

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.*

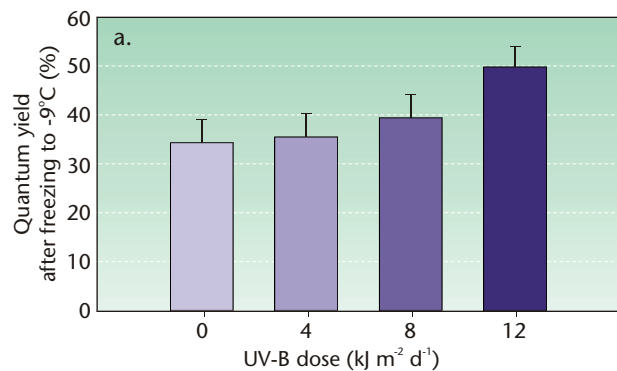


FIGURE 21a *Frost hardiness of western larch seedlings after freezing to -9°C in early October. Each bar is the mean of 54 seedlings, ± one standard error.*

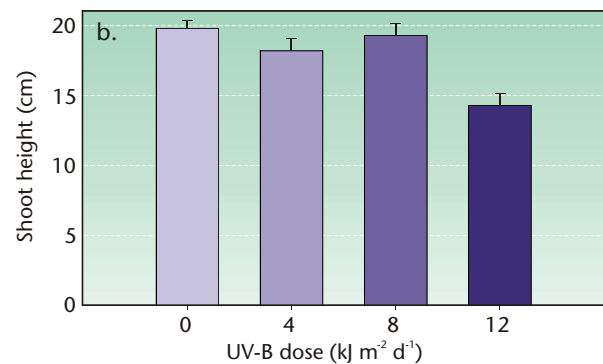


FIGURE 21b *Shoot height of western larch seedlings after 5 months of UV-B exposure. Each bar is the mean of 90 seedlings, ± one standard error.*

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).

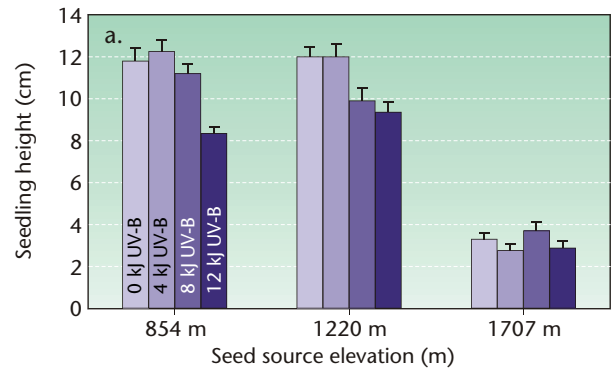


FIGURE 23a Shoot height of Engelmann spruce seedlings after 4 months of UV-B exposure. Each bar is the mean of 45 seedlings, \pm one standard error.

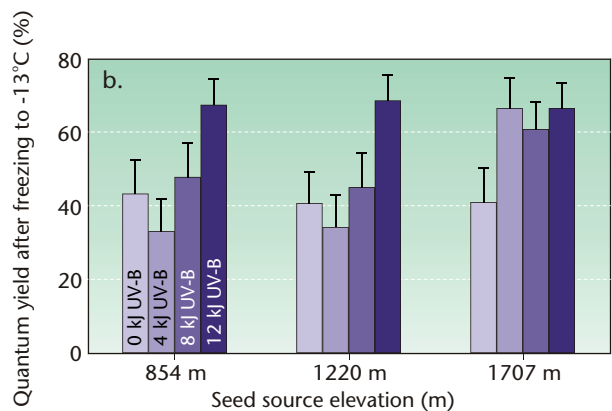


FIGURE 23b Frost hardiness of Engelmann spruce seedlings after freezing to $-13^{\circ}C$ in September. Each bar is the mean of 15 seedlings, \pm one standard error.

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.

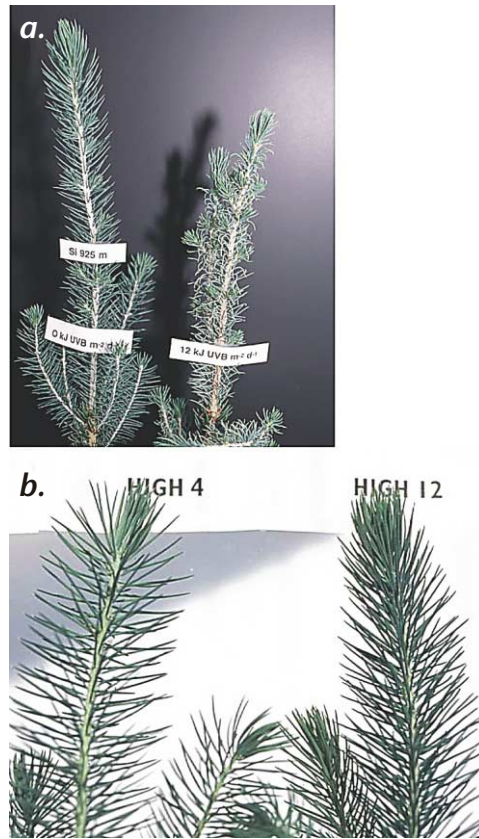


FIGURE 24 a) Interior spruce seedlings grown at 0 (left) or 12 (right) kJ UV-B m⁻² d⁻¹ for 4 months. b) Interior spruce shoots grown at high light and 4 (left) or 12 (right) kJ UV-B m⁻² d⁻¹ for 5 weeks. Note the needle angles. Photos a and b are from different studies with different seedlings.

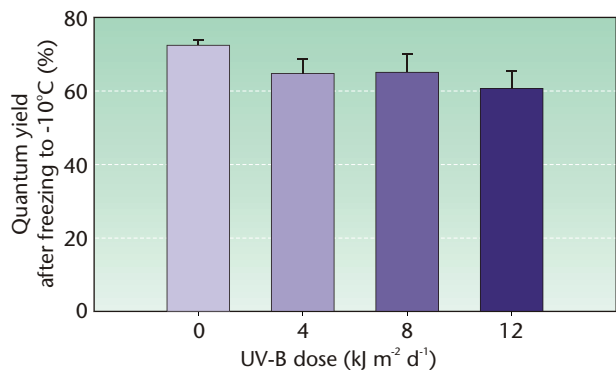


FIGURE 25 Frost hardiness of interior spruce seedlings after freezing to -10°C in September. Each bar is the mean of 15 seedlings, \pm one standard error.

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.

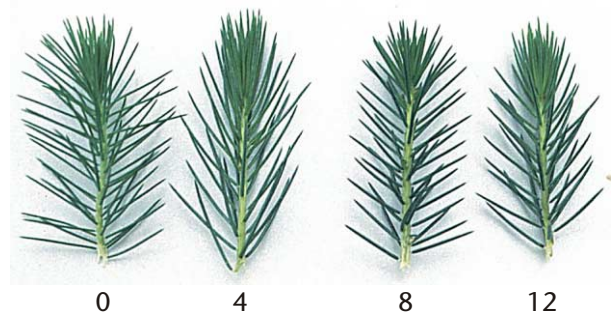


FIGURE 26 Shoot tips of Sitka spruce seedlings grown with increasing UV-B. From left to right, 0, 4, 8, 12 kJ UV-B m² d⁻¹.

