant survival may be evaluated separately.

For example, seeds may germinate in a wide range of microsites, but may fail to survive as a result of drought conditions over the summer (Potts 1985; Burton 1997). Better-than-average survival is often noted in cohorts of seedlings that germinate earlier, rather than later, in the spring (Zasada et al. 1983). Low seedling densities may not be due to the seedbed, but rather to the limited availability of seeds, the seed-shedding behaviour of associated vegetation, or local activity and habitat preferences of seed predators. Conversely, high numbers of seedlings in a particular microsite may be due to the capture of seeds drifting on a crusted snow surface, to microsites of exposed mineral soil, or to unusually abundant soil water during the growing season (Matlack 1989). If the factors (and their interactions) promoting good regeneration are not understood, site preparation methods cannot be successfully applied to other locations.

8.4 Combined Studies

Studies of seed germination and seedling establishment can be combined with seed rain monitoring to select the optimal width for patch cuts and strip cuts for natural regeneration (see Noble and Ronco 1978; McDonald and Abbott 1994). By coupling seed rain with seedling survival, estimates can be made of the seed-to-seedling ratios required to establish a single seedling that survives to a given age (e.g., 5 years) (see Alexander 1986; Walker et al. 1986).

Seed-to-seedling estimates help us understand the dynamics of major factors influencing successful reforestation of a site. Even with good seed supplies and high emergence, seedling survival can differ significantly among sites and seedbeds, in different years, and between clearcut and forest conditions. For example, in the first growing season, heat and drought accounted for 60% of red alder seedling mortality in clearcuts compared to only 5% of red alder mortality in forests (Haeussler et al. 1995). Later other factors became more important. During the first winter, soil erosion, frost heaving, and freezing together caused over 60% of mortality in clearcuts; during the second growing season, crushing under litter or vegetation (40%) was the primary mortality factor.

Because young seedlings usually require some protection during the first growing season, the interactions between site preparation and shade treatments are often evaluated. For example, Alexander (1986) found that germination and survival of Engelmann spruce in Colorado was poorer on sites that were left unscarified and/or unshaded. Cain (1991) noted that seedbed preparation resulted in better survival of understory loblolly (*Pinus taeda*) and shortleaf pine (*Pinus echinata*); however, the chemical removal of hardwoods in the canopy (with or without seedbed scarification) was even more important than seedbed treatments in promoting pine survival.

The Engelmann Spruce–Subalpine Fir (ESSF) biogeoclimatic zone is one of the most extensive forest zones in British Columbia, but it is also one of the province's most severe climates for forest growth. To determine the best conditions in this area for the natural regeneration of subalpine fir and Engelmann spruce, germination plots received a number of seeding and silvicultural treatments: screefed and seeded (DS), screefed and not seeded (DN), undisturbed and seeded (US), or undisturbed and not seeded (UN) (Jull et al. 1996). Disturbed forest floor, created either by screefing or logging disturbance, dramatically improved the germination of both spruce and subalpine fir seeds (Figure 8.5). Direct seeding of the plots with undisturbed forest floor only slightly improved the total number of germinants relative to unseeded plots. Very small numbers of germinants were observed in clearcut areas when additional seeds were not supplied, even though 1993 (the year in which the study was conducted) was a year of relatively high seed production in the surrounding stands. These results indicate that natural seed supplies cannot be relied on for the reforestation of clearcuts in this area.

8.5 Summary

Seeds, by virtue of their small size, respond to the environmental conditions prevailing within a relatively small microsite. Much of the research and documentation of seed germination ecology under natural conditions thus involves the classification, modification, or monitoring of microsites and the

behaviour of seeds and seedlings within them. Farmer (1997) provides a useful summary of forest microsites as regeneration niches, and how these microsites might be studied and manipulated.

Even the simplest field investigations of seedbed and canopy effects (whether natural or manipulated) constitute a challenging exercise in ecosystem ecology. The potential of a site to support natural regeneration or successful regeneration by direct seeding cannot be

evaluated by a single factor isolated from other environmental or site variables. Even though canopy and seedbed influences are, in themselves, complex meta-factors, careful consideration must also be given to a range of other influences, including local climate, the silvics of different tree species, the microsite attributes of vegetation and soil, and many of the other factors that comprise the physical and biological matrix upon which successful natural regeneration depends.

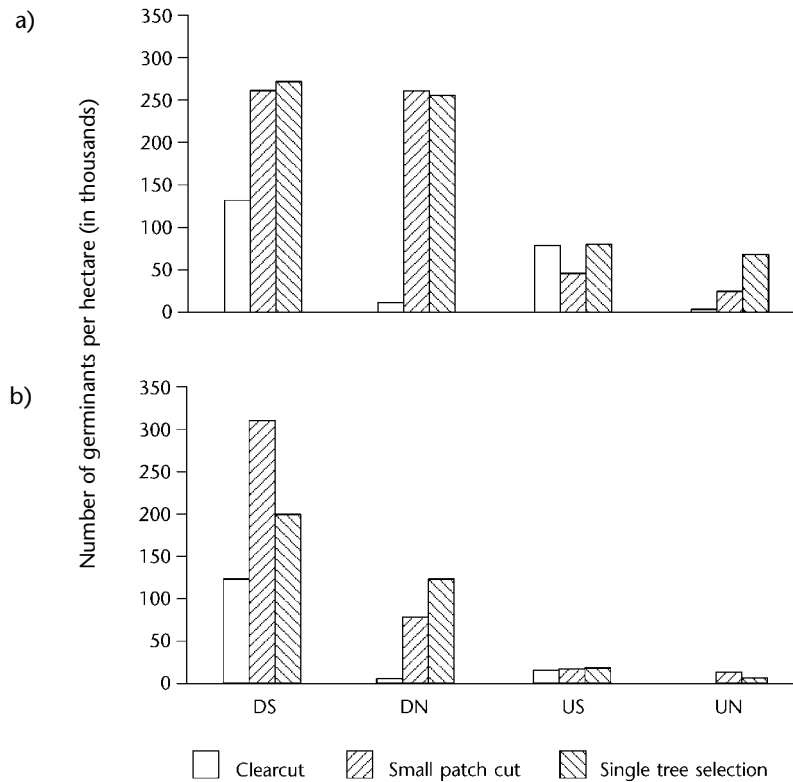


FIGURE 8.5 Number of (a) subalpine fir and (b) Engelmann spruce germinants per hectare within three silvicultural treatments at the Lucille Mountain Project, Prince George Forest Region, British Columbia (Jull et al. 1996). Results are shown for treatments illustrated in Figure 8.2a, b, and e. DS = screeded and seeded, DN = screeded and not seeded, US = undisturbed and seeded, UN = undisturbed and not seeded.

