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49

Ultraviolet-B Radiation Impacts on Tree Seedlings in British Columbia

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Ministry of Forests
Forest Science Program

Ultraviolet-B Radiation Impacts on Tree Seedlings in British Columbia

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British Columbia
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Since the discovery of the ozone hole over Antarctica in 1985 (Farman et al. 1985), attention has been directed towards changes in the stratospheric ozone layer and the implications for living things. Reductions in ozone layer thickness over North America have been reported during the past decade (Kerr and McElroy 1993), along with increases in ultraviolet-B (UV-B) radiation reaching the earth's surface (Madronich et al. 1998). The magnitude of the changes was alarming to some people, who began asking scientists and government agencies how our ecosystems might be affected.

When we (Figure 1)began studying the response of tree seedlings to UV-B in 1995, there was little information on how this energetic form of radiation would affect tree species in our forests. There had been no research done in British Columbia and only a few studies in other countries. The prevailing wisdom was that the thick waxy coating on conifer needles would block almost all UV-B from entering living cells (DeLucia et al. 1992). It was expected that there would be minimal damage to conifers, with effects limited to the time of needle expansion before the waxes are fully formed. As for our native hardwoods (such as paper birch), any predictions of damage were educated guesses.

Our first studies were supported by the Research Branch of the Ministry of Forests, after which Forest Renewal BC granted funds for a 4-year project. Entitled "Risk Assessment for Ultraviolet-B Radiation Damage to Economically Important Tree Species in British Columbia," this was planned as a greenhouse study (Figure 2) using tree seedlings. Over the 4 years we were able to test a dozen British Columbia tree species, with a range of seed sources from different latitudes and elevations. We designed and constructed exposure chambers, learned how to measure and apply UV-B radiation, and spent countless hours refining a variety of methods for detecting the effects of UV-B exposure on plant tissues.

Along the way there were some predictable results and some surprises. We now have a greater understanding of how British Columbia tree seedlings respond to increasing levels of UV-B radiation, at least under controlled conditions. It is possible to predict which species and seed sources will be most at risk at the seedling stage. The considerable genetic variation in UV-B sensitivity within and among species can be used to plan the most appropriate ways of coping with increasing UV-B.

In this report, we provide some background information on the thinning ozone layer and how UV-B affects plants, summarize the logistics of UV-B exposure studies, and show results for each tree species studied. We make an initial ranking of UV-B sensitivity, compare our results to those of other studies, and make recommendations for future directions.

FIGURE 1 *The research team: Dr. Wolfgang Binder and Dr. Sylvia L'Hirondelle.*

FIGURE 2 *The UV-B research greenhouse in Victoria, B.C.*

2.1 Solar Radiation

Our sun emits light energy in a wide range of wavelengths found in the electromagnetic spectrum (Figure 3). Light wavelengths are measured in nanometres (nm); one billion (10^9) nm = 1 m. As wavelengths get shorter (towards the right in Figure 3), their energy level increases.

About half of the solar irradiance (amount of energy per unit area) reaching the earth (Gibson 1999) is in the 750–25,000 nm range, which includes infrared and is not visible to the human eye. Another 42% of the total energy arrives as visible wavelengths (400–750 nm), which include the familiar colours of the rainbow. Plants use visible light for photosynthesis.

Ultraviolet (UV) light makes up the remaining 8% of solar irradiance reaching the earth. UV is divided by wavelength into three types. The longest, UV-A (320–400 nm) gives us suntans. The middle, UV-B (290–320 nm), gives us sunburns. The shortest, UV-C (1–290 nm) is highly energetic and extremely dangerous to all living cells. Most UV-B and all UV-C rays are now screened out by the ozone layer (see section 2.2) before they can reach the earth's surface (Figure 4).

The irradiance of UV-B at ground level varies with latitude, time of day and year, elevation, cloud cover, and thickness of the ozone layer (Frederick 1993). The sun's angle above the horizon affects the distance light travels through the ozone layer. UV-B levels are highest at the equator (where the sun is directly overhead and the ozone layer is thinnest), at solar noon (when the sun reaches its high point), and in the summer at higher latitudes. Total UV-B dose increases rapidly as latitude decreases and moderately with increasing elevation (10-fold increase from sea level in the arctic to 4000 m at the equator; 14–18% increase per 1000 m elevation) (Caldwell et al. 1980). Clouds scatter UV rays and usually decrease UV-B intensity, but partial cloud cover can result in patches of higher radiation (Mims and Frederick 1994; Sabburg and Wong 1998).

Biologists studying how living things respond to UV-B need to know how effective the energy is at damaging cells. By exposing organisms to known wavelengths, they can measure a damage response curve, also called an action spectrum (Diffey 1991). This curve can be multiplied by the irradiance reaching the earth for each wavelength, to give a weighted function. This is called biologically effective UV-B or UV-B_{be} (Caldwell and Flint 1997) and is expressed as watts per metre squared (W m^{-2}) or kilo Joules per metre squared per day (kJ m^{-2} d^{-1}).

Values of UV-B_{be} for southern British Columbia at sea level average about 4 kJ m^{-2} d^{-1} in the summer, with some days having doses of 8 kJ or higher (Environment Canada 2000b). UV-B_{be} levels at the equator are typically 12 kJ m^{-2} d^{-1}.

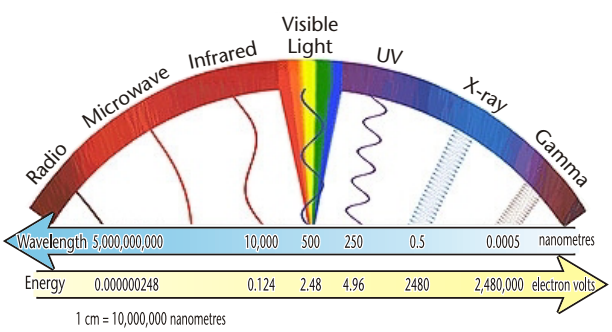

FIGURE 3 *The electromagnetic spectrum, with the full range of wavelengths and energy that characterizes light. Light waves are fluctuations of electric and magnetic fields in space. Solar radiation is part of this spectrum.*

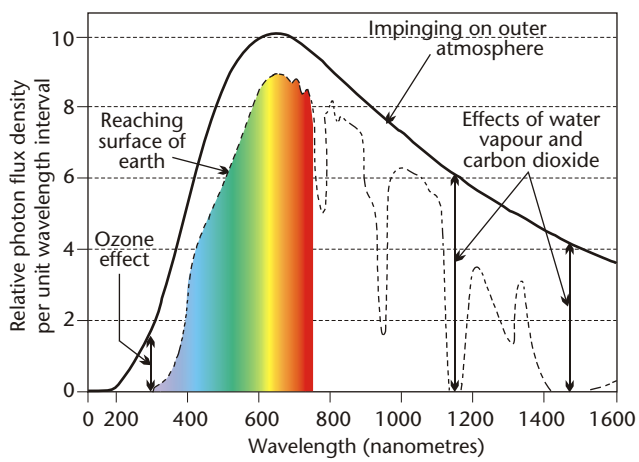

FIGURE 4 *Wavelengths of sunlight reaching earth. Gases in the atmosphere absorb strongly in some wavelengths, reducing the amount of energy reaching ground level. (Figure adapted from Nobel, P.S. 1991.* Physicochemical and Environmental Plant Physiology. *Academic Press, San Diego, Calif., page 238).*

2.2 The Ozone Layer and its Depletion

Ozone is naturally formed when UV radiation splits oxygen molecules (O_2) into atomic oxygen (O). O_2 combines with O to form ozone (O_3), a bluish gas. About 90% of our planet's ozone is in the stratosphere, 10–50 km above the earth's surface (USEPA 1999). At sea-level pressure and temperature, this ozone layer would form a shell averaging only 3 mm thick, thickest at the poles and thinnest at the equator. This layer is our main defence against UV rays, absorbing all UV-C and most UV-B as they pass through the atmosphere (Figure 4). Ozone constantly forms and dissociates in the stratosphere, but the total amount has been relatively stable for centuries.

In recent decades the ozone layer has been thinning, especially at high latitudes, due to the release of anthropogenic chemicals (Wardle et al. 1997). Ozone-depleting substances (ODSs) include chlorofluorocarbons, halons, carbon tetrachloride, methyl bromide, and methyl chloroform (USEPA 1999). When sunlight promotes the break-up of ODSs molecules in the stratosphere, they release active chlorine and bromine atoms (radicals). Each radical can destroy many thousands of ozone molecules, much faster than ozone is created.

Almost 200 countries have signed the Montreal Protocol, an agreement to phase out ODSs, but it will take a century for their stratospheric levels to decline to normal (World Meteorological Organization 1995; Wardle et al. 1997). Recovery of the ozone layer is expected to begin in the next few decades, but it is difficult to predict when it will fully recover. There are complex reactions and interactions not fully understood in atmospheric chemistry (Wennberg et al. 1994), including interactions among ozone and greenhouse gases (Kerr 1998b).

An example of this complexity is the stratospheric chlorine–ozone reactions that take place above the polar regions. The production of chlorine radicals takes place relatively slowly in the gas phase, but much faster on surfaces. The particles found in polar stratospheric clouds (PSCs) promote these reactions (Figure 5). These particles contain nitric acid, leading to a reduction in gaseous forms of nitrogen oxide (denitrification) (Waibel et al. 1999; Tabazadeh et al. 2000). High levels of active chlorine are maintained under these conditions. When sunlight returns in the spring, chlorine radicals rapidly destroy ozone and an ozone "hole" forms. The antarctic ozone hole has reached a maximum area of 26–28 million square kilometres (Kerr 1998a; British Antarctic Survey Ozone 2000).

PSCs may form earlier and persist longer owing to the greenhouse effect, which traps heat near the earth's surface, resulting in a colder stratosphere and changed patterns of polar air circulation (Salawitch 1998; Shindell et al. 1998; Waibel et al. 1999; Aldhous 2000; Tabazadeh et al. 2000). Greenhouse gases may also change the water vapour cycle, affecting halogen activation and polar ozone loss (Kirk-Davidoff et al. 1999). Model results predict increasing polar ozone losses for the next 20 years, with up to 65% losses of ozone in the arctic (Shindell et al. 1998).

Although ozone losses are greatest over arctic regions, significant decreases have already occurred over the rest of Canada. Over southern Canada, the ozone layer has thinned 7–8% on average in the past two decades (Wardle et al. 1997; Environment Canada 1999; Randel et al. 1999), with peak losses usually found in winter and spring (UNEP 1998). In 1995 in southern British Columbia, ozone depth was 9% lower than pre-1980 norms (Environment Canada 2000a).

Decreased stratospheric ozone is linked with increased ground-level UV-B (Wardle et al. 1997). An ozone loss of 1% translates into a UV-B increase of 1.1% at low levels of ozone depletion, but the UV-B increase is steeper (2%) as ozone loss increases (UNEP 1998). Ozone losses of 50%, such as found in polar regions, may lead to UV-B surface level increases of 100% or more.

FIGURE 5 *Long-lasting polar clouds in the arctic stratosphere contribute to major ozone loss in the spring. Photo Credit: NASA Ames Home Page*

2.3 Changes in Plants with Increasing UV-B

When plants absorb UV-B radiation, changes occur at levels ranging from the molecular to the ecosystem (Figure 6). The degree and direction of changes are affected by many factors, especially by how much radiation penetrates the epidermal layers (Day et al. 1994). Seasonal and daily variation in UV-B levels determine the exposure dose. Protective features such as waxy and reflective layers, surface hairs, thick epidermis, and production of UV-absorbing pigments affect how much UV-B is absorbed. The intensity of response to absorbed radiation depends on genetic variation in UV-B tolerance, the presence of other stresses such as drought and air pollutants, and the developmental stage of the plant (Teramura and Sullivan 1991; Balakumar et al. 1993; Cen and Bornman 1993).

More than 300 plant species and cultivars have been screened for responses to UV-B radiation, with about two-thirds of them apparently sensitive (Teramura and Sullivan 1991; Farrell 1993). Some plants are negatively affected by even ambient levels of UV-B (Krizek 1997; Schumaker et al. 1997).

Most tests have been done in growth chambers or greenhouses under simulated increases in UV-B radiation. There have been some studies done outdoors, but these are relatively few (Caldwell et al. 1994). Light effects limit greenhouse and chamber studies; photosynthetically active radiation is less intense and spectrally different than outdoors (National Research Council 1982; Caldwell et al. 1989; Teramura and Sullivan 1991), and water and nutrients may be more available than in the field.

Controlled environment studies are not accurate representations of the "real world" that plants experience, but they do offer the ability to quantify potential responses of plants to UV-B increases. They can produce precise data for establishing cause-and-effect relationships. Rather than dismissing them as unrealistic and biased, we can view them as a starting point for species and population comparisons, and for linking the numerous pathways involved in plant responses to changes in solar radiation (Caldwell et al. 1994).