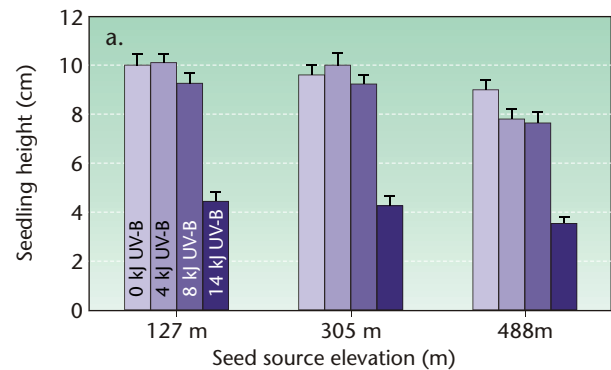


FIGURE 27a Shoot height of Sitka spruce seedlings after 4 months of UV-B exposure. Each bar is the mean of 30 seedlings, \pm one standard error.

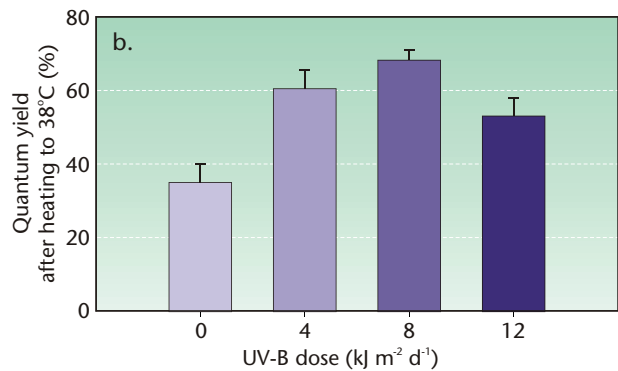


FIGURE 27b Heat resistance of Sitka spruce seedlings after heating to 38°C for 30 minutes. Needles from 1-year-old seedlings from an 84-m seed source were tested. Each bar is the mean of 15 seedlings, \pm one standard error.

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.

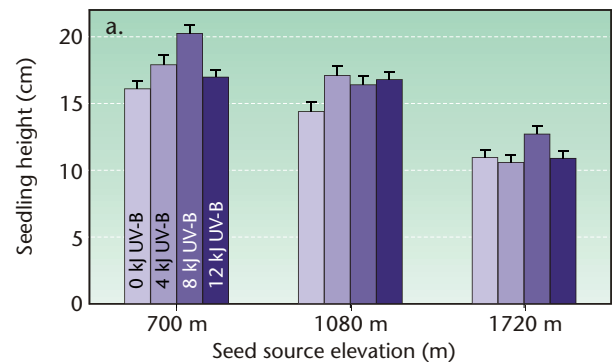


FIGURE 29a Shoot height of lodgepole pine seedlings after 5 months of UV-B exposure. Each bar is the mean of 45 seedlings, \pm one standard error.

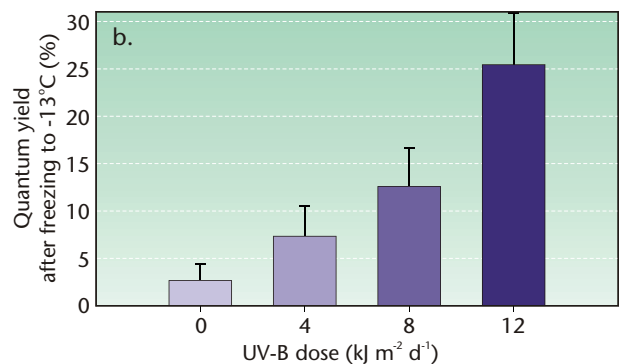


FIGURE 29b Frost hardiness of lodgepole pine seedlings after freezing to -13°C in early September. Each bar is the mean of 45 seedlings, \pm one standard error.

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.

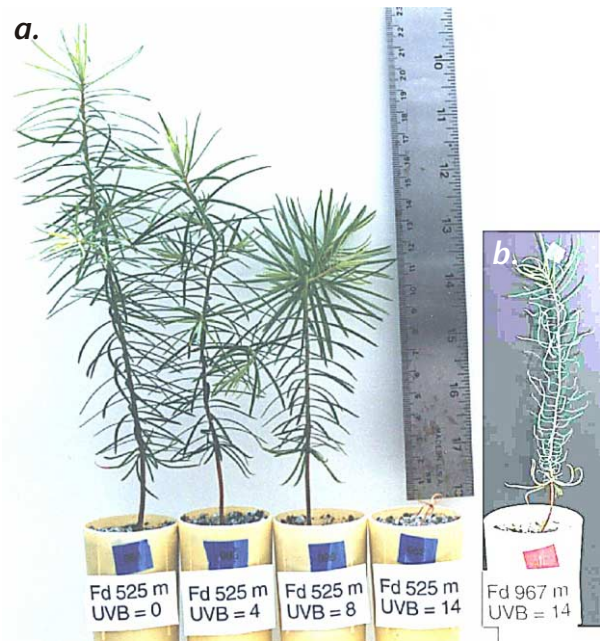


FIGURE 30 a) Seedlings of mid-elevation coastal Douglas-fir grown with increasing UV-B (seedling at 14 is dead). Units for UV-B are kJ m⁻² d⁻¹. b) High-elevation seedling grown at highest UV-B level.

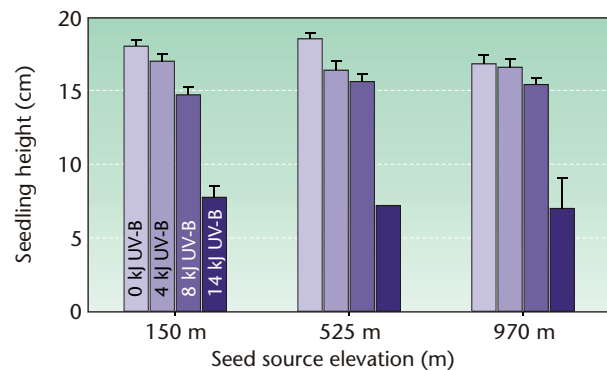


FIGURE 31 Shoot height of coastal Douglas-fir seedlings after 4 months of UV-B exposure in a glasshouse. Each bar is the mean of 30 seedlings, \pm one standard error, except for the 14 kJ treatment in which most seedlings died.

**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 m² d⁻¹. There were no striking morphological changes in interior Douglas-fir seedlings.

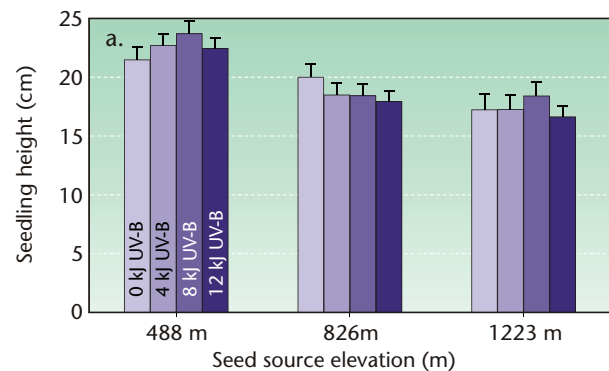


FIGURE 33a Shoot height of interior Douglas-fir seedlings after 5 months of UV-B exposure. Each bar is the mean of 45 seedlings, \pm one standard error.