APPENDIX A Tree Species Occurring in British Columbia**Gymnosperms**

Scientific name/authority	Common name
<i>Abies amabilis</i> (Dougl. ex Loud.) Forbes	amabilis fir
<i>Abies grandis</i> (Dougl. ex D.Don in Lamb.) Lindl.	grand fir
<i>Abies lasiocarpa</i> (Hook.) Nutt.	subalpine fir
<i>Chamaecyparis nootkatensis</i> (D.Don in Lamb.) Spach	yellow-cedar
<i>Juniperus scopulorum</i> Sarg.	Rocky Mountain juniper
<i>Larix laricina</i> (Du Roi) K.Koch	tamarack
<i>Larix lyallii</i> Parl. in DC.	subalpine larch
<i>Larix occidentalis</i> Nutt.	western larch
<i>Picea engelmannii</i> (Parry ex Engelm.)	Engelmann spruce
<i>Picea glauca</i> (Moench) Voss	white spruce
<i>Picea mariana</i> (P.Mill.) B.S.P.	black spruce
<i>Picea sitchensis</i> (Bong.) Carr.	Sitka spruce
<i>Pinus albicaulis</i> Engelm.	whitebark pine
<i>Pinus banksiana</i> Lamb.	jack pine
<i>Pinus contorta</i> Dougl. ex Loud. var. <i>contorta</i>	shore pine
<i>Pinus contorta</i> Dougl. ex Loud. var. <i>latifolia</i> Engelm.	lodgepole pine
<i>Pinus flexilis</i> James	limber pine
<i>Pinus monticola</i> Dougl. ex D.Don in Lamb.	western white pine
<i>Pinus ponderosa</i> Dougl. P. & C. Lawson	ponderosa pine
<i>Pseudotsuga menziesii</i> (Mirb.) Franco var. <i>glauca</i> (Beissn.) Franco	Rocky Mountain (interior) Douglas-fir
<i>Pseudotsuga menziesii</i> (Mirb.) Franco var. <i>menziesii</i>	coastal Douglas-fir
<i>Taxus brevifolia</i> Nutt.	Pacific yew
<i>Thuja plicata</i> Donn ex D.Don in Lamb.	western redcedar
<i>Tsuga heterophylla</i> (Raf.) Sarg.	western hemlock
<i>Tsuga mertensiana</i> (Bong.) Carr.	mountain hemlock

Angiosperms

Scientific name/authority	Common name
<i>Acer macrophyllum</i> Pursh	bigleaf maple
<i>Alnus rubra</i> Bong.	red alder
<i>Arbutus menziesii</i> Pursh	arbutus
<i>Betula papyrifera</i> Marsh.	paper birch
<i>Betula papyrifera</i> var. <i>neoalaskana</i> (Sarg.) Raup.	Alaska paper birch
<i>Cornus nuttallii</i> Aud. ex T. & G.	Pacific dogwood
<i>Fraxinus latifolia</i> Benth.	Oregon ash
<i>Malus fusca</i> (Raf.) Schneid.	Pacific crab apple
<i>Populus balsamifera</i> L. ssp. <i>balsamifera</i>	balsam poplar
<i>Populus balsamifera</i> L. ssp. <i>trichocarpa</i> (T. & G.) Brayshaw	black cottonwood
<i>Populus tremuloides</i> Michx.	trembling aspen
<i>Prunus emarginata</i> (Dougl.) Walp.	bitter cherry
<i>Prunus pensylvanica</i> L.	pin cherry
<i>Quercus garryana</i> Dougl.	Garry oak
<i>Rhamnus purshiana</i> DC.	cascara
<i>Salix amygdaloides</i> Anderss.	peach-leaf willow
<i>Salix bebbiana</i> Sarg.	Bebb's willow
<i>Salix discolor</i> Muhlenb.	pussy willow
<i>Salix exigua</i> Nutt.	sandbar willow
<i>Salix lucida</i> Muhl. ssp. <i>lasiandra</i> (Benth.) E. Murray	Pacific willow
<i>Salix scouleriana</i> Barratt ex Hook.	Scouler's willow

Standard species names and codes for British Columbia can be found in both ACCESS 2.0 and EXCEL 4.0 files at the B.C. Ministry of Forests Research Branch FTP site (142.36.141.53) (anonymous login) in the directory /pub/provspp. They are regularly revised and updated.

APPENDIX B Conversion Factors

Imperial units		SI equivalents	Approximate conversion factors for light	
Length			Daylight, full sun*	
1 chain = 66 feet	=	20.1168 m (exactly), or a 50 or 75 m nylon tape	950 W m ⁻² = 1.36 cal cm ⁻² min ⁻¹ ≅ 95,000 lux of this PAR (400–700 nm) is: 1800 μmol photons m ⁻² s ⁻¹ ≅ 399 W m ⁻² = 0.572 cal cm ⁻² min ⁻¹ = 42% of total. ∴ 1 W m ⁻² (total) ≅ 1.895 μmol photons m ⁻² s ⁻¹ (PAR)	
1 foot	=	0.3048 m (exactly)		
1 inch	=	2.54 cm (exactly)		
1 mile	=	1.6093 km		
1 yard	=	0.9144 m (exactly)		
Area			Blue sky light*	
1 acre	=	0.4047 hectare	72 W m ⁻² = 0.103 cal cm ⁻² min ⁻¹ ≅ 9000 lux of this PAR is: 200 μmol photons m ⁻² s ⁻¹ ≅ 45 W m ⁻² = 0.065 cal cm ⁻² min ⁻¹ = 63% of total. ∴ 1 W m ⁻² (total) ≅ 2.778 μmol photons m ⁻² s ⁻¹ (PAR)	
1 square foot	=	0.0929 m ²		
1 square inch	=	6.4516 cm ² (exactly)		
1 square mile	=	2.5900 km ²		
1 square yard	=	0.8361 m ²		
Mass				
1 ounce	=	28.3495 g		
1 pound	=	453.60 g		
1 ton (2,000 lb.)	=	0.9072 t		
Volume or Capacity (dry measure)				
1 US bushel = 2150.42 cu. in.	=	approx. 35.24 L		
1 UK bushel (liq & dry) = 8 imp gal	=	approx. 36.37 L		
1 US peck = (¼ US bushel)	=	8.81 L		
1 UK peck = 2 gals. or 8 imp qts.	=	9.0925 L		
1 imp gal	=	4.54609 L (exactly)		
1 U.S. gal	=	3.78541 L		
2.838 US bushels	=	100 L or 1 hectolitre		

*Data from Coombs et al. (1985).