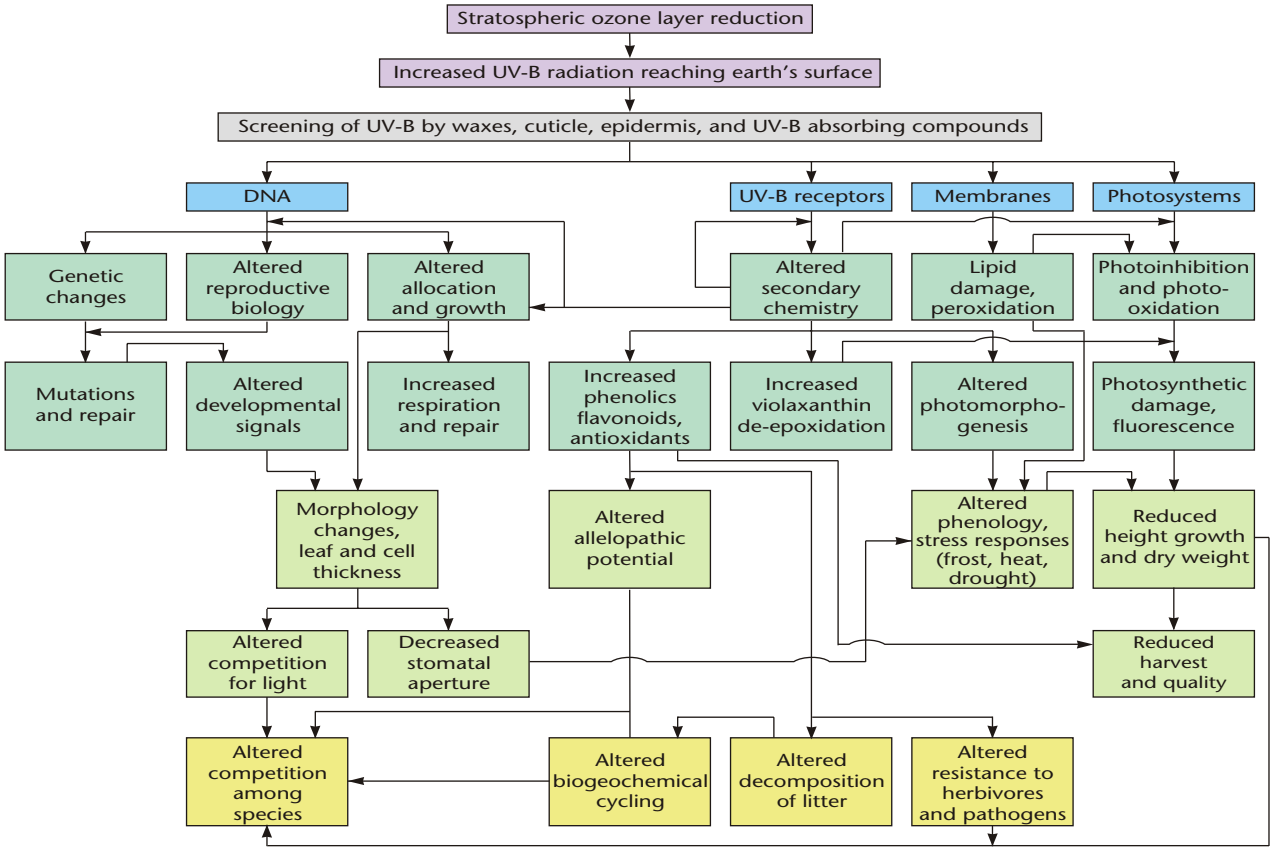

FIGURE 6 *Potential effects of increased UV-B radiation on vascular plants from molecular (blue) to tissue (dark green), whole plant (light green), and ecosystem (yellow) levels. Adapted from Caldwell et al. (1989) and Caldwell et al. (1994).*

What are some changes described in these studies? At the molecular level, photoreceptors for UV-B have not yet been identified (Casal 1999), although flavins may be involved (Ballaré et al. 1995a). UV-B exposure can cause DNA to break, forming pyrimidine dimers, (Diffey 1991; Murphy et al. 1993; Jansen et al. 1998; Ries et al. 2000), which can lead to mutations passed on to offspring (particularly in pollen). Under adequate levels of visible light and UV-A, photoreactivation of repair enzymes takes place and much of the damage is undone (McLennan 1987; Fernbach and Mohr 1992; Britt et al. 1993; Björn 1996).

Other changes at the molecular level, such as peroxidation of fatty acids in membranes (Britt 1996), can lead to changes in enzyme synthesis and activity, and altered membrane structure and permeability (Murphy 1983; Björn 1996; Lao and Glazer 1996; Ries et al. 2000). Damaged membranes may lead to lowered stress resistance.

Pigments and proteins involved in photosynthesis and photoinhibition suffer UV damage, and their repair processes decrease, leading to lower photosynthesis and higher respiration rates and shifts in carbon allocation (Britt et al. 1993; Day and Vogelmann 1995; Björn 1996; Tosserams and de Sà 1996; Hao et al. 1997; Jansen et al. 1998). UV triggers photooxidative stress, which can disrupt metabolism (Foyer et al. 1994). Both pigment content and distribution in leaves can change (Day and Vogelmann 1995). Chlorophyll fluorescence and photosynthesis under higher UV-B may be more affected at winter than at summer temperatures (Bavcon et al. 1996).

UV-B effects on photobiology and photochemistry may be exaggerated in controlled environments where light levels are lower than outdoors (Mirecki and Teramura 1984; Caldwell et al. 1989; Teramura and Sullivan 1991; Björn 1996). This is because protective and repair mechanisms may be impaired; more UV-B can be absorbed, more damage results, and less repair can take place. Both visible light and UV-A are important in modulating UV-B effects (Caldwell et al. 1994; Björn 1996), as is the ratio of visible light to UV-B (Deckmyn and Impens 1997).

Another major effect of UV-B exposure is altered secondary chemistry through the phenylpropanoid pathway (Middleton and Teramura 1993b; Liu and McClure 1995; van de Staaij et al. 1995; Björn 1996; Shirley 1996). Flavonoid biosynthesis is triggered by exposure to UV-B (Caldwell et al. 1983; Ensminger 1993; Ballaré et al. 1995b), and increases in response to increasing UV-B dose in many plants (Day and Vogelmann 1995; Ambasht and Agrawal 1998). At excessive UV-B doses it may be inhibited (Liu and McClure 1995; Liu et al. 1995). Flavonoids are concentrated in the upper layers of leaves, where they act as UV-B filters by absorbing radiation (Cen and Bornman 1993). Along with glutathione and ascorbate, flavonoids can also react with free radicals to increase UV-B protection (Björn 1996; Jansen et al. 1998). Flavonoid content varies with season and tissue age (Kinnunen 1999), and may change from initially high levels to lower levels after prolonged UV-B exposure (Sullivan and Teramura 1989; Kinnunen 1999).

Some plants deficient in flavonoids are extremely sensitive to UV-B radiation (Li et al. 1993; Ormrod et al. 1995), but there is not always a clear relationship between flavonoid content and UV-B response (Barnes et al. 1987; Singh 1996), because other factors affect plant sensitivity. *Arabidopsis* plants lacking hydroxycinnamic acids (produced by the phenylpropanoid pathway) are very sensitive to UV-B (Landry et al. 1995).

At the tissue level, exposure to UV-B can decrease stomatal aperture, lower leaf water content, and reduce cell division and growth (Dai et al. 1992; Björn 1996; Ambasht and Agrawal 1998). Visible evidence of damage shows as bronzing, glazing, or chlorosis on the upper leaf surface (Figure 7) (Teramura 1983). Photomorphogenesis (the ability of light to affect plant growth and development) includes UV-B effects, leading to changes in growth form (e.g., switching from shade to sun leaves), leaf curling, reduced internode length, increased leaf loss, and lower yield (Curry et al. 1956; Murali et al. 1988; Barnes et al. 1990; Cen and Bornman 1993; Ensminger 1993; Björn 1996; Hao et al. 1997; Jansen et al. 1998; Krol et al. 2000). High UV-B may increase the thickness of epidermal layers, mesophyll cells, and leaves. Some UV-induced changes in growth form and phototropism (stem and leaf curling) result from effects on growth hormones or photosynthesis (Jansen et al. 1998); others may be

FIGURE 7 *Exposure of paper birch to high UV-B levels led to smaller leaves with pigment breakdown (chlorosis) between veins.*

regulated by DNA damage and altered developmental stimuli (Ensminger 1993).

Morphological and biochemical effects of UV can change whole-plant stress resistance. UV-B stress confers increased drought resistance, and vice versa (Murali and Teramura 1986; Sullivan and Teramura 1990; Teramura and Sullivan 1991; Balakumar et al. 1993; Petropoulou et al. 1995). Exposure to high UV-B can also increase frost hardiness (Dunning et al. 1994). Combining other stresses such as toxic metals with UV-B can have a greater impact than the sum of the single stresses (Dubé and Bornman 1992). For air pollutant stresses, pre-exposure to ground-level ozone can decrease UV-B sensitivity in a flavonoid-deficient *Arabidopsis* mutant (Rao and Ormrod 1995). In Norway spruce and Scots pine grown at increased ozone levels, excluding UV-B radiation has ameliorated the negative effects of ozone (Schnitzler et al. 1999).

Changes in stress resistance from UV-B exposure may differ with tissue age and developmental stage. Because development is itself altered by UV-B, plants can show changes in phenology (the timing of plant life-phases relative to seasonal and climatic cycles). Timing and number of flowers change with UV-B exposure in some species (Caldwell 1968; Ziska et al. 1992; Staxén and Bornman 1994). Reproductive capacity can also decrease through UV-B effects on pollen germination and mutation (Flint and Caldwell 1984; Walbot 1999).

Because of climate change, global temperature and CO_2 are increasing along with UV-B. Growth increases from high levels of CO_2 can be negated by UV-B damage (Teramura et al. 1990; Yakimchuk and Hoddinott 1994), and high levels of CO_2 may even enhance UV-B damage in some species (Hao et al. 1997). There may also be shifts in carbon allocation patterns when high levels of CO_2 and UV-B are both present (Sullivan and Teramura 1994). In addition, higher temperatures can affect growth rates under UV-B exposure (Tevini et al. 1991).

At the population level, UV-B induced declines in plant growth and shifts in morphology may lead to plant community changes (Teramura 1983; Caldwell et al. 1989; Barnes et al. 1990; Dai et al. 1992; Bothwell et al. 1994; Sato et al. 1994; Musil 1996). Changes in secondary chemistry may alter the allelopathic potential of plant exudates, change the production of and decomposition rates for litter, and affect resistance to herbivores and pathogens, leading to changes in biogeochemical cycling (Caldwell et al. 1989; Caldwell et al. 1994; Manning and Tiedemann 1995; Tosserams and de Sà 1996; Cybulski et al. 2000). Along with morphological modifications that affect competition for light and water, and subsequent differences in growth rates and biomass, these changes can lead to altered competition among species (Gold and Caldwell 1983).

There is a wide range of variation among species in response to increased UV-B, from no apparent changes to large changes in appearance, reduced growth, and decreased survival (Barnes et al. 1990; Sullivan et al. 1992). Within species, there are also differences in UV-B sensitivity (Dai et al. 1992; Day et al. 1992; Barnes et al. 1993), sometimes related to the UV-B environment of the plant source. There may be genotype-by-environment interactions, with the sensitivity of some populations or varieties affected by microclimate (Teramura and Sullivan 1991). And genotype-by-age interactions are likely, because plants and populations can acclimate to seasonal changes and transfers to new locations (Caldwell et al. 1983). Inheritance of UV-B resistance may be controlled by recessive polygenes in some species (Sato et al. 1994).

Gradients of sensitivity to UV-B have been found among ecotypes growing along gradients of natural UV-B levels (Figure 8) (Robberecht et al. 1980; Caldwell et al. 1982; Ziska et al. 1992). Although large differences in flavonoids have been found among tree populations (Kaundun et al. 1998) and along environmental gradients, flavonoid content and UV-B sensitivity are not directly related (Caldwell et al. 1982; Barnes et al. 1987).

There is still much to learn about how plants and ecosystems will be affected by increasing levels of UV-B radiation. The studies done so far indicate a wide range in responses. Some species and varieties will show decreased growth, reproduction, and survival, while others will continue to be productive and competitive.

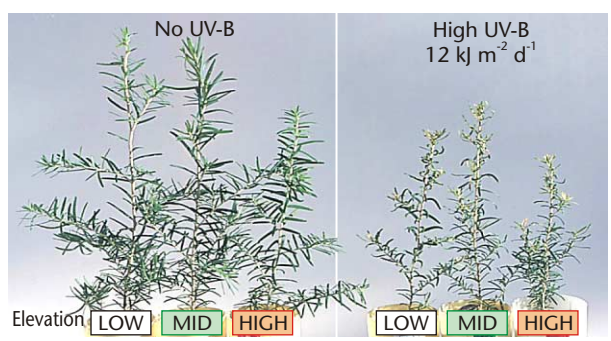

FIGURE 8 *Western hemlock seedlings from three elevations grown without or with UV-B. The growth decrease was proportionately greater for low than for high-elevation seedlings.*

2.4 Tree Response to Increasing UV-B

Less work has been done on the effects of UV-B on woody plants than on crop plants, and not much is known about interactions of UV-B with other stresses (Björn 1996; UNEP 1998). Some studies have used seedlings grown and exposed under controlled conditions in greenhouses or growth chambers; a few have done multi-season field evaluations with seedlings or mature trees. Exclusion studies (no UV radiation) have also been used (Robson et al. 2000; Turunen et al. 2000). Some populations and species are negatively affected by UV-B, even at ambient levels, others are resistant, and some may benefit from exposure to UV-B (Table 1) (Teramura and Sullivan 1991; Laakso and Huttunen 1998).

Mature evergreen conifer needles have UV-resistant surface layers that protect them from damage (DeLucia et al. 1991; Day et al. 1994), but young foliage may be sensitive to UV during early growth because more UV-B can penetrate (Kossuth and Biggs 1981; DeLucia et al. 1991, 1992; Day et al. 1994; Laakso 2000). As needles mature, they usually develop thickened epidermal layers (Day 1993) and a glaucous surface, especially in high-elevation species. Less than 1% of biologically effective UV penetrates to the mesophyll in some species (DeLucia et al. 1992; Sullivan et al. 1996). The epidermal layer of Scots pine contains up to 90% of the needle content of soluble and wall-bound flavonoids, effectively screening almost all UV-B (Schnitzler et al. 1996). Deciduous conifers such as western larch may be more sensitive to UV-B under some conditions (Krol et al. 2000), although needles of mature trees are highly effective at screening UV-B in the epidermis (Day et al. 1992).