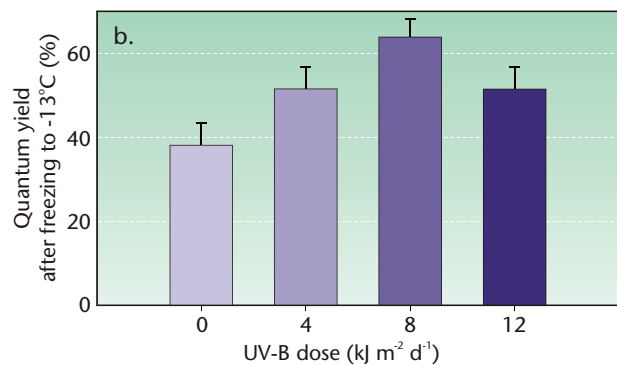


FIGURE 33b Frost hardiness of interior Douglas-fir seedlings after freezing to -13°C in early September. Each bar is the mean of 45 seedlings, \pm one standard error.

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.

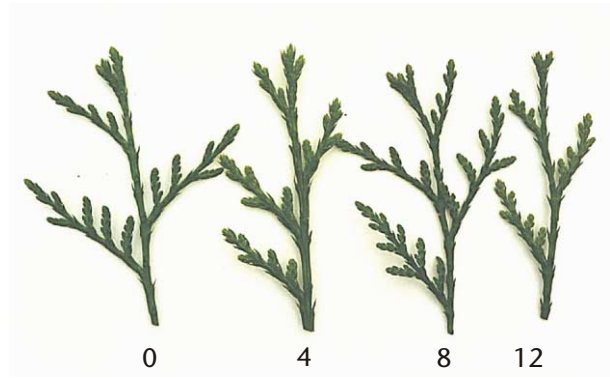


FIGURE 34 Shoots of western redcedar grown at (left to right) 0, 4, 8, and 12 $\text{kJ UV-B m}^{-2} \text{d}^{-1}$. There appeared to be changes in branchlet angle as UV-B levels increased.

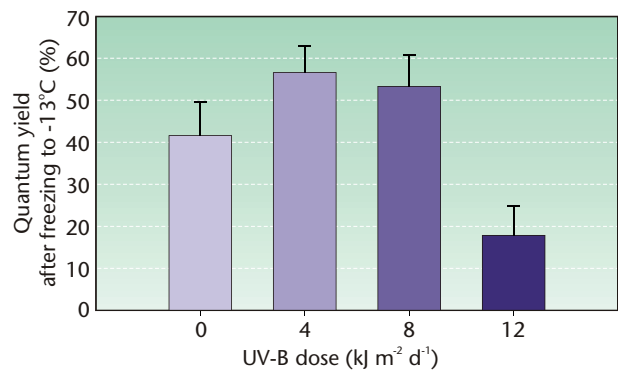


FIGURE 35 Frost hardiness of western redcedar seedlings after freezing to -13°C in September. Each bar is the mean of 15 seedlings, \pm one standard error.

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.

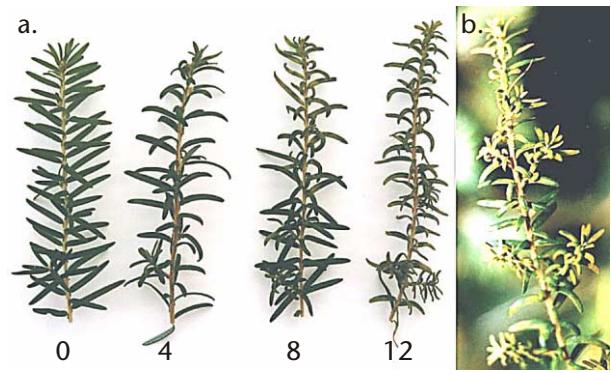


FIGURE 36 a) Shoots of western hemlock grown at (left to right) 0, 4, 8, and 12 kJ UV-B $m^{-2} d^{-1}$. Note the needle curling as UV-B levels increased. b) Bronzing on needles of western hemlock grown at the highest UV-B dose.

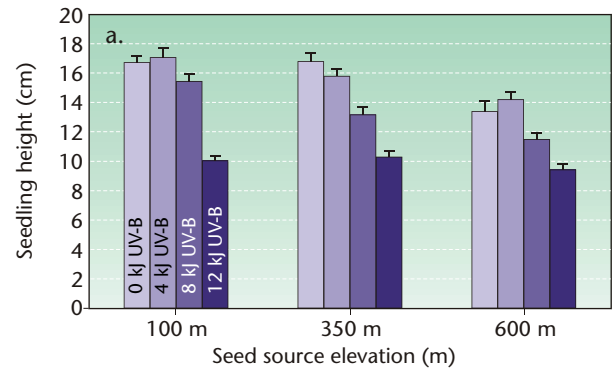


FIGURE 37a Shoot height of western hemlock seedlings after 4 months of UV-B exposure. Each bar is the mean of 45 seedlings, \pm one standard error.

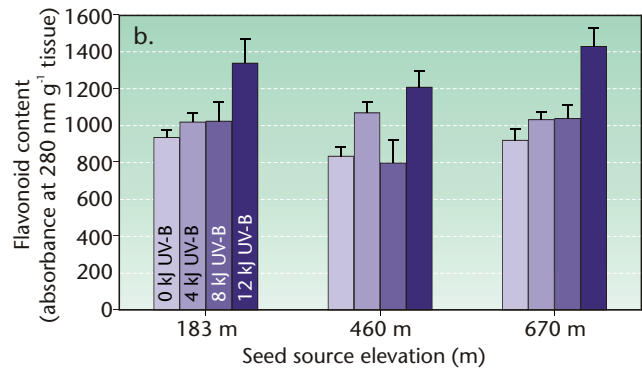


FIGURE 37b Flavonoid content of western hemlock seedlings after 5 months of UV-B exposure. Each bar is the mean of nine seedlings, \pm one standard error.

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.

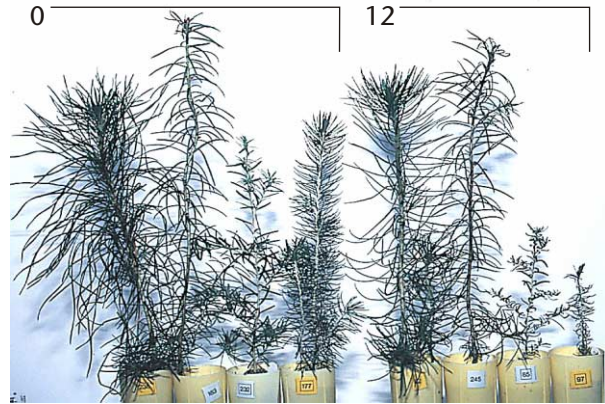


FIGURE 38 *Lodgepole pine, interior Douglas-fir, western hemlock, and Engelmann spruce grown at 0 (four seedlings on left) or 12 kJ UV-B m² d⁻¹. The hemlock and spruce showed strong morphological changes with increased UV-B, while the pine and Douglas-fir did not.*