CONE AND SEED ANALYSIS COMPANIES AND SUPPLIERS

For a current list of cone and seed analysis companies and suppliers, please refer to Portlock (compiler, 1996).

INTERNET RESOURCES

Solar noon estimates

<http://www.crhnwscr.noaa.gov/grr/sunlat.htm>

B.C. Ministry of Forests Internet resources

homepage: <http://www.for.gov.bc.ca/>

Glossary of terms: <http://www.for.gov.bc.ca/pab/publctns/glossary/glossary.htm>

Publication catalogue: <http://www.for.gov.bc.ca/hfd/pubs/search/index.htm>

Forest Practices Code homepage: <http://www.for.gov.bc.ca/tasb/legregs/fpc/fpc.htm>

Current species lists: Res. Br. FTP site (142.36.141.53), in directory /pub/provspp.

Research Branch FTP site: address of the Cowichan server is 142.36.141.53 The directory will depend on your enquiry.

Nursery and Seed Operations Branch Homepage <http://www.for.gov.bc.ca/nursery/branch.htm>

SPAR homepage

<http://www.for.gov.bc.ca/nursery/headqtrs/spar.htm>

LI-COR (radiometer) homepage

<http://www.licor.com>

COMPUTER PROGRAMS

The computer programs mentioned in the text are familiar to the authors, but this does not imply endorsement or that they are the only programs available for the task. Further information about each program is available from the contacts and references provided below.

Sit (1992a) lists the code of a sas program for computing tree shadow lengths for different times of day and year.

GLI

Dr. Charles Canham, Institute of Ecosystem Studies, Box R, Millbrook NY 12545-0178 USA

Reference: Canham (1988)

GS+ (Professional Geostatistics for the PC, Version 2.0 (1992)).

Gamma Design Software, P.O. Box 201, Plainwell MI 49080 USA

HEMIPHOT

The Tropenbos Foundation, P.O. Box 232, 6700 AE Wageningen, The Netherlands

Reference: ter Steege (1993)

SAS (Statistical Analysis System)

SAS Institute Inc., Box 8000, Cary NC 27512-8000 USA

SiteTools Software

(for estimating site series from species and height)

B.C. Ministry of Forests, Research Branch, P.O. Box 9519, Stn. Prov. Govt., Victoria, BC V8W 9C2

SOLARCALC

Dr. Robin Chazdon, Department of Ecology and Evolutionary Biology, University of Connecticut, Box U-42, Storrs CT 06269-3042 USA

Reference: Chazdon and Field (1987)

COMPUTER PROGRAMS (*continued*)

SUNSHINE

Mr. W. Rick Smith, Research Forester, USDA Forest Service, Southern Forest Experiment Station, 701 Loyola Ave., New Orleans LA 70113 USA
Reference: Smith and Somers (1991)

SYSTAT/SYGRAPH

SPSS Inc., 444 North Michigan Avenue, Chicago IL 60611-3962 USA

VENUS

VENUS is a computer data entry and reporting tool for describing site data (soil, mensuration, vegetation), and is based on the FS882 forms available from B.C. Ministry of Forests Sales. The program is available from the B.C. Ministry of Forests Research Branch FTP site (address: 142.36.141.53) in directory / pub/venus. For further information, contact the Ecology Data Analyst (Greg Britton):

B.C. Ministry of Forests, Research Branch, P.O. Box 9519, Stn. Prov. Govt., Victoria, BC V8W 9C2

OTHER RESOURCES

LI-COR RADIOMETER

LI-COR Inc., 4421 Superior St., P.O. Box 4425
Lincoln NE 68504, USA
Telephone 1-800-447-3576 (U.S. and Canada)
or 402-467-3576; FAX: 402-467-2819
email: envsales@env.licor.com

(SPAR) Seedling Planning and Registry System

SPAR is an on-line registry, intended for use by B.C. Ministry of Forests staff, licensee, and nursery staff whose job responsibilities require it. The registry facilitates entering Seedling Requests, managing the Tree Seed Register for seedlots and the Cutting Registry for cutting lots, and monitoring Seedling and other Cone and Seed Service Requests. Services also include electronic access for all Ministry and non-Ministry clients and data entry of seedling request and seedlot provenance information at the forest district level.

Internet: SPAR homepage at <http://www.for.gov.bc.ca/nursery/headqtrs/spar.htm>

Biogeoclimatic Ecosystem Classification System

The biogeoclimatic ecosystem classification (BEC) is a hierarchical land classification system used in British Columbia that delineates ecological units based on vegetation, soils, and climate. BEC information for specific regions in British Columbia can be found in the following publications:

Forest region	References
Cariboo	Steen et al. [1997]
Kamloops	Lloyd et al. (1990)
Nelson	Braumandl and Curran (1992)
Prince George	DeLong (1996a) DeLong (1996b) DeLong et al. (1993) DeLong et al. (1994) MacKinnon et al. (1990) Meidinger et al. (1996)
Prince Rupert	Banner et al. (1993)
Vancouver	Green and Klinka (1994)

The BEC climate summary database is not yet available on the Internet. For information, contact David Spittlehouse, Research Branch, B.C. Ministry of Forests, P.O. Box 9519, Stn. Prov. Govt., Victoria, BC V8W 9C2

Forest Practices Code Guidebooks

Information about the B.C. Forest Practices Code and a list of current guidebooks is available on the Forest Practices Code homepage. Guidebooks can be ordered through the Guidebook page or by telephone, fax, or mail from the address below.