Conifers seem to be less sensitive during a single growing season than crop plants, but are still damaged by UV-B (Figure 9). Responses include reduced photosynthesis, variable chlorophyll fluorescence, and chlorophyll levels, often accompanied by reduced growth or changes in carbon allocation to plant parts (Kossuth and Biggs 1981; Sullivan and Teramura 1988, 1992; Naidu et al. 1993; Stewart and Hoddinott 1993; Bavcon et al. 1996). Altered wax synthesis, needle thickness and needle area often occur (Gordon et al. 1998b; Krol et al. 2000; Laakso 2000). There may also be increases in stomatal density and UV-absorbing pigments in some species (Kossuth and Biggs 1981; Sullivan and Teramura 1988, 1989, 1992; Naidu et al. 1993; Stewart and Hoddinott 1993).

UV-B responses are more pronounced in shade-tolerant (e.g., spruces) than sun-tolerant species (Yakimchuk and Hoddinott 1994; Hunt et al. 1996; Gordon et al. 1998b), but have also been found in loblolly pine, a commercial species in the south-eastern United States. Photosynthetic rates fell and biomass decreased 20–40% when seedlings were exposed to increased doses of UV-B for up to 3 years (Sullivan and Teramura 1989, 1992; Naidu et al. 1993; Sullivan 1994; Sullivan et al. 1996).

TABLE 1 *Response of some tree species to increased UV-B radiation*

Species	Effect	References
Abies concolor (white fir)	↑	Kossuth and Biggs 1981
Abies fraseri (Fraser fir)	↑	Sullivan and Teramura 1988
Abies procera (noble fir)	↓	Kossuth and Biggs 1981
Acer saccharum (sugar maple)	↓	Gordon et al. 1998a
Betula pendula (silver birch)	○	Lavola et al. 1997; Lavola 1998
Betula resinifera (Alaska birch)	○	Lavola 1998
Liquidambar styraciflua (sweetgum)	○ ↓	Sullivan et al. 1994b; Sullivan et al. 1996
Picea abies (Norway spruce)	↓	Dub and Bornman 1992; Bavcon et al. 1996; Gordon et al. 1998b, Laakso and Huttunen 1998
Picea engelmannii (Engelmann spruce)	↑ ○ ↓	Kaufmann 1978; Sullivan and Teramura 1988; Bassman et al. 2000
Picea glauca (white spruce)	○ ↓	Sullivan and Teramura 1988; Yakimchuk and Hoddinott 1994; Gordon et al. 1998b
Picea mariana (black spruce)	○ ↓	Yakimchuk and Hoddinott 1994; Gordon et al. 1998b
Picea rubens (red spruce)	○	Gordon et al. 1998b
Pinus banksiana (jack pine)	○ ↓	Stewart and Hoddinott 1993; Yakimchuk and Hoddinott 1994
Pinus contorta (lodgepole pine)	○ ↓	Kaufmann 1978; Kossuth and Biggs 1981; Sullivan and Teramura 1988
Pinus edulis (pinyon)	○	Sullivan and Teramura 1988
Pinus elliottii (slash pine)	↓	Kossuth and Biggs 1981
Pinus halepensis (Aleppo pine)	○	Petropoulou et al. 1995
Pinus nigra (Austrian pine)	○	Sullivan and Teramura 1988
Pinus pinea (Italian stone pine)	○	Petropoulou et al. 1995
Pinus ponderosa (ponderosa pine)	↑ ○ ↓	Kossuth and Biggs 1981; Bassman et al. 2000
Pinus resinosa (red pine)	↓	Sullivan and Teramura 1988
Pinus sylvestris (Scots pine)	○ ↓	Sullivan and Teramura 1988; Fernbach and Mohr 1992; Kinnunen 1999; Laakso 2000
Pinus taeda (loblolly pine)	↓	Kossuth and Biggs 1981; Sullivan and Teramura 1988, 1989, 1992, 1994; Naidu et al. 1993; Sullivan et al. 1996
Populus trichocarpa, P. trichocarpa x *deltoides* (hybrid poplar)	○ ↓	Schumaker et al. 1997; Bassman et al. 2000
Pseudotsuga menziesii (Douglas-fir)	↑ ○ ↓	Kossuth and Biggs 1981; Bassman et al. 2000
Quercus rubra (red oak)	↑ ○	Bassman et al. 2000

↑ = positive effect, ○ = tolerant (no change), ↓ = negative effect

Evergreen conifers, with their long needle life span may be vulnerable to UV-B because damage is suspected to depend on cumulative exposure (Sullivan and Teramura 1992; Caldwell et al. 1994; Björn 1996). If even minor decreases in annual productivity occur, the cumulative effects could be large over the lifetime of a tree. There is further risk from effects on pollen germination (Weirich 1996) and increased mutation, which may affect the reproductive potential of trees in forests and seed orchards.

More UV-B penetrates into the leaf mesophyll of broadleaf than of coniferous trees (Day et al. 1992; Day 1993; Day et al. 1994; Sullivan et al. 1996), so there is greater potential for responses. In some broadleaf species (e.g., olive, medlar, and quince), dense trichomes on young leaves protect tissues from UV-B damage until phenolic production and other avoidance mechanisms increase (Karabourniotis et al. 1995). In sugar maple, UV-B decreases wax biosynthesis, changing the micromorphology of the upper leaf surface (Gordon et al. 1998a).

Leaf content of flavonoids and other phenolics often increases with increasing UV-B in broadleaved trees (Karabourniotis et al. 1995; Lavola et al. 1997; Schumaker et al. 1997; Lavola 1998). Although even ambient UV-B may decrease photosynthesis and stomatal conductance (Schumaker et al. 1997), corresponding changes in growth are not always found. For silver birch and Alaskan paper birch seedlings, there were no significant changes in growth, morphology, or leaf area at 5–7 kJ m^{-2} d^{-1} of UV-B (Lavola et al. 1997; Lavola 1998). Similarly, supplemental UV-B did not decrease total biomass of sweetgum, but leaf area decreased and carbon allocation to branches and roots increased (Sullivan et al. 1994b).

Resistance of woody plants to stress, pests, and pathogens may also change as a result of UV-B effects on biochemistry. Increased cold hardiness after UV-B exposure was reported in *Rhododendron*, an evergreen shrub (Dunning et al. 1994). The freezing response was related to an increased production of phenolic compounds. And increased UV-B exposure alleviated the negative effects of water stress on field-grown Mediterranean pines (Petropoulou et al. 1995).

There may be changes in species composition in forest communities, because differing sensitivities to UV-B may change the competitive relationships among species (Tevini and Teramura 1989). Because there is genetic variation within species for UV-B sensitivity (Sullivan and Teramura 1992), it may be possible to select resistant populations, families, or individuals for planting in areas with potentially high UV-B levels. There may be a trade-off between UV resistance and growth, so the optimal seed source chosen would combine high growth potential and UV-B resistance.

Many of the observations about UV-B effects on tree growth are preliminary, because most of the studies done to date have tested tree seedlings in controlled conditions for one growing season. Some longer studies found that UV-B responses varied within and among seasons (Bavcon et al. 1996; Kinnunen 1999; Laakso 2000; Turunen et al. 2000).

Short-term greenhouse studies provide tentative relative rankings among species and populations, but extrapolation to field conditions is full of uncertainty. Although expensive and logistically challenging (Caldwell et al. 1994), more field studies are needed to confirm conclusions from greenhouse studies.

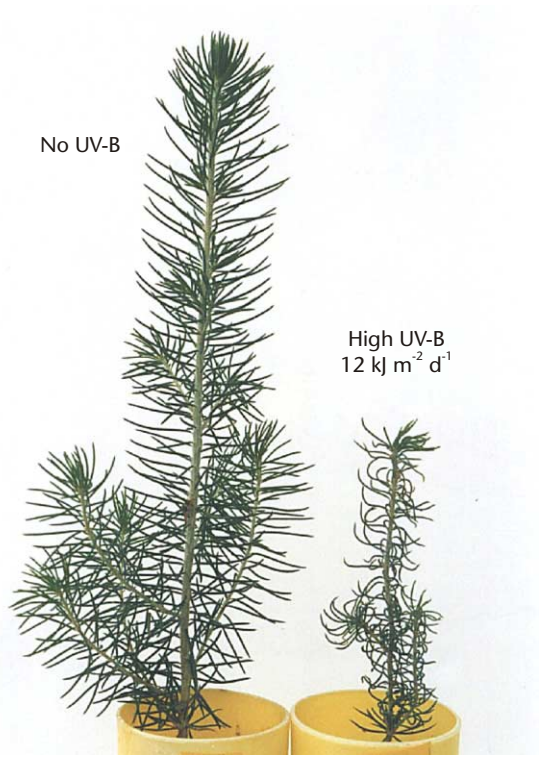

FIGURE 9 *Engelmann spruce seedlings from low elevation are sensitive to high levels of UV-B.*

3.1 Methods

Studying the effects of UV-B on plants can be logistically challenging and expensive. Greenhouse and growth chamber experiments give the greatest control over environmental conditions, and the ability to establish cause-and-effect relationships. However they may alter the patterns and intensity of incoming radiation, so that the ratios of UV-B, UV-A, and visible light are different from outdoors (Caldwell et al. 1994). This can make plants more sensitive to increasing levels of UV-B. The most realistic assessments of UV-B effects are studies done in the field on seedlings and mature plants, and use modulated exposure systems that supplement ambient radiation levels (Sullivan et al. 1994a). However, these studies are expensive, labour-intensive, and difficult to establish (Caldwell et al. 1994) because of the cost of hardware and meeting environmental and regulatory constraints.

Our UV-B project was limited to a few years with a relatively modest budget, with plans to test several species of British Columbia trees. Given these constraints, we chose to modify existing greenhouse facilities for immediate use rather than spend a large proportion of time and money developing field facilities. We built UV-B chambers and developed exposure regimes based on findings of previous researchers (Björn 1989; Adamse and Britz 1992; Björn and Teramura 1993; Middleton and Teramura 1993a).

In the 4 year project, we conducted five studies on the effects of increasing UV-B on tree seedlings. Details of exposure conditions, sampling methods, and data analyses are found in working plans (L'Hirondelle and Binder 1996, 1997a, 1997b).

All studies were done in polycarbonate greenhouses (see Figure 2) at the Research Laboratory in Victoria, B.C. (48°39' N, 123°26'W, 100 m elevation). Greenhouses had roof and side vents, supplemental lighting, cooling fans, and fan-jet tubes. Temperatures inside greenhouses were one to several degrees above the outside temperature, and light levels were less than full sun due to shading from the structure. Hourly temperatures and light levels were recorded.

Our tests were done between spring and early autumn, when outdoor light levels were high, except for one test with western redcedar. It was done in midwinter when the collaborator supplied seed. Halogen lamps provided supplemental lighting.

The polycarbonate greenhouse covering screened out incoming UV-B, so doses of UV-B were entirely supplied by lamps. We built 24 UV-B chambers of angle aluminum (Figures 10 and 11). Each chamber had 10 UVB-313 lamps controlled by dimming ballasts. Cellulose acetate filters (pre-solarized for 10 hours, changed biweekly) screened out UV-C, and Mylar filters screened out UV between adjacent chambers. Lamps were pre-aged for at least 70 hours to give standard outputs (Adamse and Britz 1992). Seedlings were placed 60–90 cm below the lamps.

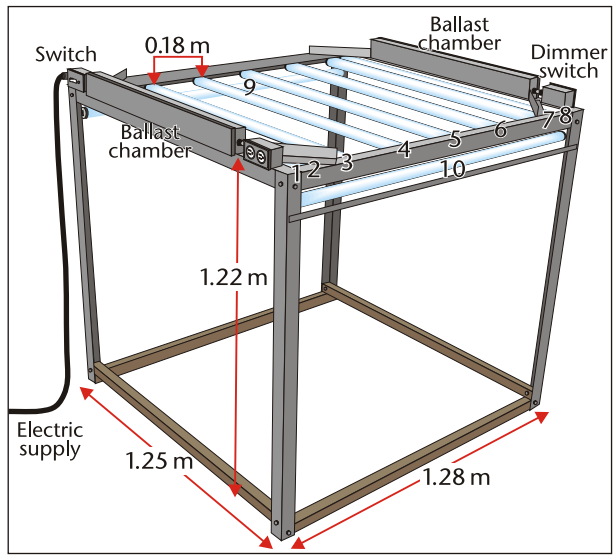

FIGURE 10 *Diagram of UV-B exposure chamber.*

FIGURE 11 *UV-B exposure chamber with seedlings.*

UV-B radiation was applied 6 hours a day, centred on solar noon. We measured UV-B weekly in each chamber with a spectroradiometer and bulk sensor with a solar blind filter.

Instruments and sensors were calibrated regularly. Curves were developed to convert bulk sensor readings into biologically effective UV-B (UV-B_{be}) in kJ m^{-2} d^{-1}. We converted W m^{-2} to kJ m^{-2} d^{-1} with weighting factors from the Caldwell plant action spectrum, normalized to 300 nm (Björn and Teramura 1993).

Seed was obtained from the Ministry of Forests Tree Seed Centre and Research Branch forest genetics staff. Seed was stratified and germinated according to recommended protocols for each species. Germinants (newly germinated seedlings) were grown in 164-ml containers, and 1-year-old seedlings in 262- or 656-ml containers in a peat mix or vermiculite. Containers were watered and fertilized daily.

Most studies used four levels of UV-B_{be} dose: 0, 4, 8, or 12 kJ m^{-2} d^{-1}. Average ambient UV-B levels for Victoria are about 4 kJ m^{-2} d^{-1}, so the 8 and 12 kJ treatments represented double and triple ambient levels for Victoria. These levels are realistic in that they already occur farther south and at high elevations. The experimental unit for UV-B treatment was the chamber. One of the four doses was randomly applied to each chamber.