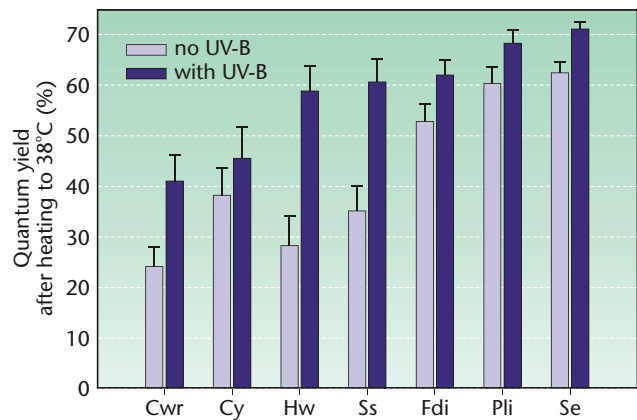


FIGURE 39 *Heat resistance of conifer species grown with or without UV-B. Cwr = western redcedar, Cy = yellow-cedar, Hw = western hemlock, Ss = Sitka spruce, Fdi = interior Douglas-fir, Pli = interior lodgepole pine, Se = Engelmann spruce. The "with UV-B" column is the mean of the 4, 8, and 12 kJ UV-B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

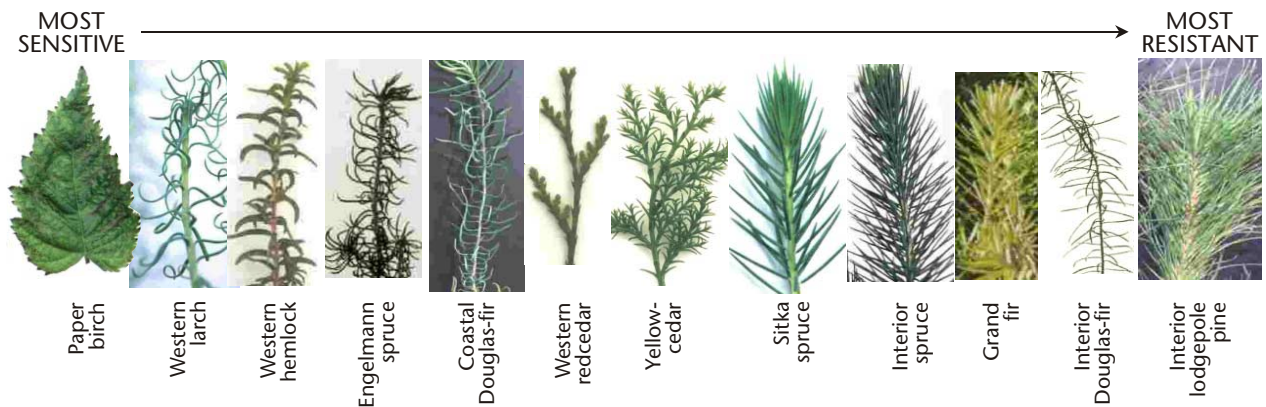


FIGURE 40 Predicted ranking of some British Columbia tree species for resistance to increased UV-B, based on greenhouse testing.

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.*

REFERENCES

- Adamse, P. and S.J. Britz. 1992. Spectral quality of two fluorescent UV sources during long-term use. *Photochem. Photobiol.* 56: 641–644.
- Aldhous, P. 2000. Global warming could be bad news for Arctic ozone layer. *Nature* 404: 531.
- Ambasht, N.K. and M. Agrawal. 1998. Physiological and biochemical responses of *Sorghum vulgare* plants to supplemental ultraviolet-B radiation. *Can. J. Bot.* 76: 1290–1294.
- Ashton, P.M.S., L.P. Olander, G.P. Berlyn, R. Thadani, and I.R. Cameron. 1998. Changes in leaf structure in relation to crown position and tree size of *Betula papyrifera* within fire-origin stands of interior cedar-hemlock. *Can. J. Bot.* 76: 1180–1187.
- Balakumar, T., V.H.B. Vincent, and K. Paliwal. 1993. On the interaction of UV-B radiation (280–315 nm) with water stress in crop plants. *Physiol. Plant.* 87: 217–222.
- Ballaré, C.L., P.W. Barnes, and S.D. Flint. 1995a. Inhibition of hypocotyl elongation by ultraviolet-B radiation in de-etiolating tomato seedlings. I. The photoreceptor. *Physiol. Plant.* 93: 584–592.
- Ballaré, C.L., P.W. Barnes, S.D. Flint, and S. Price. 1995b. Inhibition of hypocotyl elongation by ultraviolet-B radiation in de-etiolating tomato seedlings. II. Time course, comparison with flavonoid responses and adaptive significance. *Physiol. Plant.* 93: 593–601.
- Barnes, P.W., S.D. Flint, and M.M. Caldwell. 1987. Photosynthesis damage and protective pigments in plants from a latitudinal arctic/alpine gradient exposed to supplemental UV-B radiation in the field. *Arctic Alpine Res.* 19: 21–27.
- _____. 1990. Morphological responses of crop and weed species of different growth forms to ultraviolet-B radiation. *Am. J. Bot.* 77: 1354–1360.
- Barnes, P.W., S. Maggard, S.R. Holman, and B.S. Vergara. 1993. Intraspecific variation in sensitivity to UV-B radiation in rice. *Crop Sci.* 33: 1041–1046.
- Bavcon, J., A. Gaberščik, and F. Batic. 1996. Influence of UV-B radiation on photosynthetic activity and chlorophyll fluorescence kinetics in Norway spruce [*Picea abies* (L.) Karst.] seedlings. *Trees* 10: 172–176.
- Björn, L.O. 1989. Computer programs for estimating ultraviolet radiation in daylight. *In* Radiation measurements in photobiology. B.L. Diffey (editor). Academic Press, New York, N.Y., pp. 161–189.
- _____. 1996. Effects of ozone depletion and increased UV-B on terrestrial ecosystems. *Int. J. Environ. Stud.* 51: 217–243.
- Björn, L.O. and A.H. Teramura. 1993. Simulation of daylight ultraviolet radiation and effects of ozone depletion. *In* Environmental UV photobiology. A.R. Young, L.O. Björn, J. Moan, and W. Nultsch (editors). Plenum Press, New York, N.Y., pp. 41–71.
- Bothwell, M.L., D.M.J. Sherbot, and C.M. Pollock. 1994. Ecosystem response to solar ultraviolet-B radiation: influence of trophic-level interactions. *Science* 265: 97–100.
- British Antarctic Survey Ozone. 2000. Ozone at Halley, Rothera, and Vernadsky/Faraday. <http://www.nbs.ac.uk/public/icd/jds/ozone/>
- Britt, A.B. 1996. DNA damage and repair in plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 47: 75–100.
- Britt, A.B., J.J. Chen, D. Wykoff, and D. Mitchell. 1993. A UV-sensitive mutant of *Arabidopsis* defective in the repair of pyrimidine-pyrimidinone (6-4) dimers. *Science* 261: 1571–1574.
- Burr, K.E., C.D.B. Hawkins, S.J. L'Hirondelle, W.D. Binder, M.F. George, and T. Repo. 2001. Methods for measuring cold hardiness of conifers. *In* Conifer cold hardiness. F. Bigras and S. Colombo (editors). Kluwer Academic Press, Dordrecht, Netherlands.
- Caldwell, M.M. 1968. Solar ultraviolet radiation as an ecological factor for alpine plants. *Ecol. Monogr.* 38: 243–268.