Forest Practices Code homepage: <http://www.for.gov.bc.ca/tasb/legregs/fpc/fpc.htm>

Forest Practices Code Guidebooks, Public Affairs Branch, B.C. Ministry of Forests, P.O. Box 9517 Stn. Prov. Govt., Victoria, BC V8W 9C2
Telephone: 1-800-994-5899 or 250-387-7964
FAX: 250-387-7009

GLOSSARY

Felix que potuit rerum cognoscere causas.
—Happy he who can understand the causes of things.
(Virgil)

abscission The separation of an appendage (petiole, fruit stalk, etc.) as a result of the programmed death of a specialized zone of cells (the abscission layer) found at the base of the appendage.

achene A dry, indehiscent (non-opening) one-seeded fruit (e.g., fruit of *Betula*).

accuracy The closeness of a set of estimates to the true population parameter, considered together with how closely they are grouped together (their precision). Compare *precision*.

acorn The one-seeded fruit of oaks; consists of a cup-like base and the nut (e.g., fruit of *Quercus garryana*).

adjusted coefficient of determination See *coefficient of determination*.

allometric Refers to the study and measurement of the growth of part of an organism relative to the whole.

analysis of covariance (ANCOVA) A statistical tool that combines both ANOVA and regression. The treatment means of the dependent variable are adjusted by using a covariate which controls error and increases precision. See ANOVA, *regression*, *precision*.

analysis of variance (ANOVA) A statistical tool used to analyze differences observed in the means of treated samples, to determine whether the differences in the means are due to the treatment or to random variation in the population.

anemometer An instrument for measuring wind speed, which may give direct or recorded readings.

angiosperms Flowering plants, distinguished from gymnosperms by having the ovules enclosed within the ovary; after fertilization the ovary becomes a fruit, enclosing one or more seeds. Compare *gymnosperms*.

aril Exterior covering or appendage that develops after fertilization as an outgrowth from the point of attachment of the ovule (e.g., fleshy fruit of yew containing a single seed).

artificial regeneration Establishing a new forest by planting seedlings or by direct seeding. Compare *natural regeneration*.

aspect The direction toward which a slope faces, expressed in degrees azimuth (clockwise from north), or categorized according to 4 (N, S, E, or W), 8, or 16 compass points.

auger A tool used to bore into wood or soil to retrieve a cylindrical sample or core.

autocorrelation The correlation between a point in a set and other points within the same set.

berry A pulpy fruit developed from a single pistil and containing one or more immersed seeds, but no true stone (e.g., fruit of *Arbutus menziesii*).

biogeoclimatic ecosystem classification (BEC) A hierarchical land classification system used in British

Columbia that delineates ecological units based on vegetation, soils, and climate.

biogeoclimatic site series within the BEC system all sites capable of producing the same mature or climax plant communities within a biogeoclimatic subzone or variant. Site series are described by the site and soil conditions as well as the vegetation community.

biogeoclimatic subzone geographic areas influenced by one regional climate. Subzones are divided into variants and site series.

biogeoclimatic variant subzones are sometimes further divided into areas called variants which reflect variations in climate (e.g., drier, wetter, snowier, warmer, or colder) within the subzone.

biogeoclimatic zone within the BEC system, generalized units representing extensive areas of broad, homogeneous macroclimates. Zones are divided into subzones.

biological diversity (biodiversity) The diversity of plants, animals, and other living organisms in all their forms and levels of organization, including genes, species, ecosystems, and the evolutionary and functional processes that link them.

Bonferroni technique A statistical method for making several non-independent pairwise comparisons, usually performed after ANOVA.

bract In gymnosperms, a modified leaf that extends underneath a scale in a female cone.

breast height age The number of annual growth rings measured on a tree at breast height, 1.3 m above high side ground level. See also *dbh*.

canopy (1) The cover of branches and foliage formed by tree crowns. (2) The branches and foliage of any vegetation.

canopy bank All seeds retained in cones or fruits on the tree, as opposed to seeds being retained in the soil. Compare *soil seed bank*.

capsule A dry, many-seeded fruit composed of two or more fused carpels that split at maturity to release their seeds (e.g., fruit of *Alnus*, *Betula*, *Populus*).

categorical variable See *variable*.

catkin In gymnosperms, a male strobilus which produces pollen. In angiosperms, a spike-like inflorescence, usually pendulous, of unisexual flowers (either staminate or pistillate) (e.g., *Alnus*, *Betula*, *Populus*, *Salix*).

central tendency A measure of the “middle” of a distribution. Common measures of central tendency are mean (the average), the median (the middle value of an ordered set), and the mode (the value with highest frequency).

chi-square test A statistical test for analyzing categorical variables measured for two or more populations. See *variable - categorical*.

chord An aeronautics term: an imaginary straight line between the leading and trailing edges of an airfoil.

chromosome The genetic material of organisms; composed of DNA and proteins.

clearcut (n. or adj.) An area of forest land from which all trees have been harvested. **clear-cut** (v.) A timber harvesting method and an even-aged silvicultural system in which all trees (typically >3 m tall) are removed to maximize the recovery of fibre and to provide growing space for the next crop.

closed canopy Describes a stand in which the crowns of the main level of trees forming the canopy are touching and intermingled so that light cannot reach the forest floor directly. See *canopy*.

codominant In stands with a closed canopy, those trees whose crowns form the general level of the canopy and receive full light from above, but comparatively little from the sides. In young stands, those trees with above-average height growth. See *canopy*, *crown class*.

coefficient of determination (r^2) A statistic that assesses how clearly a regression model describes the

relationship between the dependent and independent variables. Adjusted r^2 is the coefficient of determination adjusted by the model degrees of freedom, and is more appropriate than r^2 for comparing several models using the same data.

coefficient of variation (cv) A measure of variation relative to the mean; the ratio of standard deviation to the mean.

cohort A group of organisms of more or less the same age (e.g., all seedlings that germinated in the month of May).

cone The dry multiple fruit of conifers. A female cone consists of a central axis supporting scales which bear naked seeds. A male cone consists of a central axis supporting spirally arranged microsporophylls bearing pollen sacs that contain pollen grains. Syn. *strobilus*. See *conelet*, *microsporophyll*.

conelet In gymnosperms, the immature stages of development of a female flower following pollination. See *cone*, *female flower*.