Germinants or older seedlings were randomly assigned to racks for each chamber, and within a rack the different elevations were randomly assigned to rows. Racks were randomly assigned to positions within each chamber.

In the spring and early summer of 1998, we tested the combined effects of UV-B and PAR (photosynthetically active radiation) on 1-year-old seedlings. There were two PAR levels: high (about 600 µmol m^{-2} s^{-1}) and low (chambers covered with shadecloth to reduce PAR levels to 300 µmol m^{-2} s^{-1}). There were also two UV-B levels: 4 and 12 kJ m^{-2} d^{-1}. The four PAR by UV-B treatments were randomly assigned to eight chambers in the greenhouse. Racks of 1-year-old seedlings of paper birch, interior spruce, western hemlock, and coastal Douglas-fir were randomly assigned positions in each chamber and grown for 6 weeks.

We measured changes in morphology, phenology, biomass, and physiological response to various stresses. Non-destructive measures induded height, visible injury, root collar diameter, and number of branches. Destructive measures included needle length and thickness, dry weight of shoots and roots, and sampling of needles for pigments, electrolyte leakage, and chlorophyll fluorescence (Figure 12). Measurements were made weekly or biweekly, or at the end of each experiment, using 5–10 seedlings per seed source per chamber.

Frost hardiness was estimated with stress-enhanced electrolyte leakage (SEEL) or quantum yield (QY) from chlorophyll fluorescence (Burr et al. 2000). For SEEL, needles or stem sections were removed from seedlings, frozen in containers in a programmable freezer, thawed, and soaked for a day in deionized water to release electrolytes. Electrical conductivity was measured with a conductivity meter, samples were killed by oven heating, then soaked again, and final conductivity was measured. For QY, needles or shoots were frozen (as above), thawed, and pre-conditioned under bright light (1200 µmol m^{-2} s^{-1}) for at least 1 hour. After 20–30 minutes of dark acclimation, QY was read with a pulse-modulated fluorometer. For heat resistance, needles or shoots were placed in vials and heated for

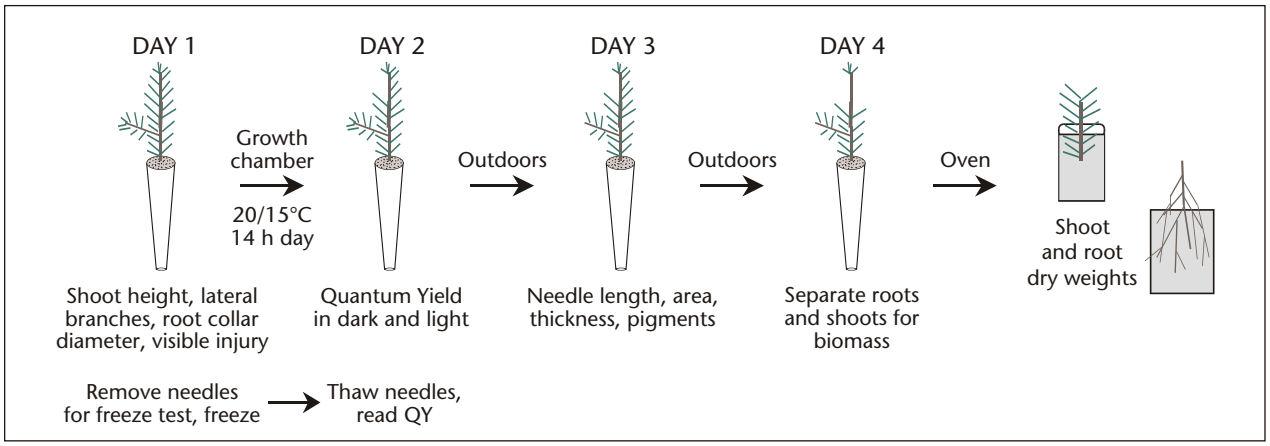

FIGURE 12 *Sampling methods.*

1 hour in a growth chamber under bright light. Samples were dark-acclimated and QY was read as above. Low values of QY indicated that needles were damaged. For all tests, control samples (not frozen or heated) were included.

For pigment analyses, needles were removed from seedlings, frozen in liquid nitrogen, and freeze-dried. Chlorophyll content (Moran and Porath 1980; Moran 1982) and amount of UV-B–absorbing compounds (Dai et al. 1992; Day et al. 1994) were measured from tissue extracts.

Experimental designs included split-plot, nested, randomized block, and factorial. UV-B dose, PAR, and elevation were fixed effects; block, chamber, and family were random effects. Analyses of variance were run on dependent variables, and regression analyses were used to describe relationships among variables. Testing was done at $p < 0.10$ for main effects and interactions because these were exploratory studies and small differences were expected.

3.2 Results by Species

We tested several species and seed sources of conifers and one hardwood. Species tested included the following:

- *Abies grandis* (Dougl. ex D.Don.) Lindl. – grand fir
- *Betula papyrifera* Marsh – paper birch
- *Chamaecyparis nootkatensis* (D.Don) Spach – yellow-cedar
- *Larix occidentalis* Nutt. – western larch
- *Picea engelmannii* Parry ex Engelmann – Engelmann spruce
- *Picea glauca* (Moench) Voss x *engelmannii* – interior spruce
- *Picea sitchensis* (Bong.) Carr – Sitka spruce
- *Pinus contorta* Dougl. ex Loud. var. *latifolia* Englem. – lodgepole pine
- *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* – coastal Douglas-fir
- *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco – interior Douglas-fir
- *Thuja plicata* Donn ex D.Don – western redcedar
- *Tsuga heterophylla* (Raf.) Sarg. – western hemlock

Seed sources came from a fairly wide range of geographical locations (Figure 13). For most species, three seed sources were tested, usually low, middle, and high elevations from the same latitude. The difference between low and high elevations ranged from about 500 to 1000 m.

There was much variation in UV-B responses among and within species, and also among individuals within chambers. This was partly due to the random location of each source within chambers–sometimes slower-growing species were partially shaded by faster-growing ones, so they would have received a lower UV-B dose in those chambers. There was variation in visible light levels across the greenhouse, and also in temperature and humidity. Variable conditions also exist at field sites. Repeated tests on the same seed sources usually gave the same trends, but the degree of response varied.

Even with this level of variation, we found many trends and significant effects of UV-B dose and seed source on the measured morphological and physiological traits of seedlings in our experiments.

In the following pages we present some of the results of our studies, including photographs of morphological responses to increased UV-B and graphs of measured traits.

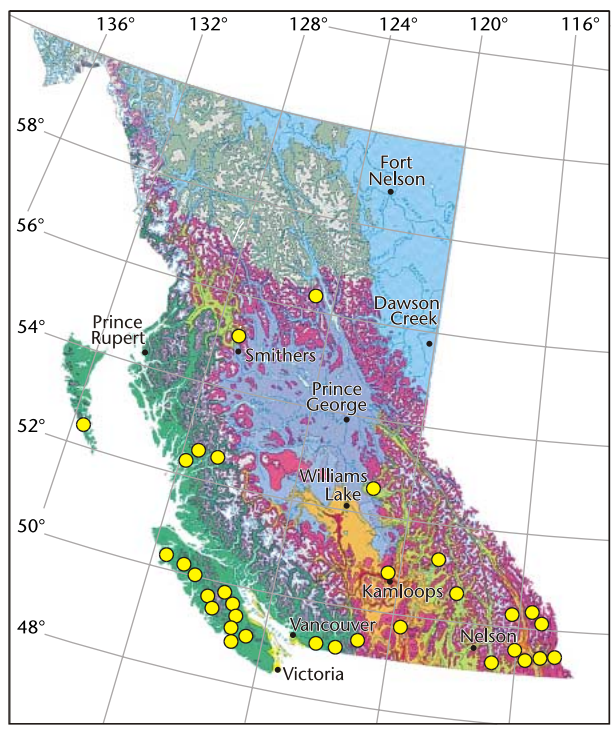

FIGURE 13 *Biogeoclimatic map of British Columbia showing locations of seed sources used in UV-B testing.*

3.2.1 *Abies grandis* (grand fir)

Grand fir ranges from southern British Columbia to California, generally at low elevations on moist sites (Farrar 1995). Its upper limit in British Columbia is usually less than 300 m (Xie and Ying 1993), while farther south it may be found up to 2000 m (USDA Forest Service 2001). Although seedlings grow well in moderate shade, mature trees of this species do best in full sun. In British Columbia, grand fir is a climax species. Relative to associated conifers, it has thinner, longer-lived needles, which might be vulnerable to the cumulative effects of UV-B exposure. The major cause of seedling mortality in natural regeneration is drought, so interactions between UV-B and water stress may be important.

The seed sources we used were from a fairly narrow range of elevation (260–680 m) from the District of Chilliwack in southern British Columbia, and all grew fairly slowly (Figure 14). Height growth was affected both by elevation of the seed source and UV-B exposure (Figure 15).

The low-elevation seedlings were the slowest-growing, not a typical result for this species (Xie and Ying 1993). They had an average height of only 5 cm after 4 months of summer growth, about 45% shorter than the high-elevation seedlings at 9.5 cm. Low-elevation seedlings grew best at zero or ambient UV-B exposure. Height decreased by about 25% between the two lowest and the two highest UV-B doses.

Middle-elevation seedlings were intermediate in height between low- and high-elevation sources. They grew best at ambient UV-B, where they were about 18% taller than seedlings grown without UV-B. Growth decreased somewhat as UV-B increased, but not as much as for the low-elevation seedlings.

High-elevation seedlings showed the greatest height growth, and they grew best at the highest UV-B dose. Growth in the 8 kJ treatment was anomalous, showing an apparent decrease relative to the other UV doses. The reason for this is not clear.

Based on our greenhouse test, we suggest that the resistance of grand fir to UV-B has a high degree of genetic control, so choice of seed source will be important in regeneration. The geographical location of the seed sources may have differed in more than elevation (moisture levels, aspect, etc.), so increased UV-B resistance cannot be attributed to elevation alone. There may also be an interaction between seed source and growing conditions that modifies the response of seedlings to UV-B. The next step would be to test a range of seed sources from gradients of elevation and latitude to establish the range of UV-B resistance, and to test foliage of mature trees as well.

In general, grand fir seedlings appear to be fairly resistant to UV-B, although seedlings from the lowest elevations may show reduced growth with an increase in UV-B dose above ambient levels.

FIGURE 14 *Grand fir seedlings.*

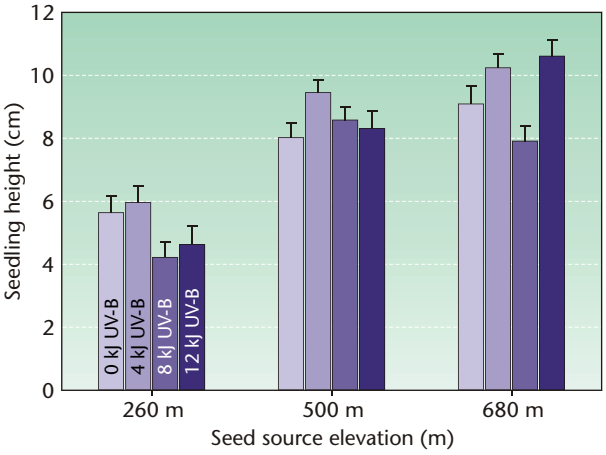

FIGURE 15 *Shoot height of grand fir seedlings after 16 weeks of UV-B exposure in greenhouses. Each bar is the mean of 25 seedlings, ± one standard error.*

3.2.2 *Betula papyrifera* (paper birch)

Paper birch has a wide distribution across Canada, from coast to coast and north to Alaska (Farrar 1995). Although generally a low-elevation species, it is found near timberline in the northeastern United States. Paper birch is a short-lived and shade-intolerant pioneer species (USDA Forest Service 2001), so it is well-adapted to high light intensities. Leaf morphology changes as light level increases: sun leaves are thicker, have a higher density of stomata, and have a larger surface area than shade leaves in young trees (Ashton et al. 1998). Other birch species have the ability to increase flavonoid production in response to increased UV-B, and are relatively insensitive to higher UV-B levels (Lavola 1998).

We tested 1-year-old seedlings of paper birch (one seed source, from the British Columbia interior) immediately after removal from over-winter cold storage, so their leaves expanded in the presence of UV-B. In this test only two levels of UV-B were used (ambient at 4 kJ m^{-2} d^{-1} and triple ambient at 12), along with two levels of visible light (low at 300 µmol m^{-2} s^{-1} and high at 600). After only 5 weeks of UV-B exposure, there were very striking differences in appearance of the seedlings and the leaves (Figure 16).

Leaves grown at low light tended to be larger in area (Figure 17a) and dry weight than those grown at higher visible light levels. But the most pronounced effect was that of UV-B. The total surface area of leaves 5, 6, and 7 from the apex was 35% lower at 12 than at 4 kJ UV-B (Figure 17a). Leaves at high UV-B had a bumpy surface (Figure 16) and curled margins, and sometimes developed chlorotic patches between the veins (Figure 7).

When leaves were heat stressed (exposure of leaf discs to 46°C for 30 minutes in bright light), those grown at high UV-B were more resistant than those grown at ambient (Figure 17b). It appears that growth under additional UV-B stress increases the ability of birch leaves to survive high temperatures, likely because similar mechanisms are used to dissipate excess energy.

Paper birch seedlings from this seed source were very sensitive to UV-B radiation, with pronounced decreases in growth and morphology at high UV-B levels. However, they also showed an increase in resistance to heat. It may be possible to find sources that combine a greater degree of UV-B resistance with the ability to tolerate heat. The next step would be to test a wider range of seed sources at more UV-B levels, to give a more comprehensive estimate of the sensitivity of this hardwood species.