- Caldwell, M.M. and S.D. Flint. 1997. Uses of biological spectral weighting functions and the need of scaling for the ozone reduction problem. *Plant Ecol.* 128: 66–76.
- Caldwell, M.M., R. Robberecht, and W.E. Billings. 1980. A steep latitudinal gradient of solar ultraviolet-B radiation in the arctic-alpine life zone. *Ecology* 61: 600–611.
- Caldwell, M.M., R. Robberecht, and S.D. Flint. 1983. Internal filters: prospects for UV-acclimation in higher plants. *Physiol. Plant.* 58: 445–450.
- Caldwell, M.M., R. Robberecht, R.S. Novak, and W.D. Billings. 1982. Differential photosynthetic inhibition by ultraviolet radiation in species from the arctic-alpine life zone. *Arctic Alpine Res.* 14: 195–202.
- Caldwell, M.M., A.H. Teramura, and M. Tevini. 1989. The changing solar ultraviolet climate and the ecological consequences for higher plants. *Trends Ecol. Evol.* 4: 363–367.
- Caldwell, M.M., A.H. Teramura, M. Tevini, J.F. Bornman, L.O. Björn, and G. Kulandaivelu. 1994. Environmental Effects of Ozone Depletion Chapter 3: Effects of increased solar ultraviolet radiation on terrestrial plants. <http://sedac.ciesin.org/ozone/UNEP/chap3.html>
- Casal, J.J. 1999. Phytochromes, cryptochromes, phototropin: photoreceptor interactions in plants. *Photochem. Photobiol.* 71: 1–11.
- Cen, Y.P. and J.F. Bornman. 1993. The effect of exposure to enhanced UV-B radiation on the penetration of monochromatic and polychromatic UV-B radiation in leaves of *Brassica napus*. *Physiol. Plant.* 87: 249–255.
- Curry, G.M., K.V. Thimann, and P.M. Ray. 1956. Base curvature response of *Avena* seedlings to the ultraviolet. *Physiol. Plant.* 9: 429–440.
- Cybulski, W.J., W.T. Peterjohn, and J.H. Sullivan. 2000. The influence of elevated ultraviolet radiation (UV-B) on the litter quality and decomposition of loblolly pine (*Pinus taeda* L.). *Environ. Exp. Bot.* 44: 231–241.
- Dai, Q., V.P. Coronel, B.C. Vergara, P.W. Barnes, and A.T. Quintos. 1992. Ultraviolet-B radiation effects on growth and physiology of four rice cultivars. *Crop Sci.* 32: 1269–1274.
- Daubenmire, R. 1974. Taxonomic and ecologic relationships between *Picea glauca* and *Picea engelmannii*. *Can. J. Bot.* 52: 1545–1560.
- Day, T.A. 1993. Relating UV-B radiation screening effectiveness of foliage to absorbing-compound concentration and anatomical characteristics in a diverse group of plants. *Oecologia* 95: 542–550.
- Day, T.A., B.W. Howells, and W.J. Rice. 1994. Ultraviolet absorption and epidermal-transmittance spectra in foliage. *Physiol. Plant.* 92: 207–218.
- Day, T.A. and T.C. Vogelmann. 1995. Alterations in photosynthesis and pigment distributions in pea leaves following UV-B exposure. *Physiol. Plant.* 94: 433–440.
- Day, T.A., T.C. Vogelmann, and E.H. DeLucia. 1992. Are some plant life forms more effective than others in screening out ultraviolet-B radiation? *Oecologia* 92: 513–519.
- De Fabo, E.C. (editor). 1992. Effects of increased ultraviolet radiation on biological systems. Scientific Committee on Problems of the Environment (SCOPE), Paris, France.
- Deckmyn, G. and I. Impens. 1997. The ratio UV-B /photosynthetically active radiation (PAR) determines the sensitivity of rye to increased UV-B radiation. *Environ. Exp. Bot.* 37: 3–12.
- DeLucia, E.H., T.A. Day, and T.C. Vogelmann. 1991. Ultraviolet-B radiation and the Rocky Mountain environment: measurement of incident light and penetration into foliage. *Current Topics in Plant Biochemistry and Physiology* 10: 32–48.
- _____. 1992. Ultraviolet-B and visible light penetration into needles of two species of subalpine conifers during foliar development. *Plant Cell Environ.* 15: 921–929.
- Diffey, B.L. 1991. Solar ultraviolet radiation effects on biological systems. *Phys. Med. Biol.* 36: 299–328.

- Dubé, S.L. and J.F. Bornman. 1992. Response of spruce seedlings to simultaneous exposure to ultraviolet-B radiation and cadmium. *Plant Physiol. Bioch.* 30: 761–767.
- Dunning, C.A., L. Chalker-Scott, and J.D. Scott. 1994. Exposure to ultraviolet-B radiation increases cold hardiness in *Rhododendron*. *Physiol. Plant.* 92: 516–520.
- Ensminger, P.A. 1993. Control of development in plants and fungi by far-UV radiation. *Physiol. Plant.* 88: 501–508.
- Environment Canada. 1999. A primer on ozone depletion. <http://www.ec.gc.ca/ozone/primer/>
- _____. 2000a. State of Canada's ozone layer. Annual averages 1995. <http://www.cmc.ec.gc.ca/cmc/images/ozone/ozon95.gif>
- _____. 2000b. State of the ozone layer over Canada. <http://www.cmc.ec.gc.ca/cmc/htmls/A-ozone.html>
- Farman, J.C., B.G. Gardiner, and J.D. Shanklin. 1985. Large losses of ozone in Antarctica reveal seasonal ClO_x/NO_x interaction. *Nature* 315: 207–210.
- Farrar, J.L. 1995. Trees in Canada. Canadian Forest Service, Ottawa, Ont.
- Fernbach, E. and H. Mohr. 1992. Photoreactivation of the UV light effects on growth of Scots pine (*Pinus sylvestris* L.) seedlings. *Trees* 6: 232–235.
- Flint, S.D. and M.M. Caldwell. 1984. Partial inhibition of in vitro pollen germination by simulated solar ultraviolet-B radiation. *Ecology* 65: 792–795.
- Foyer, C.H., M. Lelandais, and K.J. Kunert. 1994. Photooxidative stress in plants. *Physiol. Plant.* 92: 696–717.
- Frederick, J.E. 1993. Ultraviolet sunlight reaching the earth's surface: A review of recent research. *Photochem. Photobiol.* 57: 175–178.
- Gibson, J.H. 1999. UVB Radiation: definition and characteristics. http://uvb.nrel.colostate.edu/UVB/publications/uvb_primer.pdf
- Gold, W.G. and M.M. Caldwell. 1983. The effects of ultraviolet-B radiation on plant competition in terrestrial ecosystems. *Physiol. Plant.* 58: 435–444.
- Gordon, D.C., K. Percy, and R.T. Riding. 1998a. Effects of enhanced UV-B radiation on adaxial leaf surface micromorphology and epicuticular wax biosynthesis of sugar maple. *Chemosphere* 36: 853–858.
- _____. 1998b. Effects of UV-B radiation on epicuticular wax production and chemical composition of four *Picea* species. *New Phytol.* 138: 441–449.
- Hao, X., B.A. Hale, and D.P. Ormrod. 1997. The effects of ultraviolet-B radiation and carbon dioxide on growth and photosynthesis of tomato. *Can. J. Bot.* 75: 213–219.
- Hunt, J.E., F.M. Kelliher, and D.L. McNeil. 1996. Response in chlorophyll *a* fluorescence of six New Zealand tree species to a step-wise increase in ultraviolet-B irradiance. *N. Z. J. Bot.* 34: 401–410.
- Jansen, M.A.K., V. Gaba, and B.M. Greenberg. 1998. Higher plants and UV-B radiation: balancing damage, repair and acclimation. *Trends Plant Sci.* 3: 131–135.
- Jaquish, B. and Y.A. El-Kassaby. 1998. Genetic variation of western larch in British Columbia and its conservation. *J. Hered.* 89: 248–253.
- Karabourniotis, G., D. Kotsabassidis, and Y. Manetas. 1995. Trichome density and its protective potential against ultraviolet-B radiation damage during leaf development. *Can. J. Bot.* 73: 376–383.
- Kaufmann, M.R. 1978. The effects of ultraviolet radiation on Engelmann spruce and lodgepole pine seedlings. *In* EPA-IAG-DG-0168: Research Report on the Impacts of Ultraviolet-B Radiation on Biological Systems: A study related to atmospheric ozone depletion. SIRA File 142.22. U.S. E.P.A., Washington, DC.
- Kaundun, S.S., P. Lebreton, and A. Bailly. 1998. Needle flavonoid variation in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) populations. *Can. J. Bot.* 76: 2076–2083.