confidence interval A range of possible values above and below an estimate of some population parameter, expressing the likelihood (e.g., 95%) that the true value lies between the bounds of that range. The confidence level is the probability that a confidence interval will enclose the true value of the parameter; $1 - \text{confidence level} = \text{level of significance}$. Compare *level of significance*.

continuous (of data or a variable). See *variable*.

coppice A silvicultural system that takes advantage of the tendency of some trees to produce many shoots when the main stem is removed and the root system is left intact.

cotyledon The first leaf produced by the embryo of a seed plant. In conifers, cotyledons appear needle-like.

cover The vertical projection of the crown or stem of a plant onto the ground surface; usually expressed as a percentage of the total ground area being considered.

crown The live branches and foliage of a tree.

crown class A group of trees in a forest having crowns of similar development and occupying a similar position in the canopy. See *canopy*, *dominant*, *codominant*.

cutting test A method to determine seed maturity; the seed is bisected longitudinally and the morphological development of the embryo and the storage tissue are assessed.

datalogger A portable, rugged simple computer, typically used in the field to automatically record data from environmental sensors over a period of time. The data can then be transferred to a computer and returned to the lab for analysis.

dbh Diameter at breast height; a standard forestry measurement used to indicate stem diameter 1.3 m above ground level.

detection limit The resolution or finest distinction that can be measured with a particular instrument or methodology.

dioecious (Literally *two houses*). Describes plants in which the male (staminate) and female (pistillate) flowers are borne on different plants. Compare *monoecious*.

direct count A method for determining the number and species of seeds found in a soil seed bank by separating seeds from the soil, then counting and identifying them directly. Compare *sample germination*. See *elutriation*.

direct seeding The practice of sowing seeds in or on the soil, rather than planting seedlings to reforest a harvested area. See *artificial regeneration*.

discrete See *variable*.

dispersal Movement of individuals away from a source, as in the spread of seeds away from a parent plant.

dispersal curve The frequency distribution of dispersed seed versus the distance that seeds are found from the seed source.

dispersion The spatial arrangement of objects, often described as random, clumped, or regular.

dominant Trees with crowns extending above the general level of the canopy and receiving full light from above and partly from the side; taller than the average trees in the stand and with well-developed crowns. See *canopy*, *crown class*, *codominant*.

dormancy Physical or physiological condition of a viable seed that prevents germination even in the presence of otherwise favourable germination conditions.

drupe Fleshy indehiscent fruit, usually one-seeded, containing a seed enclosed in a hard, bony endocarp (pericarp), (e.g., fruit of *Cornus*, *Prunus*). *Syn.* stone fruit.

elutriation The process of separating soil and particles from seeds. See *root elutriator*.

embryo The rudimentary plant within the seed; that part of a seed that develops from the union of the egg cell and sperm cell, which after germination becomes the young plant.

emergence (1) Protrusion of the radicle through the seed coat, or (2) under nursery or field conditions, protrusion of the hypocotyl and cotyledon above the soil surface.

emittance The radiant flux emitted per unit area of a surface. Compare *irradiance*.

empty seed A seed that does not contain all the tissues essential for germination. Compare *filled seed*.

endosperm Nutritive tissue (3N) of an angiosperm seed, which surrounds and nourishes the embryo. Compare *megagametophyte*.

epicotyl That portion of the seedling stem above the cotyledons.

epigeal Seed germination in which there is considerable elongation of the hypocotyl so that the cotyledons are raised above the surface of the ground to form the first green leaves of the plant. Compare *hypogeal*.

even-aged Describes a forest, stand, or forest type in which relatively small age differences (10–20 years) exist between individual trees which could be considered members of a single *cohort*. Compare *uneven-aged*.

excised embryo test: A quick test for evaluating the growth potential of an embryo that has been removed from the seed.

exclosure A cage placed around a field plot to exclude predators of seeds or seedlings, or other animal activity.

experimental unit. The smallest collection of the experimental material to which one level of a factor or some combination of factor levels is applied.

factor Some influence that is thought to cause a response (e.g., soil moisture or soil type may affect germination rate). Often used as a synonym for “treatment.” A factor may be either fixed or random. The levels of a fixed factor (e.g., soil moisture) are chosen by the experimenter, and replication of the experiment would involve those same factor levels. The levels of a random factor (e.g., soil type) are chosen in a random manner from the population of all possible levels, and replication of the experiment would (possibly) involve a new random set of levels.

female flowers (1) The female strobili of conifers before and during pollination. (2) The flowers of angiosperms that contain female structures (ovary and style), but not male structures. See *cone*, *conelet*, *strobilus*.

fertilization Penetration of a pollen tube into the ovule; the male sperm nucleus is discharged into the ovule to unite with the egg nucleus.

filled seed A seed that contains both storage tissue and an embryo, as opposed to being empty or partially empty. Compare *empty seed*.

fixed factor See *factor*.

flora The plant life characteristic of a particular geographic area.

frugivore (adj. **frugivorous**): An animal that eats fruit.

gamma radiation High-energy electromagnetic radiation emitted by excited atomic nuclei passing to a lower excitation state; a useful tag for retrieving seeds. See *radioactive*.

gap The space left in the canopy when one or more trees die or are removed. See *canopy*.

genotype The hereditary constitution of an individual organism, which may or may not be expressed as observable features. Compare *phenotype*.

geostatistics A branch of applied statistics that focuses on the detection, modelling, and estimation of spatial patterns.

germinant A young seedling, just after emergence from the seed, but before full establishment as an independent plant.

germination Resumption of active growth in the embryo, which results in emergence of the embryo from the seed and development of the embryo into an independent plant.

germination percentage An expression of how many seeds germinated as a percentage of the total number of seeds sown; = number of seeds germinated ÷ number of seeds sown × 100.

germination rate (R₅₀) The number of days it takes for 50% of the total number of sown seeds to germinate.

germination speed (R_{50'}) The number of days it takes for 50% of the germinating seeds to germinate.

germination value (GV) An expression that combines the speed and completeness of germination into a single number; $GV = \text{peak value (PV)} \times \text{mean daily germination (MDG)}$. $PV = \text{maximum quotient obtained by dividing the number of accumulated daily germination by the corresponding number of days}$. $MDG = \text{total germination divided by the number of days in the test}$. Compare *germination rate*, *germination speed*.

global radiation See *solar radiation*.

group selection system A harvesting and silvicultural

system designed to regenerate an uneven-aged stand by removing trees in small groups. See *silvicultural system*, *uneven-aged*.