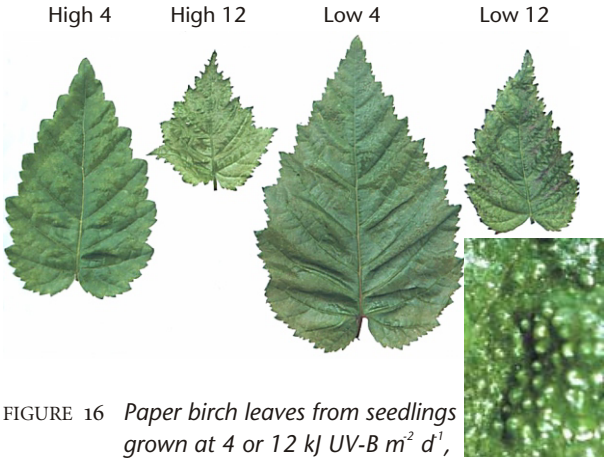

FIGURE 16 *Paper birch leaves from seedlings grown at 4 or 12 kJ UV-B m^{-2} d^{-1}, under high or low visible light levels. At right, close-up of High 12 leaf surface.*

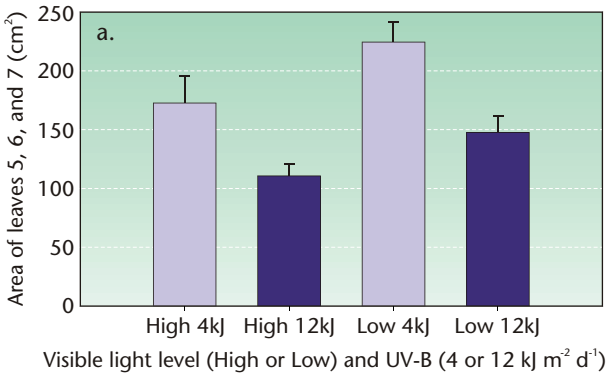

FIGURE 17a *Leaf area of paper birch seedlings after 5 weeks of UV-B exposure at high or low visible light. Each bar is the mean of 12 seedlings, ± one standard error.*

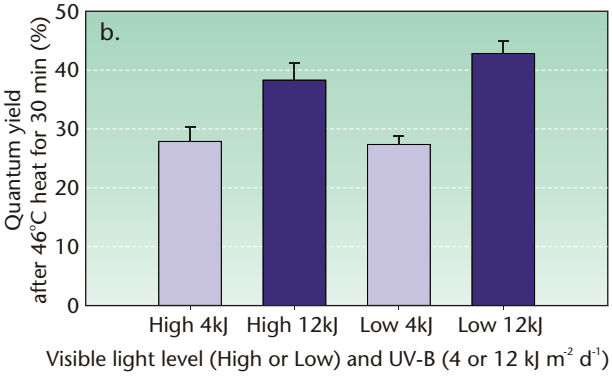

FIGURE 17b *Quantum yield of paper birch seedlings after heat stress. Higher quantum yield indicates less damage. Each bar is the mean of 12 seedlings, ± one standard error.*

3.2.3 *Chamaecyparis nootkatensis* (yellow-cedar)

Yellow-cedar, also known as Alaska-cedar, is a long-lived coastal species ranging from Alaska to northern California. It grows relatively slowly but can reach 3500 years of age, at elevations from sea level to 2200 m (USDA Forest Service 2001). The leaves of yellow-cedar are small and scale-like (Figure 18), and are quite shade tolerant (Farrar 1995), although this species also grows well in full sun as a climax species.

We tested yellow-cedar seedlings of a Vancouver Island seed source from 750 m elevation. Seedlings were 1 year old when they were placed under four levels of UV-B and grown for 5 months. New foliage at the higher UV-B levels appeared quite different from that grown without UV-B (Figure 18). The leaves retained a more juvenile appearance, and were strongly curled.

Although there were no large changes in total biomass of the seedlings, there were changes in frost hardiness and pigment levels (Figure 19a,b). Seedlings freeze-tested in early September showed a pattern of increasing frost hardiness with increasing UV-B levels from 0 to 8 kJ m^{-2} d^{-1}, but then a decrease in hardiness at the highest UV-B level (Figure 19a). At this level, their frost hardiness was lower than that of seedlings grown without UV-B.

Foliar levels of the photosynthesis pigments, chlorophylls *a* and *b*, were significantly affected by growth under increased UV-B. Leaf content of chlorophyll *a* increased by 120% and chlorophyll *b* by 105% between the zero and 12 kJ UV-B treatments, so the total chlorophyll content increased by 118% (Figure 19b). We did not measure photosynthetic rates, so we do not know if they were affected by this change.

These results suggest that yellow-cedar seedlings from this seed source are fairly sensitive to UV-B increases, but have the capacity to acclimate to changes in UV-B levels without large short-term effects on biomass. However, with large increases in UV-B, they may become more sensitive to fall freezing events.

The next step would be to test a wider range of seed sources from a gradient of latitudes and elevations, preferably under field conditions. There is moderate genetic variation in other adaptive traits of this species, related to latitude and elevation of seed origin (Russell 1993).

FIGURE 18 *Yellow-cedar branches from seedlings grown at 0 (left) or 12 (right) kJ UV-B m^{-2} d^{-1} for 5 months.*

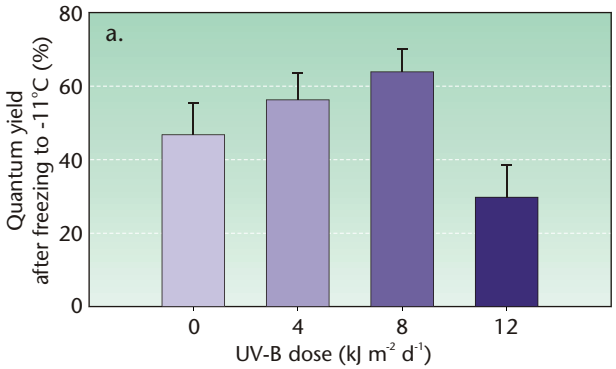

FIGURE 19a *Frost hardiness of yellow-cedar seedlings after freezing to -11°C in early September. Each bar is the mean of 15 seedlings, ± one standard error.*

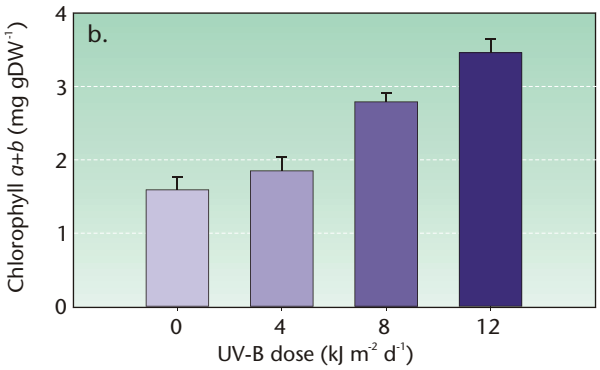

FIGURE 19b *Chlorophyll a+b content of yellow-cedar foliage after 5 months of UV-B exposure. Each bar is the mean of 15 seedlings, ± one standard error.*

3.2.4 *Larix occidentalis* (western larch)

Western larch is distributed over a relatively small range from southeastern British Columbia to Idaho and northern Oregon (Farrar 1995). It is a fast-growing deciduous conifer that typically regenerates disturbed areas, particularly after fire (USDA Forest Service 2001). Western larch can be found as high as 1600–2500 m elevation; it is quite frost-tolerant but not very drought-tolerant. Its deciduous needles are very shade-intolerant and have high photosynthetic rates. Because of their short life, the needles require less of a carbon investment than do evergreen needles of other conifer species.

We tested 1-year-old western larch seedlings from 800 m elevation, and younger seedlings from 940, 1160, and 1560 m elevation seed sources. Growth was reduced by increasing doses of UV-B radiation, and needle morphology changed dramatically. Instead of growing long, straight, and flat, the needles became shorter, twisted, and corkscrewed (Figure 20). Seedlings grown for 5 months under the highest level of UV-B were 28% shorter than seedlings grown without UV-B (Figure 21b). However, there was little change in height between seedlings grown without UV-B and those grown at twice the ambient levels.

In addition to their morphological changes, seedlings also showed changes in stress physiology. Frost hardiness in mid-October increased with increasing UV-B dose (Figure 21a). Seedlings grown without any UV-B had about one-third more damage than those grown at the highest UV-B dose. This response was similar for seedlings from all three elevations.

Western larch may be considered sensitive to UV-B because of its changes in morphology, height growth, and physiology. Because its needles are deciduous, there would be no direct cumulative effects on foliage productivity, but changes in carbon allocation would be expected to affect stem and root biomass. Because there is significant genetic variation among populations (Jaquish and El-Kassaby 1998), testing of more sources and trees in field situations is needed to estimate the potential for future effects.

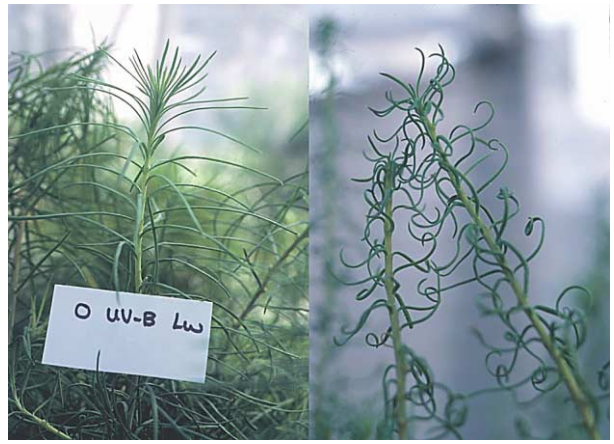

FIGURE 20 *Western larch seedlings grown with no UV-B (left) had long, straight needles. Those grown at high UV-B (12 kJ m^{-2} d^{-1}) (right) had shorter, twisted needles.*

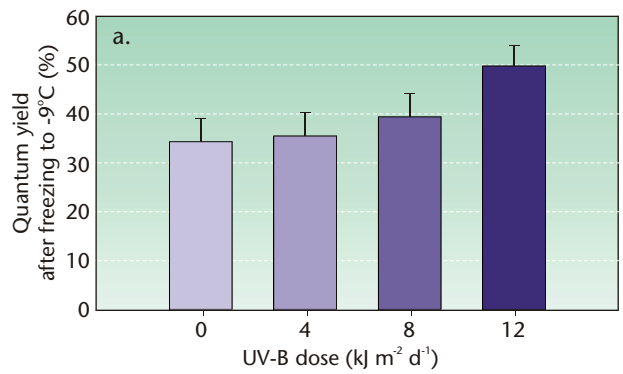

FIGURE 21a *Frost hardiness of western larch seedlings after freezing to -9°C in early October. Each bar is the mean of 54 seedlings, ± one standard error.*

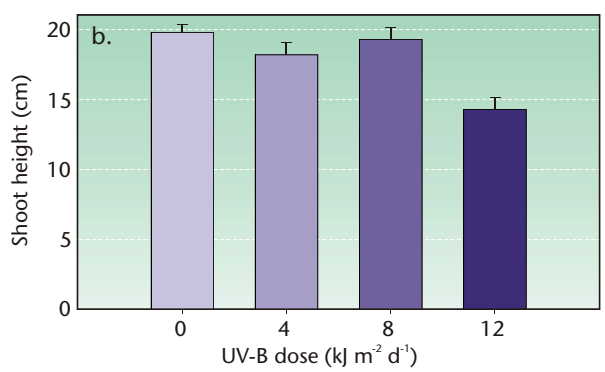

FIGURE 21b *Shoot height of western larch seedlings after 5 months of UV-B exposure. Each bar is the mean of 90 seedlings, ± one standard error.*

3.2.5 *Picea engelmannii* (Engelmann spruce)

Engelmann spruce is a high-elevation species ranging from northern British Columbia south through Idaho to Arizona, usually growing above 1000 m and up to treeline (Farrar 1995). Seedlings are very shade- and frost-tolerant and slow-growing in their natural environments. They do not compete well with faster-growing and less shade-tolerant associates when regenerating under open canopies or on disturbed sites (USDA Forest Service 2001).

We tested Engelmann spruce seedlings from three seed sources covering a 900 m range in elevation. High-elevation seedlings were very slow-growing under greenhouse conditions (Figure 23a), with a height of less than 4 cm after 4 months of growth. However, they did not appear to be negatively affected by increased doses of UV-B.

In contrast, low- and middle-elevation seedlings grew about three times as fast, but were affected by UV-B. They grew best at 0 and ambient UV-B levels (Figures 9, 22, and 23a). At the highest level of UV-B, they were about 25% shorter than at ambient UV. Even with this decrease, they were still more than double the size of the high-elevation seedlings.

Along with decreased height, seedlings grown at the higher UV-B levels also had smaller root collar diameter, fewer branches, shorter needles, more visible injury, and lower biomass.

As with several other species, Engelmann spruce seedlings showed increased stress resistance when exposed to increasing levels of UV-B. Frost hardiness in September increased by more than 60% for seedlings grown at the highest UV-B levels, relative to those grown without any UV-B (Figure 23b). This happened for seedlings from all three elevations, with the only notable difference being that high-elevation seedlings showed high levels of frost hardiness at all three UV-B levels–only the seedlings grown without UV-B were damaged. It seems that exposure to UV-B triggers metabolic and biochemical changes that make photosynthetic and cellular membranes more resistant to disruption from freezing temperatures.

Test results for this species again show that generalizations for a species must be made cautiously. Engelmann spruce, being a high-elevation species, would be expected to be very resistant to UV-B, but the resistance is affected by population source. There is likely also a difference in resistance between seedlings and mature trees, and between sun and shade foliage. Tests, including a larger combination of genetic and environmental treatments, are needed to establish a range of UV-B resistance in this species.