- Kerr, J.B. and C.T. McElroy. 1993. Evidence for large upward trends of ultraviolet-B radiation linked to ozone depletion. *Science* 262: 1032–1034.
- Kerr, R.A. 1998a. Deep chill triggers record ozone hole. *Science* 282: 391.
- _____. 1998b. Ozone loss, greenhouse gases linked. *Science* 280: 202.
- Kinnunen, H. 1999. Surface structure, wax and methanol-extractable compounds in Scots pine and Norway spruce needles enhanced UV-B. Faculty of Science, University of Oulu, Oulu, Finland.
- Kirk-Davidoff, D.B., E.J. Hintsala, J.G. Anderson, and D.W. Keith. 1999. The effect of climate change on ozone depletion through changes in stratospheric water vapour. *Nature* 402: 399–401.
- Kossuth, S.V. and R.H. Biggs. 1981. Ultraviolet-B radiation effects on early seedling growth of Pinaceae species. *Can. J. For. Res.* 11: 243–248.
- Krizek, D.T. 1997. Inhibitory effects of ambient levels of solar UV-A and UV-B radiation on growth of cucumber. *Physiol. Plant.* 100: 886–893.
- Krol, P.M., D.P. Ormrod, W.D. Binder, and S.J. L'Hirondelle. 2000. Effects of ultraviolet-B radiation on needle anatomy and morphology of western larch, interior spruce, and lodgepole pine. *J. Sustain. For.* 10: 141–148.
- Laakso, K. 2000. Effects of ultraviolet-B radiation (UV-B) on needle anatomy and glutathione status of field-grown pines. Department of Biology, University of Oulu, Oulu, Finland.
- Laakso, K. and S. Huttunen. 1998. Effects of the ultraviolet-B radiation (UV-B) on conifers: A review. *Environ. Pollut.* 99: 319–328.
- Landry, L.G., C.S.C. Clark, and R.L. Last. 1995. *Arabidopsis* mutants lacking phenolic sunscreens exhibit enhanced UV-B injury and photooxidative damage. *Plant Physiol.* 109: 1159–1166.
- Lao, K. and A.N. Glazer. 1996. Ultraviolet-B photodestruction of a light-harvesting complex. *Proc. Natl. Acad. Sci.* 93: 5258–5263.
- Lavola, A. 1998. Accumulation of flavonoids and related compounds in birch induced by UV-B irradiance. *Tree Physiol.* 18: 53–58.
- Lavola, A., R. Julkunen-Tiitto, P. Aphalo, T. De La Rosa, and T. Lehto. 1997. The effect of u.v.-B radiation on u.v.-absorbing secondary metabolites in birch seedlings grown under simulated forest soil conditions. *New Phytol.* 137: 617–621.
- L'Hirondelle, S.J. and W.D. Binder. 1996. Ultraviolet-B radiation effects on British Columbia conifers. 3) Morphology and physiology of germinants (four species from three elevations) and seedlings (three species) after exposure to UV-B in a greenhouse. EP1118.11, B.C. Min. For. Res. Br., Victoria, B.C. (unpublished)
- _____. 1997a. Ultraviolet-B radiation effects on British Columbia conifers. 4) Morphology and physiology of ten families of western redcedar after exposure to UV-B in a greenhouse. EP1118.13, B.C. Min. For. Res. Br., Victoria, B.C. (unpublished)
- _____. 1997b. Ultraviolet-B radiation effects on British Columbia conifers. 5) Morphology and physiology of germinants (four species from three elevations) or seedlings (four species) after exposure to UV-B in a greenhouse. EP1118.14, B.C. Min. For. Res. Br., Victoria, B.C. (unpublished)
- Li, J., T.-M. Ou-Lee, R. Raba, R.G. Amundson, and R.L. Last. 1993. *Arabidopsis* flavonoid mutants are hypersensitive to UV-B irradiation. *Plant Cell* 5: 171–179.
- Liu, L., D.C. Gitz, and J.W. McClure. 1995. Effects of UV-B on flavonoids, ferulic acid, growth and photosynthesis in barley primary leaves. *Physiol. Plant.* 93: 725–733.
- Liu, L. and J.W. McClure. 1995. Effects of UV-B on activities of enzymes of secondary phenolic metabolism in barley primary leaves. *Physiol. Plant.* 93: 734–739.
- Madronich, S., R.L. McKenzie, L.O. Björn, and M.M. Caldwell. 1998. Changes in biologically active ultraviolet radiation reaching the earth's surface. *J. Photochem. Photobiol. B* 46: 5–19.