growing degree-days (GDD) A cumulative sum of the degrees of temperature above a threshold (generally 5°C) counted on each day that the daily mean temperature exceeds that threshold.

gymnosperms Conifers and their allies; distinguished from angiosperms by having unprotected ovules (not enclosed in a fruit). Compare *angiosperms*.

half-face The cut surface of one side of a cone that has been bisected longitudinally.

hybrid The offspring produced by crossing individuals of different species or unrelated genetic lines. Usually refers to crossing of two true-breeding individuals (homozygous) with different forms of a trait (e.g., green or yellow seeds); the offspring are heterozygous hybrids.

hydration (of seeds) Uptake of water by seed tissues.

hypocotyl Part of the axis of an embryo or stem of a seedling between the cotyledons and the radicle; usually identifiable as the region between the root collar and the base of the cotyledons.

hypogeal Seed germination in which the cotyledons remain below the ground. Compare *epigeal*.

in situ Literally, in place; to describe experiments conducted in the field or in their natural environment (*in vivo*), as opposed to in the laboratory (*in vitro*).

independent variable See *variable*.

insect-species complex A group of different insect species that feed on a single tree species.

integument The outer cell layer or layers that surround the ovule and give rise to the seed coat.

irradiance The electromagnetic radiant energy received per unit area of a plane surface. Compare *emittance*.

isopleth A line joining points of equal value; for example, a contour map consists of isopleths of elevation.

level of significance A statistical term expressing the probability that an apparently significant difference is not real but simply due to chance; the level is pre-set for an experiment, typically at 1% or 5%.

LFH layers Litter, fermentation, and humus layers of the soil profile, consisting of the surface organic layers (forest floor or duff in forest soils).

life table A tabulation of mortality and survivorship of a population; static, time-specific, or vertical life tables are based on a cross-section of a population at a given time; dynamic, cohort, or horizontal life tables are based on a cohort of organisms followed throughout life.

linear regression See *regression*.

longwave radiation Electromagnetic radiation with wavelength 3.0–100 μm ; also known as thermal radiation.

male flowers (1) The male strobili of conifers that produce pollen. (2) The flowers of angiosperms that contain no female structures, only male (anthers).

MANOVA See multivariate analysis of variance.

mast year A year of unusually good seed production; generally applied to hardwoods.

maturation Final stage of seed development characterized by dehydration of seed tissues and, usually, the induction of dormancy.

mechanical site preparation The use of machines to prepare a site for reforestation; may consist of dragging anchor chains or shark-fin barrels, disc trenching, plowing, or mounding. See *site preparation*.

megagametophyte The nutritive tissue (1N) of gymnosperm seeds, which surrounds and nourishes the embryo. Often incorrectly called *endosperm*.

meristem Undifferentiated tissue that is capable of undergoing cell division; located in root and shoot tips where growth in length occurs in axillary buds of male and female cones, or in the secondary meristem tissue (cambium) where growth in girth occurs.

metafactor A complex factor or a set of independent variables which are tightly associated, and hence often treated as a single factor. See *factor*.

microclimate The small-scale climates of hill and hollow, field and forest; the physical environment of plant communities, insects, fish, and wildlife; may differ significantly from the general climate of the region. See *microsite*.

micropyle A minute opening into an ovule of an angiosperm plant through which the pollen grain normally passes to reach the egg cell; usually closed in the mature seed to form a superficial scar. See *ovule*.

microsite The specific spot or local habitat occupied by an organism; the environmental conditions sensed by an individual organism.

microsporophyll. The spore-producing structure of plants; in angiosperms, the stamen. See *male flowers*.

moisture content (mc) A measure of the amount of water present in a seed; can be expressed as a percentage of either fresh or dry weight.

monoecious Literally, *one house*. Describes plants in which both male (staminate) and female (pistillate) flowers are borne on the same plant. Compare *dioecious*.

multistage sampling Experimental design where samples are taken at successive layers of randomization. For example, two-stage sampling involves selection of a sample of secondary units from the primary units; three-stage sampling involves selection of a third level of samples from the secondary units; higher-order multistage designs are also possible.

multivariate analysis of variance (MANOVA) An extension of ANOVA with comparisons made on a group of dependent variables.

natural regeneration The renewal of a forested area by natural as opposed to human means (e.g., by seeds derived from adjacent stands, or by seeds transported by wind, birds, or animals).

nonlinear regression See *regression*.

nonparametric Statistical methods for analyzing data when a “classical” or specified distribution is inappropriate. See *normal distribution*. Compare *parametric*.

normal distribution A symmetrical, bell-shaped distribution curve, with the mean, median, and mode coinciding (see *central tendency* for definitions). Such data fulfill the requirements for analysis using *parametric* statistics.

normal probability plot A diagnostic plot used to check whether data (or residuals) are normally distributed. The plot is a graph of the cumulative distribution of the data (or residuals) on normal probability paper (paper scaled in such a way that the cumulative normal distribution plots as a straight line). See *normal distribution*.

nut Dry, indehiscent, one-seed fruit with a hard wall (e.g., fruit of *Quercus*).

nutlet A small nut or nut-like fruit (e.g., fruit of *Betula*).

orthodox A term to describe seeds that can be stored for long periods at low moisture content (5–10%) and below zero temperatures; this group includes all British Columbia conifer seeds, and many hardwoods. Compare *recalcitrant*.

ovule A female organ surrounded by integument, within which an egg cell (1N) is produced, and which, following fertilization, matures into a seed (2N).

parametric Statistical methods for analyzing data from a specified distribution. Compare *nonparametric*.

partial cutting Logging practices in which only certain individuals are removed from a stand of harvestable trees. Compare *clearcutting*.