FIGURE 22 *Young Engelmann spruce seedlings grown without any UV-B (on right) or at 12 kJ UV-B m^{-2} d^{-1} (three times ambient, on left).*

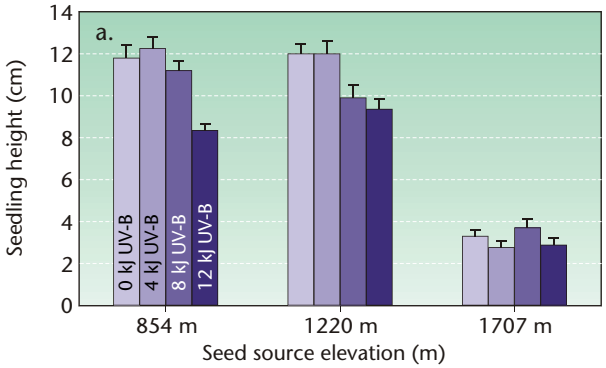

FIGURE 23a *Shoot height of Engelmann spruce seedlings after 4 months of UV-B exposure. Each bar is the mean of 45 seedlings, ± one standard error.*

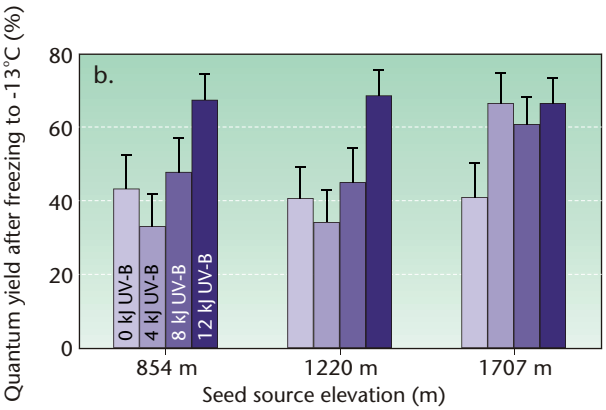

FIGURE 23b *Frost hardiness of Engelmann spruce seedlings after freezing to -13°C in September. Each bar is the mean of 15 seedlings, ± one standard error.*

3.2.6 *Picea glauca* x *engelmannii* (interior spruce)

In many parts of its range, Engelmann spruce hybridizes freely with other spruce species (Daubenmire 1974). Hybrids between Engelmann and white spruce are common throughout central British Columbia, mostly at lower elevations, where they are called interior spruce (Xie et al. 1998). These hybrids most closely resemble white spruce, but cannot be readily distinguished from Engelmann spruce.

The most frequently planted seedlings in British Columbia are interior spruce, which have a large economic value (Xie et al. 1998). Because the hybrids include a range of characteristics of the two pure species, they might be expected to exhibit a range of responses to increased UV-B radiation.

We tested 1-year-old seedlings from 925 m elevation in northern British Columbia, and younger seedlings from three elevations in the southeastern part of the province. This last group suffered from water stress in the early part of the test, so here we present the results for the older seedlings.

Interior spruce seedlings for the most part were fairly resistant to increases in UV-B levels. At the highest UV-B dose, some seedlings showed needle curling or changes in needle angle relative to seedlings grown at lower UV-B levels (Figure 24a, b). There did not appear to be notable changes in biomass.

Unlike several other conifer species that we tested, interior spruce seedlings showed a decrease in frost hardiness with increasing UV-B exposure (Figure 25). This was found in early September, near the beginning of fall cold acclimation. Although the difference was not large, it was significant.

Interior spruce populations probably have a fairly large range in UV-B sensitivity, depending on the genetic makeup of the hybrids. Some populations are expected to be quite sensitive, others fairly resistant. Because this complex is so widely planted in the province, it would be advisable to check a range of sources from wild stands and seed orchards for vulnerability to increased UV-B levels.

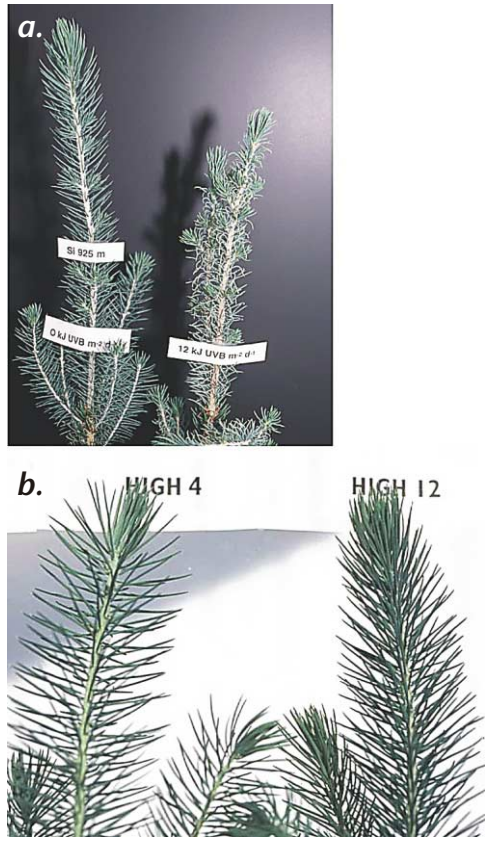

FIGURE 24 *a) Interior spruce seedlings grown at 0 (left) or 12 (right) kJ UV-B m^{-2} d^{-1} for 4 months. b) Interior spruce shoots grown at high light and 4 (left) or 12 (right) kJ UV-B m^{-2} d^{-1} for 5 weeks. Note the needle angles. Photos a and b are from different studies with different seedlings.*

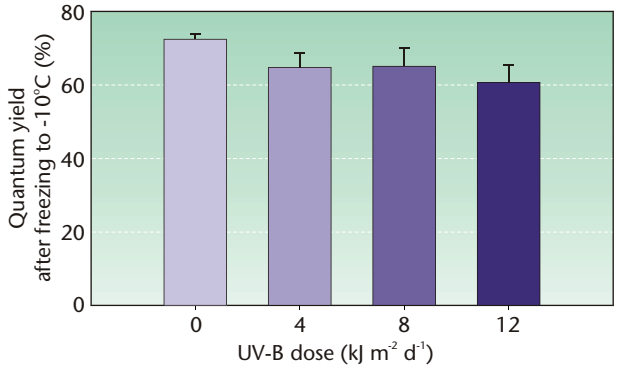

FIGURE 25 *Frost hardiness of interior spruce seedlings after freezing to -10°C in September. Each bar is the mean of 15 seedlings, ± one standard error.*

3.2.7 *Picea sitchensis* (Sitka spruce)

Sitka spruce is a low-elevation coastal species ranging from Alaska to Northern California, in many places growing in the fog belt (Farrar 1995). It prefers cool, moist summers and does best in areas of high precipitation. This long-lived species is the world's tallest spruce (USDA Forest Service 2001). Sitka spruce is shade-intolerant, and is both a pioneer and a climax species.

In a previous study, we tested Sitka spruce seedlings from 130, 300, and 490 m elevation by growing them for 4 months in late winter in a glasshouse. Height growth was strongly affected by both seed source elevation and UV-B dose (Figure 27a). Seedlings from the low and middle elevation were taller at all UV-B doses than those from the high-elevation source. Increasing UV-B had only small effects on seedling height as it increased from zero to ambient and double ambient, but, at three times ambient, many seedlings were killed and height growth dropped by more than half. In this study, the effects of high UV-B may have been exaggerated because ambient levels of visible light were relatively low from late winter to early spring.

Subsequent work with Sitka spruce used 1-year-old seedlings, which showed few effects on needle morphology (Figure 26). Needles seemed to be more angled upward in the presence of UV-B, but showed no signs of curling. However, shoot growth decreased by 16% between the 4 and 12 kJ UV-B treatments, and stress resistance changed as well. Several heat stress tests found that Sitka spruce seedlings were more heat-tolerant when UV-B levels were above zero (Figure 27b).

Because Sitka spruce is a shade-intolerant species, it may be fairly resistant to UV-B when visible light levels are also high enough to facilitate repair processes. It also seems to increase in heat resistance when grown under increasing UV-B levels. Given the wide latitudinal range of this species, further tests of populations from the north and south extremes, and of hybrids with other spruce species, would be useful for predicting variation in UV-B resistance levels.

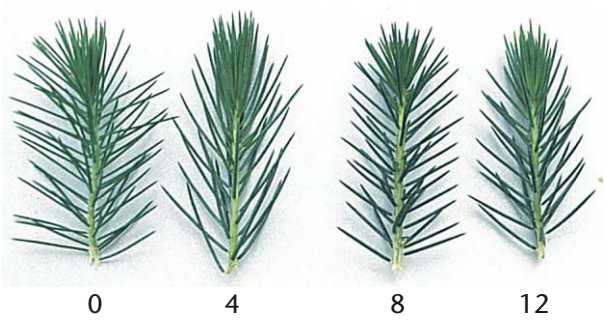

FIGURE 26 *Shoot tips of Sitka spruce seedlings grown with increasing UV-B. From left to right, 0, 4, 8, 12 kJ UV-B m^{-2} d^{-1}.*

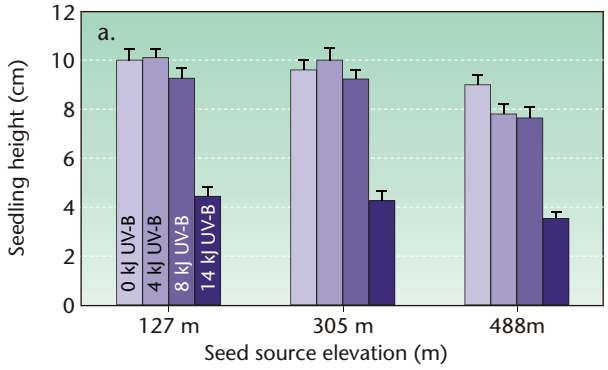

FIGURE 27a *Shoot height of Sitka spruce seedlings after 4 months of UV-B exposure. Each bar is the mean of 30 seedlings, ± one standard error.*

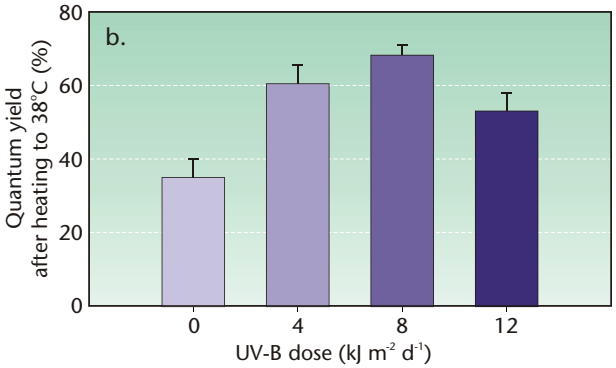

FIGURE 27b *Heat resistance of Sitka spruce seedlings after heating to 38°C for 30 minutes. Needles from 1-year-old seedlings from an 84-m seed source were tested. Each bar is the mean of 15 seedlings, ± one standard error.*

3.2.8 *Pinus contorta* var. *latifolia* (interior lodgepole pine)

One of the most common conifers in the interior of British Columbia is the interior variety of lodgepole pine. In North America, it ranges from the Yukon to Colorado, often in even-aged stands that arise after forest fires (Farrar 1995). It can be found at low elevations on relatively warm, dry sites through a range of site conditions to cool and moist at high elevations, with strong genetic variation among populations (Rehfeldt et al. 1999). This generally short-lived (less than 300 years) species is found growing as high as 3800 m in some parts of its range (USDA Forest Service 2001).

Being a shade-intolerant pioneer species, lodgepole pine might be expected to be fairly resistant to UV-B radiation. However, there is considerable variation among and within populations in growth potential and stress (cold, drought, etc.) resistance, so similar variation would be expected in UV-B resistance.

In our study we tested lodgepole pine seedlings from the southern interior of British Columbia, from three elevations up to 1720 m, and 1-year-old seedlings from 1300 m elevation (Figure 28). As expected, there were no obvious visible changes in the foliage (Figure 28), and no indication of needle curling or pigment breakdown even at triple the ambient dose of UV-B. At the morphological level, the populations we tested seemed to be very resistant to increased levels of UV-B.

For young seedlings from low elevation (700 m), height growth was positively affected by moderate levels of UV-B, increasing by 26% as dose increased from 0 to 8 kJ (Figure 29a). Growth then decreased slightly at the highest UV level. For seedlings from middle and high elevation, UV-B levels above zero had no effect or a small positive effect.

Increased exposure to UV-B increased stress resistance in seedlings from all elevations. Frost hardiness in early fall increased with increasing UV-B dose (Figure 29b), and heat resistance also increased slightly (Figure 39). From these results, it seems that some UV-B radiation is beneficial to growth and survival of this species.

At the population level, growth potential of lodgepole pine is negatively correlated with stress resistance (faster growth associated with lower stress resistance) (Rehfeldt et al. 1999). However, owing to the large amount of variation within populations, it may be possible to find parents with both high growth potential and high resistance to UV-B and other stresses.