- Manning, W.J. and A.V. Tiedemann. 1995. Climate change: potential effects of increased atmospheric carbon dioxide (CO₂), ozone (O₃), and ultraviolet-B (UV-B) radiation on plant diseases. *Environ. Pollut.* 88: 219–245.
- McLennan, A.G. 1987. The repair of ultraviolet-induced DNA damage in plant cells. *Mutation Research* 181: 1–7.
- Middleton, E.M. and A.H. Teramura. 1993a. Potential errors in the use of cellulose diacetate and mylar filters in UV-B radiation studies. *Photochem. Photobiol.* 57: 744–751.
- _____. 1993b. The role of flavonol glycosides and carotenoids in protecting soybean from ultraviolet-B damage. *Plant Physiol.* 103: 741–752.
- Mims, F.M.I. and J.E. Frederick. 1994. Cumulus clouds and UV-B. *Nature* 371: 291.
- Mirecki, R.M. and A.H. Teramura. 1984. Effects of ultraviolet-B irradiance on soybean. V. The dependence of plant sensitivity on the photosynthetic photon flux density during and after leaf expansion. *Plant Physiol.* 74: 475–480.
- Moran, R. 1982. Formulae for determination of chlorophyllous pigments extracted with N,N-dimethylformamide. *Plant Physiol.* 69: 1376–1381.
- Moran, R. and D. Porath. 1980. Chlorophyll determination in intact tissues using N,N-dimethylformamide. *Plant Physiol.* 65: 478–479.
- Murali, N.S. and A.H. Teramura. 1986. Effectiveness of UV-B radiation on the growth and physiology of field-grown soybean modified by water stress. *Photochem. Photobiol.* 44: 215–220.
- Murali, N.S., A.H. Teramura, and S.K. Randall. 1988. Response differences between two soybean cultivars with contrasting UV-B radiation sensitivities. *Photochem. Photobiol.* 48: 653–657.
- Murphy, T.M. 1983. Membranes as targets of ultraviolet radiation. *Physiol. Plant.* 58: 381–388.
- Murphy, T.M., C.P. Martin, and J. Kami. 1993. Endonuclease activity from tobacco nuclei specific for ultraviolet radiation-damaged DNA. *Physiol. Plant.* 87: 417–425.
- Musil, C.F. 1996. Accumulated effect of elevated ultraviolet-B radiation over multiple generations of the arid-environment annual *Dimporphothecca sinuata* DC. (Asteraceae). *Plant Cell Environ.* 19: 1017–1027.
- Naidu, S.L., J.H. Sullivan, A.H. Teramura, and E.H. DeLucia. 1993. The effects of ultraviolet-B radiation on photosynthesis of different aged needles in field-grown loblolly pine. *Tree Physiol.* 12: 151–162.
- National Research Council. 1982. Causes and effects of stratospheric ozone reduction: an update. National Academy Press, Washington, D.C., 340 pp.
- Ormrod, D.P., L.G. Landry, and P.L. Conklin. 1995. Short-term UV-B radiation and ozone exposure effects on aromatic secondary metabolite accumulation and shoot growth of flavonoid-deficient *Arabidopsis* mutants. *Physiol. Plant.* 93: 602–610.
- Petropoulou, Y., A. Kyparissis, D. Nikolopoulos, and Y. Manetas. 1995. Enhanced UV-B alleviates the adverse effects of summer drought in two Mediterranean pines under field conditions. *Physiol. Plant.* 94: 37–44.
- Randel, W.J., R.S. Stolarski, and D.M. Cunnold. 1999. Trends in the vertical distribution of ozone. *Science* 285: 1689–1692.
- Rao, M.V. and D.P. Ormrod. 1995. Ozone exposure decreases UV-B sensitivity in a UV-B-sensitive flavonoid mutant of *Arabidopsis*. *Photochem. Photobiol.* 61: 71–78.
- Rehfeldt, G.E. 1989. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*): a synthesis. *For. Ecol. and Manage.* 28: 203–215.
- Rehfeldt, G.E., C.C. Ying, D.L. Spittlehouse, and D.A.J. Hamilton. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecol. Monogr.* 69: 375–407.
- Ries, G., W. Heller, H. Puchta, H. Sandermann, H.K. Seidlitz, and B. Hohn. 2000. Elevated UV-B radiation reduces genome stability in plants. *Nature* 406: 98–101.

- Robberecht, R., M.M. Caldwell, and W.D. Billings. 1980. Leaf ultraviolet optical properties along a latitudinal gradient in the arctic-alpine life zone. *Ecology* 61: 612–619.
- Robson, T.M., J.G. Zaller, C.L. Ballaré, O.E. Sala, A.L. Scopel, and M.M. Caldwell. 2000. The response of *Nothofagus* tree species to UV-B radiation resulting from ozone depletion, in the forests of Tierra del Fuego. Workshop on the impacts of UV on terrestrial and aquatic ecosystems. SPARC (Stratospheric Processes and their Role in Climate), Mar del Plata, Argentina.
- Russell, J.H. 1993. Genetic architecture, genecology and phenotypic plasticity in seed and seedling traits of yellow-cedar (*Chamaecyparis nootkatensis* (D.Don) Spach). Faculty of Forestry, University of British Columbia, Vancouver, B.C.
- Sabburg, J. and J. Wong. 1998. Measurement of cloud angle for enhanced UVB at the earth's surface. <http://www.photobiology.com/UVR98/sabburg/index.htm>
- Salawitch, R.J. 1998. A greenhouse warming connection. *Nature* 392: 551–552.
- Sato, T., H.S. Kang, and T. Kumagai. 1994. Genetic study of resistance to inhibitory effects of UV radiation in rice (*Oryza sativa*). *Physiol. Plant.* 91: 234–238.
- Schnitzler, J.-P., T.P. Jungblut, W. Heller, M. Köfferlein, P. Hutzler, U. Heinzmann, E. Schmelzer, D. Ernst, C. Langebartels, and H.J. Sandermann. 1996. Tissue localization of UV-B screening pigments and of chalcone synthase mRNA in needles of Scots pine seedlings. *New Phytol.* 132: 247–258.
- Schnitzler, J.-P., C. Langebartels, W. Heller, J. Liu, M. Lippert, T. Döhring, G. Bahnweg, and H. Sandermann. 1999. Ameliorating effect of UV-B radiation on the response of Norway spruce and Scots pine to ambient ozone concentrations. *Global Change Biol.* 5: 83–94.
- Schumaker, M.A., J.H. Bassman, R. Robberecht, and K. Rademaker. 1997. Growth, leaf anatomy, and physiology of *Populus* clones in response to solar ultraviolet-B radiation. *Tree Physiol.* 17: 617–626.
- Shindell, D.T., D. Rind, and P. Lonergan. 1998. Increased polar stratospheric ozone losses and delayed eventual recovery owing to increasing greenhouse gas concentrations. *Nature* 392: 589–592.
- Shirley, B.W. 1996. Flavonoid biosynthesis: "new" functions for an "old" pathway. *Trends Plant Sci.* 1: 377–382.
- Singh, A. 1996. Growth, physiological, and biochemical responses of three tropical legumes to enhanced UV-B radiation. *Can. J. Bot.* 74: 135–139.
- Staxén, I. and J.E. Bornman. 1994. A morphological and cytological study of *Petunia hybrida* exposed to UV-B radiation. *Physiol. Plant.* 91: 735–740.
- Stewart, J.D. and J. Hoddinott. 1993. Photosynthetic acclimation to elevated atmospheric carbon dioxide and UV irradiation in *Pinus banksiana*. *Physiol. Plant.* 88: 493–500.
- Sullivan, J.H. 1994. Temporal and fluence responses of tree foliage to UV-B radiation. *In* Stratospheric ozone depletion/UV-B radiation in the biosphere. R.H. Biggs and M.E.B. Joyner (editors). Springer-Verlag, Berlin, Germany, pp. 67–76.
- Sullivan, J.H., B.W. Howells, C.T. Ruhland, and T.A. Day. 1996. Changes in leaf expansion and epidermal screening effectiveness in *Liquidambar styraciflua* and *Pinus taeda* in response to UV-B radiation. *Physiol. Plant.* 98: 349–357.
- Sullivan, J.H. and A.H. Teramura. 1988. Effects of ultraviolet radiation on seedling growth in the Pinaceae. *Am. J. Bot.* 75: 225–230.
- _____. 1989. The effects of ultraviolet-B radiation on loblolly pine. 1. Growth, photosynthesis and pigment production in greenhouse-grown saplings. *Physiol. Plant.* 77: 202–207.
- _____. 1990. Field study of the interaction between solar ultraviolet-B radiation and drought on photosynthesis and growth in soybean. *Plant Physiol.* 92: 141–146.