Pearson product-moment correlation coefficient A statistic that characterizes the strength of the linear relationship between two variables; its square is equivalent to r^2 for simple linear regression.

percentile (e.g., p -th percentile) A value such that when data are ordered from smallest to largest, at least $p\%$ of the observations are at or below this value.

periodicity A cycle of time over which a phenomenon repeats itself. For example, many conifers do not produce collectable crops every year, but depending on the species, may only produce cones at 3–10 year intervals.

phenology Study of the relationship between seasonal climatic changes and periodic biological phenomena such as flowering, fruiting, leafing, growth flushing, and dormancy.

phenotype All characteristics—morphological, anatomical, and physiological—of an organism, determined by the interaction between the genotype and the environment. Compare *genotype*.

photoinhibition A reversible loss of photosynthetic capacity that occurs when a plant is exposed to excessive sunlight. Compare *sun scald*.

photosynthetically active radiation (PAR) Electromagnetic radiation in the wavelength band 400–700 nm, which contains the wavelengths absorbed by plants for photosynthesis.

phytochrome Protein-based plant pigment that exists in two interconvertible forms; it changes from one form to the other by absorption of red (660 nm) or far-red (730 nm) light.

pollination Process by which pollen is transferred from the male structure where it is produced to the female structure. In gymnosperms, pollen is dispersed by wind from male to female cones. In angiosperms, pollen may be wind dispersed, or carried by animals from the male to female flowers.

pome Many-seeded fruit of the apple family consisting of an enlarged fleshy receptacle surrounding the

pericarp; in *Malus* the pericarp is papery and fleshy; in *Crataegus* it is hard and stony.

post-dispersal To describe events occurring after dispersal of seeds from the mother tree. Compare *pre-dispersal*.

power A statistical term, expressing the probability of detecting a difference when in fact there is a difference.

precision The degree to which a set of estimates is closely grouped together. Compare *accuracy*.

pre-dispersal To describe events occurring while the seeds are still attached to the mother tree. Compare *post-dispersal*.

provenance (of seeds) The geographical area (latitude, longitude, and elevation) and environment to which the parent trees are native, and within which their genetic constitution has evolved through natural selection; their genetic origin. Compare *seed source*.

pseudoreplication When subsamples are statistically treated as experimental units, when, in fact, they are not. Compare *replication*. See *experimental unit*.

quantum An indivisible unit or discrete packet of energy.

quartiles The three values of a variable dividing a set of ordered data into quarters: the 25th, 50th, and 75th percentiles. See *percentile*.

r² and adjusted r² See *coefficient of determination*.

R₅₀ See *germination rate*.

R₅₀' See *germination speed*.

radiation or **radiant energy** Energy transferred through space in the form of electromagnetic waves or photons.

radicle Portion of the axis of an embryo from which the root develops.

radioactive Capable of giving off high-energy particles or waves, such as the alpha, beta, and gamma rays produced by disintegration of atomic nuclei; can be used as a tag to identify an object, such as a seed, for later recovery.

radioisotope (also radioactive isotope). An unstable isotope which, upon decay, can be detected with a *scintillometer*.

random factor See *factor*.

randomization In experimental design, the assignment of treatments to the experimental material in an unbiased manner.

recalcitrant A term to describe seeds that will not germinate unless they are stored at relatively high moisture content (>15%). Seeds of this type cannot be stored successfully for long periods (generally only several weeks to several months). Compare *orthodox*.

recruitment The successful transition or graduation of an organism from one age class or stage to another (as from seed to seedling, or from seedling to sapling), or the organisms that have made this transition.

reforestation Actions taken to re-establish continuous tree cover after mature trees have been harvested or otherwise lost.

regression A statistical technique for modelling the relationship between two or more variables; linear regression assesses the relationship between variables that can be depicted by a straight line; nonlinear regression assesses the relationship between variables without assuming a linear relationship between them. See *stepwise regression*.

remay Lightweight, nonwoven white fabric, often used as a horticultural row cover. The material allows air, water, and 80–90% of light to pass through.

repeated measures analysis A special ANOVA technique applicable to data that consist of measurements collected on the same experimental unit(s) at more

than one time. That is, experimental units measured at different times cannot be treated as replicates because they are not independent—in fact, they are likely autocorrelated. See *autocorrelation*.

replication In experimental design, the independent application of treatment levels to an experimental unit. Compare *pseudoreplication*.

residuals In statistical analysis, the difference between the observed and predicted values after a model has been fitted.

root elutriator Tool designed to separate roots from soil and which can be adapted to separate seeds from soil.

samara A dry, indehiscent, winged fruit, one-seeded as in *Fraxinus* and most conifers, or two-seeded as in *Acer*.

sample germination A method for determining the number and species of seeds found in a soil seed bank by counting germinants that emerge from soil samples placed in a controlled environment. Compare *direct count*.

Satterthwaite's approximation A method of constructing approximate F-tests.

scarification (1) of seeds, the process of abrading a seed coat to make it more permeable to water, either by mechanical means or by brief exposure to hot water or to strong acids such as sulphuric acid; (2) of seedbeds, a method of seedbed preparation in which patches of mineral soil are exposed through mechanical action.

scintillometer An instrument for measuring gamma radiation emitted by a radioactive substance. Can be used to locate seeds previously tagged with a radioisotope.

screefing Removing weeds and small plants together with most of their roots from the area immediately surrounding the planting hole.

secondary dispersal Movement of seeds (by wind, water, or animals) after they have already fallen from the parent plant.

seed bank See *canopy bank*; *soil seed bank*.

seedbed In natural regeneration, the surface or substrate on which seeds falls; in nursery practice, a prepared area over which seeds are sown.

seed coat The protective outer layer of a seed derived from the integument of the ovule.

seedlot A quantity of seeds of the same species, provenance, date of collection, and handling history, which is identified by a single number.

seed orchard A plantation of specially selected trees that is managed for seed production, usually for the purpose of genetic improvement.

seed production stand A forest stand reserved and managed as a source of seeds.

seed rain The overall input of seeds on a surface per unit area per unit time.

seed shadow The area of ground with a high density of dispersed seeds, centred on (or downwind from) a seed-producing individual or stand. See *dispersal*.

seed source The place (latitude, longitude, and elevation) from which seeds are collected; their physical source. The source of a seed collection may not be identical to its *provenance*.

seed trap A device designed to collect all the seeds landing in a defined area.

seed tree (1) A seed-bearing tree. (2) An even-aged silvicultural system in which a forest stand is regenerated by removing all trees from an area except for a small number of seed-bearing trees left singly or in small groups. See *silvicultural system*; *partial cutting*.

selection system A method of harvesting and regenerating a forest stand, which maintains an uneven-aged structure by removing some trees in all size classes, either singly or in small groups. See *silvicultural system*; *partial cutting*.