FIGURE 28 *Shoots of interior lodgepole pine seedlings grown with increasing UV-B. From left to right, 0, 4, 8, and 12 kJ UV-B m^{-2} d^{-1}.*

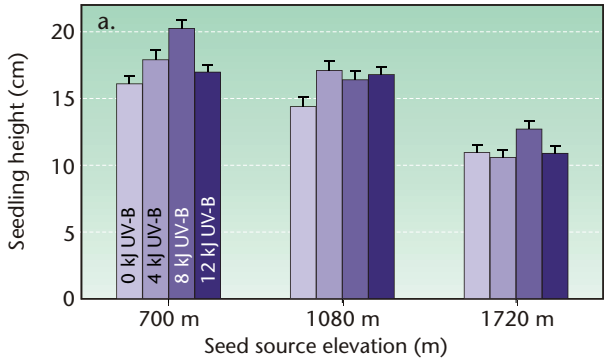

FIGURE 29a *Shoot height of lodgepole pine seedlings after 5 months of UV-B exposure. Each bar is the mean of 45 seedlings, ± one standard error.*

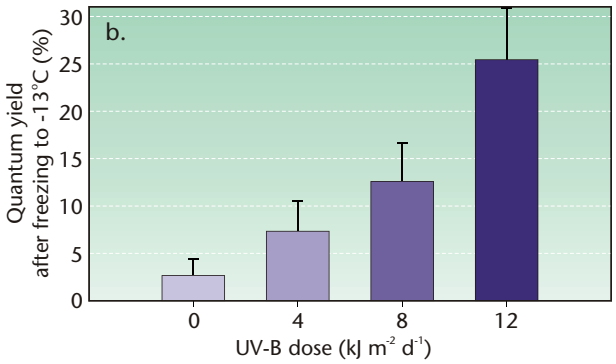

FIGURE 29b *Frost hardiness of lodgepole pine seedlings after freezing to -13°C in early September. Each bar is the mean of 45 seedlings, ± one standard error.*

3.2.9 *Pseudotsuga menziesii* var. *menziesii* (coastal Douglas-fir)

Coastal Douglas-fir is an economically valuable tree species along the west coast, ranging from mid-British Columbia to central California (Farrar 1995). This dominant long-lived species is a pioneer with moderate shade tolerance in its first year, thereafter requiring full sunlight (USDA Forest Service 2001). Damage from UV-B is most likely to occur in the first year where seedlings are growing on exposed sites. The needles last 5–8 years, so although mature needles are well-adapted to high light conditions, there may be potential for cumulative UV-B damage as surface layers change over time.

We tested young seedlings of coastal Douglas-fir in a preliminary study done in 1996. Seedlings from three elevations (150–967 m) on Vancouver Island were used. To stress seedlings when they were potentially most sensitive, we began UV-B exposure 1 week after germination. There were four doses of supplemental UV-B (0, 4, 8, and 14 kJ m^{-2} d^{-1}), with the highest dose slightly higher than that used in our other experiments. Exposure began in February 1996 in a heated glasshouse.

Within 4 days, seedlings at the highest dose showed needle curling, and in less than a week, about 90% of the Douglas-fir seedlings at that dose were dead (Figure 30a,b). Seedlings at the lower UV-B doses also showed morphological changes; after 14 weeks there was a strong effect of UV-B on height (Figure 31), root collar diameter, and dry weight. Dry weights of Douglas-fir seedlings decreased as much as 37% as UV-B increased from 0 to 8 kJ m^{-2} d^{-1}. There was no overall effect of elevation on these responses to UV-B, possibly because the range in elevation was not wide enough.

Light quality and balance (ratio of UV-B to visible) may have been confounding factors in this experiment because the test was done during the grey days of winter in Victoria, when ambient visible light levels are usually less than half of summer levels. This may have made the seedlings more vulnerable to UV-B, with less ability to undergo light-dependent repair processes.

Further testing is needed to reliably establish the sensitivity of this species to UV-B under ambient visible light levels.

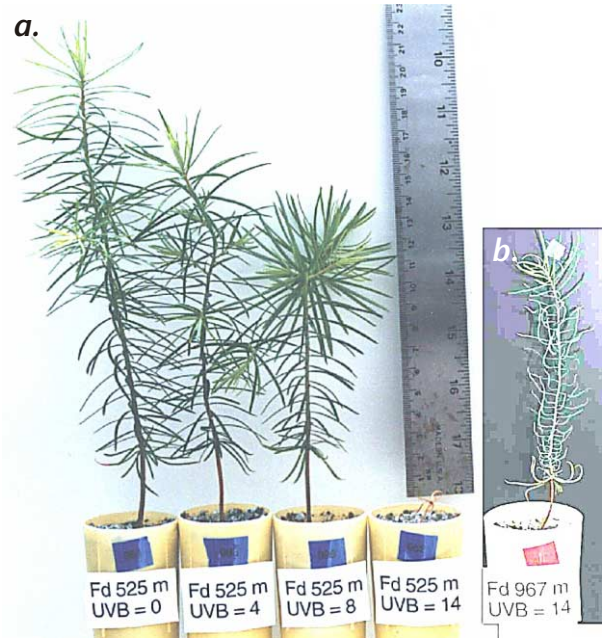

FIGURE 30 *a) Seedlings of mid-elevation coastal Douglas-fir grown with increasing UV-B (seedling at 14 is dead). Units for UV-B are kJ m^{-2} d^{-1}.*
b) High-elevation seedling grown at highest UV-B level.

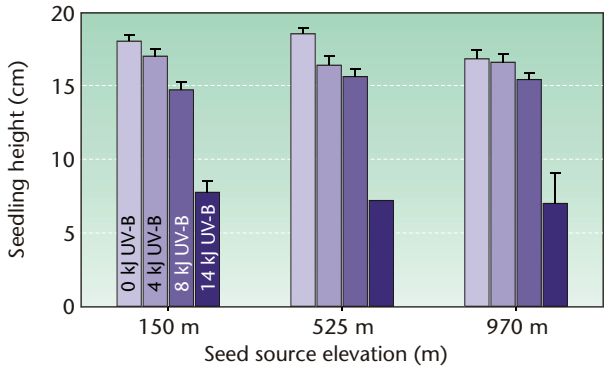

FIGURE 31 *Shoot height of coastal Douglas-fir seedlings after 4 months of UV-B exposure in a glasshouse. Each bar is the mean of 30 seedlings, ± one standard error, except for the 14 kJ treatment in which most seedlings died.*

3.2.10 *Pseudotsuga menziesii* var. *glauca* (interior Douglas-fir)

Interior or Rocky Mountain Douglas-fir ranges from the interior mountains of the Pacific Northwest south through the Rocky Mountains to Mexico (Farrar 1995), at elevations up to 3500 m. It is more cold- and drought-tolerant than the coastal variety, with which it hybridizes freely in areas of overlapping range. There is a considerable amount of genetic variation among populations following gradients of elevation and latitude (Rehfeldt 1989), with strong differences in frost hardiness and growth potential. The interior variety of Douglas-fir grows more slowly than the coastal variety and has a shorter lifespan (USDA Forest Service 2001). Seedlings regenerate best in moderate shade, where they would be exposed to less UV-B.

We tested young seedlings of interior Douglas-fir from three elevations (590, 830, and 1220 m). For the most part, seedlings grew normally and showed little evidence of UV-B–induced changes in morphology (Figure 32). Low-elevation seedlings showed greater height growth than mid- and high-elevation seedlings (Figure 33a), but were not strongly affected by increased UV-B. Height growth did not decrease significantly with increased UV-B for any of the elevations.

Similar to several other species, interior Douglas-fir seedlings showed increased frost hardiness with increased UV-B up to a point. Seedlings grown without any UV-B were the most damaged by freezing (Figure 33b), while those grown at 8 kJ (double ambient levels) were the most frost hardy. Frost hardiness was similar at 4 and 12 kJ.

Based on our preliminary results, we suggest that interior Douglas-fir is more resistant to UV-B than the coastal variety. Because there are known patterns of genetic variation in other adaptive traits, it is expected that there will also be patterns of variation in UV-B resistance. Testing of a wider range of seed sources, using seedlings and mature trees under field conditions, would be needed to describe these patterns.

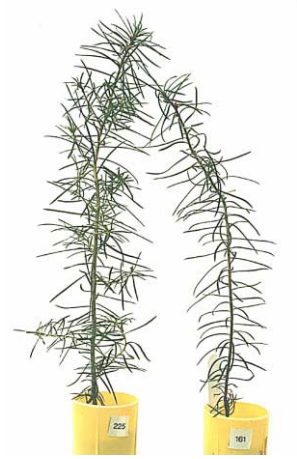

FIGURE 32 *Seedlings of mid-elevation interior Douglas-fir grown at 0 (left) or 12 (right) kJ UV-B m^{-2} d^{-1}. There were no striking morphological changes in interior Douglas-fir seedlings.*

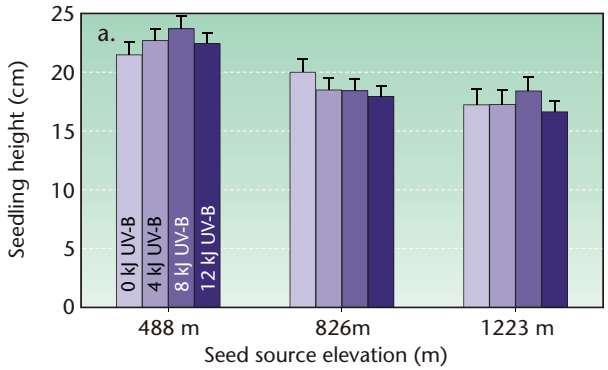

FIGURE 33a *Shoot height of interior Douglas-fir seedlings after 5 months of UV-B exposure. Each bar is the mean of 45 seedlings, ± one standard error.*

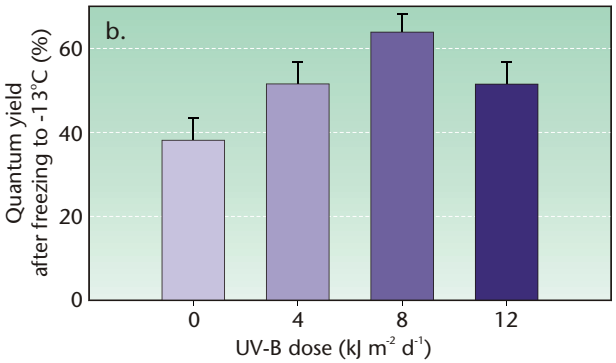

FIGURE 33b *Frost hardiness of interior Douglas-fir seedlings after freezing to -13°C in early September. Each bar is the mean of 45 seedlings, ± one standard error.*

3.2.11 *Thuja plicata* (western redcedar)

Ranging from the Pacific coast of northern British Columbia south to northern California and east through the west slopes of the Rocky Mountains, western redcedar grows to large sizes and may live for more than 1000 years (USDA Forest Service 2001). This valuable species regenerates best in partial shade; seedlings often succumb to drought and high temperature stresses in full sunlight. Although it is found at elevations up to 2000 m or more farther south, in British Columbia it is usually found at less than 1000 m elevation, with a preference for moist sites. Because seedlings are very shade-tolerant, and susceptible to drought and heat stress, we expected that they might also be sensitive to UV-B radiation.

We tested several seed sources of young seedlings and a single source of 1-year-old seedlings from 247 m elevation. Our test with young seedlings was somewhat compromised by taking place during the time of an unusually large blizzard in early 1997, during which the greenhouse nearly collapsed. We will present results here for the 1-year-old seedlings, grown the following summer.

As UV-B levels increased, there were no marked changes in the scale-like leaves, but there appeared to be small changes in the angle of branchlets (Figure 34). There was also a reduction in height growth (data not shown).

In addition to these changes, western redcedar seedlings showed strong changes in frost hardiness as UV-B dose increased (Figure 35). Seedlings grown without any UV-B were less hardy than those grown at ambient levels, but, as UV-B increased beyond ambient, frost hardiness decreased. Seedlings grown at the highest UV-B level were very sensitive to freezing.

The responses of the western redcedar seedlings in our test suggest that at least some populations of this species may be sensitive to increases in UV-B radiation. Because there is moderate genetic variation in other adaptive traits in western redcedar, it would be useful to expand testing to include more populations from across its natural range.

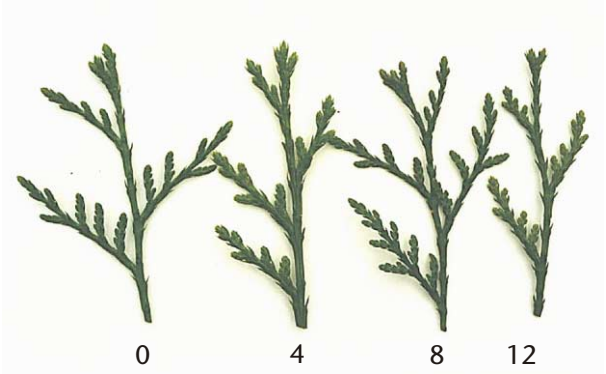

FIGURE 34 *Shoots of western redcedar grown at (left to right) 0, 4, 8, and 12 kJ UV-B m^{-2} d^{-1}. There appeared to be changes in branchlet angle as UV-B levels increased.*

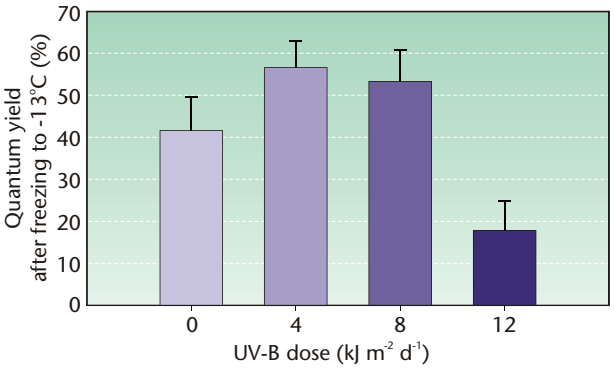

FIGURE 35 *Frost hardiness of western redcedar seedlings after freezing to -13°C in September. Each bar is the mean of 15 seedlings, ± one standard error.*

3.2.12. *Tsuga heterophylla* (western hemlock)

From Alaska to northern California, western hemlock stands are found on moist sites along the coast and also inland west of the Rocky Mountains (Farrar 1995). This fast-growing species is usually found at low to mid elevations, although farther south it grows as high as about 2000 m (USDA Forest Service 2001). The highly shade-tolerant seedlings are susceptible to frost, heat, drought, and sunscald, but mature trees can grow in high light conditions, provided there is adequate moisture. Seedlings might be expected to be relatively sensitive to increased UV-B radiation, particularly in the presence of other environmental stresses.

We tested young western hemlock seedlings from a range of elevations (100–670 m) and 1-year-old seedlings from a source at 186 m elevation. Seedlings showed typical morphological symptoms of UV-B damage early in the treatments (Figure 8, and 36a,b). Needles grown without any UV-B were straight and flat, while those grown at higher levels of UV were curled and twisted, and often showed bronzing (Figure 36b) or chlorosis. Height growth was also reduced by 25–32% as UV-B dose increased from 0 to 12 kJ (Figure 37a). High-elevation seedlings were less affected than low- or mid-elevation ones, but they also grew less at all UV-B doses.

Growth under higher levels of UV-B increased the heat resistance of young and older seedlings. Seedlings grown with no UV-B suffered two to three times as much damage from heat as seedlings grown at 12 kJ UV-B (see Figure **39**). Frost hardiness, however, did not always increase with UV-B exposure–in early September, it decreased for seedlings grown at higher levels of UV-B.

Hemlock seedlings showed pronounced changes in pigment and flavonoid content in their foliage as exposure to UV-B increased. Chlorophyll levels tended to decrease with increasing UV-B (data not shown), but flavonoids increased (Figure 37b). Averaged over all elevations, there was a 48% increase in flavonoid absorbance at 280 nm between 0 and 12 kJ UV-B.

These tests indicate that seedlings of western hemlock from British Columbia are potentially sensitive to increasing levels of UV-B radiation. Comparison with populations from farther south and higher elevations would be useful.

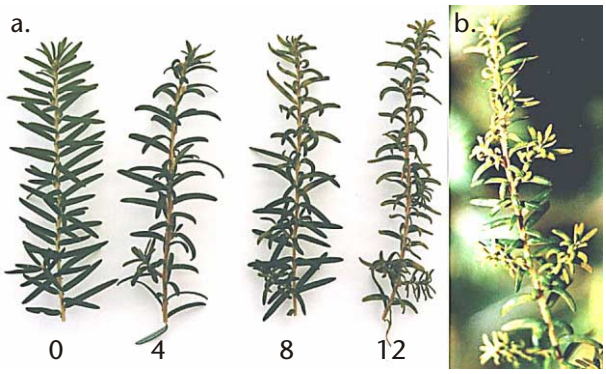

FIGURE 36 a) *Shoots of western hemlock grown at (left to right) 0, 4, 8, and 12 kJ UV-B m^{-2} d^{-1}. Note the needle curling as UV-B levels increased. b) Bronzing on needles of western hemlock grown at the highest UV-B dose.*

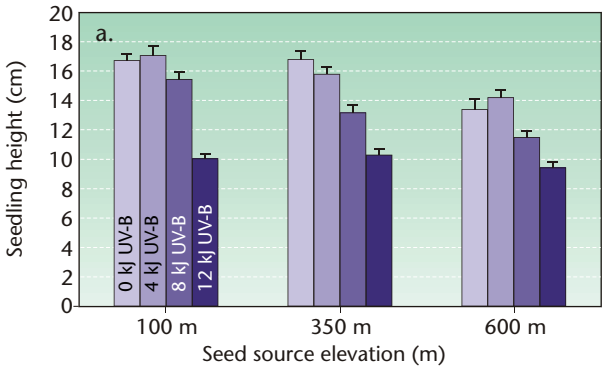

FIGURE 37a *Shoot height of western hemlock seedlings after 4 months of UV-B exposure. Each bar is the mean of 45 seedlings, ± one standard error.*

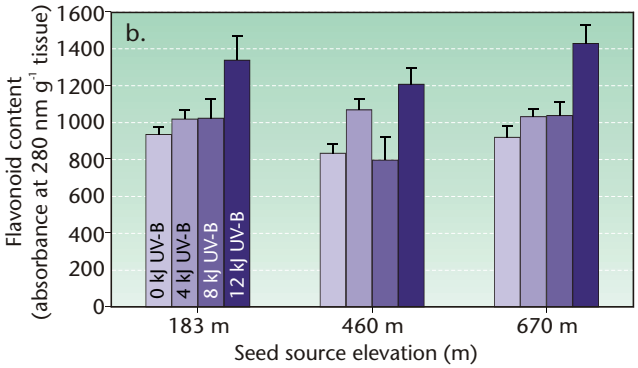

FIGURE 37b *Flavonoid content of western hemlock seedlings after 5 months of UV-B exposure. Each bar is the mean of nine seedlings, ± one standard error.*

3.3 Ranking of Species by Risk of Damage

Of the dozen species and four dozen seed sources that we tested in our UV-B chambers, several showed pronounced changes in morphology, growth, and stress tolerance, while others appeared to be resistant, showing few changes (Figure 38). UV-B exposure, in general, had more effect on low- than high-elevation seed sources. The sensitive conifers developed external changes such as curled and twisted needles, changes in needle or branchlet angle, and reduced growth. The lone hardwood tested, paper birch, showed large reductions in leaf size and changes in leaf surface morphology under high UV-B levels.

The resistant species showed few obvious external changes, but they did show increased resistance to other stresses such as freezing and heat. In fact, most of the species tested, whether UV-B sensitive or resistant, were more resistant to high temperatures when grown with supplemental UV-B radiation (Figure 39). This suggests that acclimation to increased UV-B triggers metabolic changes that are also involved in resistance to high temperatures, likely by increasing the ability to dissipate excess energy.

Our tests were done in greenhouse conditions with seedlings, so we cannot accurately extrapolate to field conditions with mature trees. We cannot, therefore, provide a definitive prediction about the effects of long-term UV-B radiation increases on overall growth and yield of the species tested. But we can provide a relative ranking of species for seedlings, and have done so in Figure 40. In the first year or two of growth, it is probable that this ranking gives a reasonable general estimate of how these species will respond to increasing levels of UV-B. However, there will be a wide range of sensitivity within most species, because populations are strongly differentiated in adaptive traits. The sensitivity will also depend on other environmental conditions at the growing site, and whether or not planted seedlings have been pre-conditioned by exposure to UV-B during early growth.

This variety of responses among and within species will help researchers and forest managers in developing solutions to deal with increased UV-B levels and their impacts on forest ecosystems.

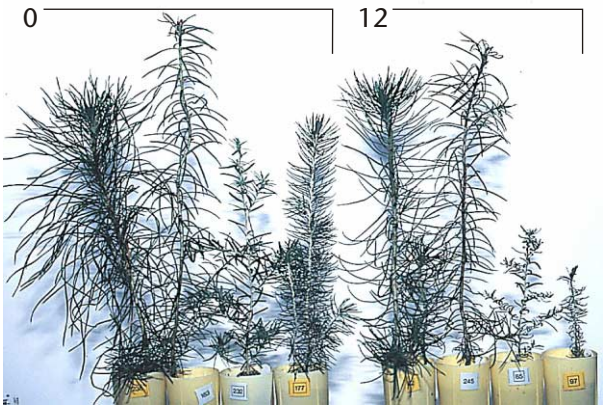

FIGURE 38 *Lodgepole pine, interior Douglas-fir, western hemlock, and Engelmann spruce grown at 0 (four seedlings on left) or 12 kJ UV-B m^{-2} d^{-1}. The hemlock and spruce showed strong morphological changes with increased UV-B, while the pine and Douglas-fir did not.*

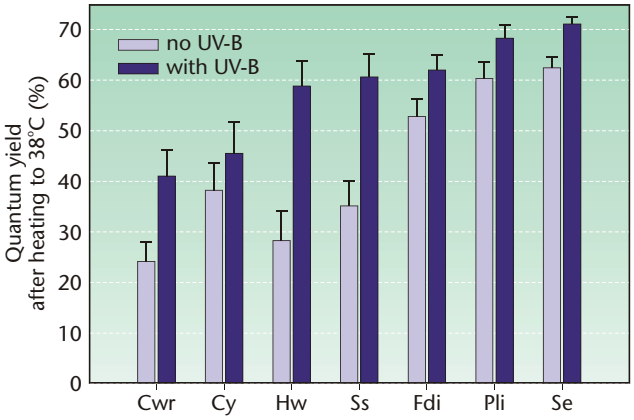

FIGURE 39 *Heat resistance of conifer species grown with or without UV-B. Cwr = western redcedar, Cy = yellow-cedar, Hw = western hemlock, Ss = Sitka spruce, Fdi = interior Douglas-fir, Pli = interior lodgepole pine, Se = Engelmann spruce. The "with UV-B" column is the mean of the 4, 8, and 12 kJ UV-B treatments.*

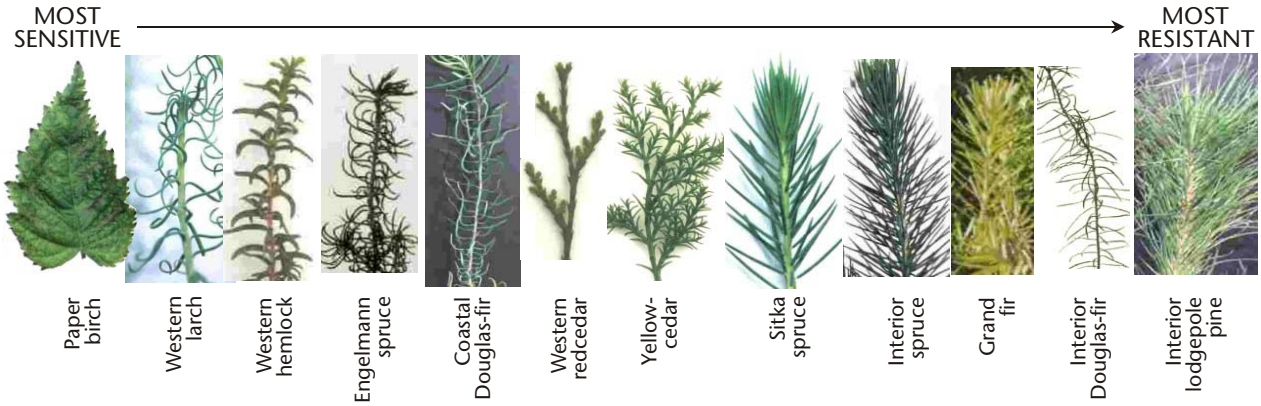

FIGURE 40 *Predicted ranking of some British Columbia tree species for resistance to increased UV-B, based on greenhouse testing.*

4 OBSERVATIONS AND RECOMMENDATIONS FOR FUTURE WORK

There were many challenges on the way to completing this project in a fairly new research area. We designed and built innovative UV-B chambers, and developed and applied fresh methods of testing seedling responses to UV-B. We dealt with the vagaries of Victoria weather (Figure 41)and obstinate irrigation systems. We gathered a truckload of data and climbed a mountain of analyses.

From all of this, benefits have emerged. We met our objectives of 1) determining the effects of increased UV-B levels on tree seedlings, 2) looking for geographic variation in responses, and 3) estimating the risk of damage to various species. We provided information and education to interested audiences, raising the awareness of ozone and UV-B in British Columbia. Our methods, hardware, and instrument calibrations have become a reference for new studies on the effects of UV-B in forestry and agriculture.

There is now enough information available on UV-B effects on British Columbia trees to help in choices for seedling management and deployment to planting sites, at least for some of the major species. We know that UV-B sensitivity is generally higher for low- versus high-elevation seed sources, for deciduous versus evergreen species, and for shade-tolerant versus shade-intolerant species. We recommend that seedlings of shade-tolerant species (e.g., western hemlock) be protected from full sun at the planting site, or gradually conditioned to UV-B in the nursery. Sharp increases in UV-B and visible light should be avoided when handling seedlings. For high-elevation or high-UV-B sites, the seed sources used should combine reasonable levels of UV-B tolerance and growth potential. Lodgepole pine seedlings appear to be well adapted to current levels of UV-B, and will likely continue to do well under moderate future increases.

The decrease in ozone levels over Canada (relative to pre-1980) was 5–45% over the past decade, and may continue for at least a few decades. This translates into UV-B increases of 10–90%, with a doubling of UV-B possible in British Columbia for some periods during the growing season. Given these changes, and that there are many unknowns (such as the interactions between UV-B and climate change),

FIGURE 41 *UV-B greenhouse with a snowfall.*

this issue cannot be considered resolved.

It is our hope that others will continue the work that we began. From the modest start made here, more extensive testing and monitoring projects in the field will determine the cumulative effects of elevated UV-B on forest productivity and sustainability in British Columbia. Our recommendations for future studies are based on our results and priorities from other scientists (de Fabo 1992; Farrell 1993). Ideally, further research and monitoring of UV-B effects on forest species in British Columbia should include the following:

- Multi-year growth studies in field conditions
- Tests of seedlings and mature trees from a wide range of species and populations
- Use of several populations for each species, and families within populations
- Identification of sensitive species and populations, not just in trees (indicators)
- Use of at least two levels of increased UV-B, preferably with modulating exposure systems
- Field sites covering gradients of latitude and elevation (range of UV-B doses)
- Measurement of effects on carbon allocation and secondary chemistry
- Identification of key symptoms of UV-B damage
- Interaction between UV-B and other stresses
- Modelling of growth processes and competitive interactions
- Testing of effects on reproductive physiology
- Evaluation of implications of UV-B–induced changes on insect and disease resistance
- Genetic selection of UV-B–resistant, productive populations and families

With this additional information, managers will be able to make appropriate choices using genecology and silviculture to minimize the risk of UV-B damage to future forest productivity.

FIGURE 42 *Rainbows are natural examples of the spectral qualities of sunlight.*

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