serotiny (adj. **serotinous**) A term to describe cones that remain closed on the tree (often for several years after maturity); some require heat (fire) to disperse their seeds.

shelterwood An even-aged silvicultural system designed to establish a new crop under the protection (overhead or side) of the old. See *silvicultural system*, *partial cutting*.

significance level See *level of significance*.

silvicultural system A process whereby forests are tended, (thinning, pruning, etc.) harvested, and replaced to produce a crop of timber and other forest products. The particular system is typically named by the cutting method used for regeneration.

single-tree selection harvesting See *selection system*.

site index The measure of the relative productive capacity of a site for a particular crop or stand, generally based on tree height at a given age.

site preparation A treatment, either mechanical, fire, chemical, or manual, to modify a site to provide favourable conditions for natural or artificial regeneration of the desired tree species.

site series See *biogeoclimatic ecosystem classification*.

slope The angle of the ground relative to horizontal, expressed in degrees or as a percentage of the run to the rise.

soil seed bank All viable seeds present on or under the surface of the soil.

solar noon The time of day at which the sun is at its highest point. For a specific location and date the information is available from website <http://www.crhnowscr.noaa.gov/grr/sunlat.htm>

solar radiation Electromagnetic energy from the sun in the 0–3000 nm wavelengths, of which the 300–3000 nm range reaches the earth's surface. It has direct and diffuse components. The former is radiation directly from the solar disc, and the latter radiation that has been scattered by the atmosphere. Syn. global radiation, shortwave radiation.

spatial statistics A branch of statistics for studying the spatial variation of positional (*x-y* coordinate) data. Many of the methods stem from or overlap with geostatistics.

Spearman's rank order correlation A correlation technique that measures the relationship between two variables, based on the rank order of the data. It assesses whether two variables have a strictly increasing or strictly decreasing relationship.

standard deviation A statistic that assesses the spread or variability of data about the mean; the square root of variance.

stepwise regression A statistical procedure for systematically reducing the number of independent variables required to model the dependent variable.

stocking A measure of the area occupied by trees, usually measured in terms of well-spaced trees per hectare, or basal area per hectare, relative to an optimum or desired level.

stratification A dormancy-breaking treatment in which seeds are exposed to moist, cold (2–5°C) conditions for several weeks (or months, depending on the species). Compare *warm stratification*.

stressing Attempts to induce tree seedling dormancy or enhanced seed production through the application of some kind of physiological stress (e.g., drought) or mechanical stress (e.g., partial girdling).

strobile (pl. **strobiles**) Spiky pistillate inflorescence of angiosperms or the resulting fruit. Syn. female *catkin*.

strobilus (pl. **strobili**) The male and female reproductive structures of gymnosperms. Syn. *cone*.

Student's t-test See *t-test*.

subsample Units within an experimental unit to be sampled for measurements. For example, if the experimental unit is a tree, the seeds from that tree could be a subsample. See *experimental unit*.

sunfleck A relatively small area of forest floor that receives direct-beam solar radiation through the interstices of overstorey foliage and branches in an otherwise closed forest canopy.

sun scald Damage to foliage and destruction of chlorophyll incurred through exposure to high light intensities when the plant is not acclimated to such conditions, also called photodamage. Compare *photoinhibition*.

t-distribution Distribution of the Student's *t*-test statistic; similar in shape to a *normal distribution*; useful for small samples.

t-test or **Student's t-test** A statistical test that assesses the differences between two groups by comparing the means.

terminal velocity The maximum velocity of a falling object, determined by the force of gravity and the shape of the object.

top height trees The largest dominant or codominant trees of the same species that are healthy, undamaged, and unsuppressed.

transformation A mathematical procedure for converting data to a different scale using one or more mathematical functions (e.g., square root, sine, natural log, exponential); often used to make the data more appropriate for a statistical test.

transpiration Release of water vapour from the aerial parts of a plant, primarily through the stomata.

Type I error In statistical analysis, the error of rejecting the null hypothesis (the hypothesis that the treatment has no effect) when it is in fact true; the probability is usually preset as the *level of significance* of the test.

Type II error In statistical analysis, the error of not rejecting the null hypothesis (the hypothesis that the treatment has no effect) when in fact it is false; the probability of avoiding which is the *power* of the test.

ultraviolet (uv) radiation Radiation in the waveband 200–400 nm. Since UV-C (200–290 nm) is filtered out by the atmosphere, UV radiation received at the earth's surface is in the 290–400 nm range.

uneven-aged Describes a forest, stand, or forest type in which relatively large age differences (>15–20 years) exist between individual trees within a stand; these age differences usually denote multiple *cohorts*. Compare *even-aged*.

variable An expression that can be assigned any of a set of values. A variable can be independent (causal) with levels set by the experimenter, or dependent (response) and responding to changes in the independent variable. The terms discrete, continuous, and categorical are used to describe data or a variable: discrete—having a distinct value, sometimes expressed in whole numbers (e.g., number of filled seeds); as opposed to continuous—able to take a continuum of values (e.g., percent germination, seed weight). Categorical describes information that has been grouped (e.g., age class, colour, species).

variance A statistic that measures the spread in the data; the square of standard deviation.

viable Alive; with respect to seeds, capable of germination and subsequent growth and development of the seedling.

vigour The combination of properties which enables seeds to germinate quickly under a wide range of environmental conditions, and which endows germinants with the ability to establish quickly and resist disease. Seeds that perform well under a wide range of environmental conditions are termed high vigour seeds and those that perform poorly are called low vigour seeds.

warm stratification A dormancy-breaking treatment of seeds in which moist seeds are held at warm temperatures (usually 20–25°C) for several weeks. The warm incubation period is usually followed by an incubation period at 2–5°C. See *stratification*.

wing loading A measure of the weight-to-area ratio of an airborne or falling object; equal to its mass times gravitational acceleration divided by its planform (projected, one-sided area).

z-test (z-score) The *z*-test and the *z*-score are examples of Wald statistics. They are computed by taking the estimated parameter, subtracting from it the parameter value under the null hypothesis, and then dividing this entire quantity by the approximated standard error of the estimated parameter. Under certain conditions, this statistic is asymptotically (i.e., large sample sizes) distributed with a standard normal distribution.

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The researches of many commentators have already thrown much darkness on this subject, and it is probable that, if they continue, we shall soon know nothing at all about it.

(Mark Twain)

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