- _____. 1992. The effects of ultraviolet-B radiation on loblolly pine. 2. Growth of field-grown seedlings. *Trees* 6: 115–120.
- _____. 1994. The effects of UV-B radiation on loblolly pine. III. Interaction with CO₂ enhancement. *Plant Cell Environ.* 17: 311–317.
- Sullivan, J.H., A.H. Teramura, P. Adamse, G.F. Kramer, A. Upadhyaya, S.J. Britz, D.T. Krizek, and R.M. Mirecki. 1994a. Comparison of the response of soybean to supplemental UV-B radiation supplied by either square-wave or modulated irradiation systems. *In* Stratospheric ozone depletion/UV-B radiation in the biosphere. R.H. Biggs and M.E.B. Joyner (editors). Springer-Verlag, Berlin, Germany, pp. 211–220.
- Sullivan, J.H., A.H. Teramura, and L.R. Dillenburg. 1994b. Growth and photosynthetic responses of field-grown sweetgum (*Liquidambar styraciflua*; Hamamelidaceae) seedlings to UV-B radiation. *Am. J. Bot.* 81: 826–832.
- Sullivan, J.H., A.H. Teramura, and L.H. Ziska. 1992. Variation in UV-B sensitivity in plants from a 3000 m elevational gradient in Hawaii. *Am. J. Bot.* 79: 737–743.
- Tabazadeh, A., M.L. Santee, M.Y. Danilin, and H.C. Pumphrey. 2000. Quantifying denitrification and its effect on ozone recovery. *Science* 288: 1407–1411.
- Teramura, A.H. 1983. Effects of ultraviolet-B radiation on the growth and yield of crop plants. *Physiol. Plant.* 58: 415–427.
- Teramura, A.H. and J.H. Sullivan. 1991. Potential impacts of increased solar UV-B on global plant productivity. *In* Photobiology. E. Riklis (editor) Plenum Press, New York, N.Y., pp. 625–634.
- Teramura, A.H., J.H. Sullivan, and L.H. Ziska. 1990. Interaction of elevated ultraviolet-B radiation and CO₂ on productivity and photosynthetic characteristics in wheat, rice, and soybean. *Plant Physiol.* 94: 470–475.
- Tevini, M., U. Mark, and M. Saile-Mark. 1991. Effects of enhanced solar UV-B radiation on growth and function of crop plant seedlings. *Curr. Top. Plant Biochem. Physiol.* 10: 13–31.
- Tevini, M. and A.H. Teramura. 1989. UV-B effects on terrestrial plants. *Photochem. Photobiol.* 50: 479–487.
- Tosserams, M. and A.P. de Sà. 1996. The effect of solar UV radiation on four plant species occurring in a coastal grassland vegetation in The Netherlands. *Physiol. Plant.* 97: 731–739.
- Turunen, M., M.-L. Sutinen, Y. Norokorpi, K. Derome, K. Masson, W. Heller, S. Stich, and H. Sandermann. 2000. Response of pine and birch seedlings to solar UV radiation at the subarctic. Workshop on the impacts of UV on terrestrial and aquatic ecosystems. SPARC (Stratospheric Processes and their Role in Climate), Mar del Plata, Argentina.
- United Nations Environmental Programme. 1998. Environmental effects of ozone depletion: 1998 assessment. <http://www.gcric.org/UNEP1998/>
- USDA Forest Service. 2001. Fire effects information system database. <http://www.fs.fed.us/database/feis/plants/tree/>
- United States Environmental Protection Agency. 1999. Questions and answers on ozone depletion. http://www.epa.gov/ozone/science/q_a.html
- U.S. Department of Energy. 1993. UV-B critical issues workshop. U.S. Department of Energy, Office of Health and Environmental Research, Center for Global Environmental Studies of Oak Ridge National Laboratory, Cocoa Beach, Fla. <http://www.ciesin.org/docs/001-536/001-536.html>
- van de Staaij, J.W.M., W.H.O. Ernst, H.W.J. Hakvoort, and J. Rozema. 1995. Ultraviolet-B (280–320 nm) absorbing pigments in the leaves of *Silene vulgaris*: their role in UV-B tolerance. *J. Plant Physiol.* 147: 75–80.
- Waibel, A.E., T. Peter, K.S. Carslaw, H. Oelhaf, G. Wetzell, J. Crutzen, U. Pöschl, A. Tsias, E. Reimer, and H. Fischer. 1999. Arctic ozone loss due to denitrification. *Science* 283: 2064–2069.

- Walbot, V. 1999. UV-B damage amplified by transposons in maize. *Nature* 397: 398–399.
- Wardle, D.I., J.B. Kerr, C.T. McElroy, and D.R. Francis (editors). 1997. *Ozone science: a Canadian perspective on the changing ozone layer*. Environment Canada, Toronto, Ont.
- Weirich, S. 1996. The effect of ultraviolet-B radiation on some aspects of plant reproduction. Unpublished manuscript Available from B.C. Min. For. Res. Br. Library.
- Wennberg, P.O., R.C. Cohen, R.M. Stimpfle, J.P. Koplow, J.G. Anderson, R.J. Salawitch, D.W. Fahey, E.L. Woodbridge, E.R. Keim, R.S. Gao, C.R. Webster, R.D. May, D.W. Toohey, L.M. Avallone, M.H. Proffitt, M. Loewenstein, J.R. Podolske, K.R. Chan, and S.C. Wofsy. 1994. Removal of stratospheric O₃ by radicals: in situ measurements of OH, HO₂, NO, NO₂, ClO, and BrO. *Science* 266: 398–404.
- World Meteorological Organization. 1995. Scientific assessment of ozone depletion: 1994. <http://www.al.noaa.gov/WWWHHD/pubdocs/Assessment94.html>
- Xie, C.-Y., A.Y. Yanchuk, and G.K. Kiss. 1998. Genetics of interior spruce in British Columbia: performance and variability of open-pollinated families in the East Kootenays. B.C. Min. For. Res. Br., Victoria, B.C. Res. Rep. 07.
- Xie, C.-Y. and C.C. Ying. 1993. Geographic variation of grand fir (*Abies grandis*) in the Pacific coast region: 10-year results from a provenance trial. *Can. J. For. Res.* 23: 1065–1072.
- Yakimchuk, R. and J. Hoddinott. 1994. The influence of ultraviolet-B light and carbon dioxide enrichment on the growth and physiology of seedlings of three conifer species. *Can. J. For. Res.* 24: 1–8.
- Ziska, L.H., A.H. Teramura, and J.H. Sullivan. 1992. Physiological sensitivity of plants along an elevational gradient to UV-B radiation. *Am. J. Bot.* 79: 863–871.

Additional Internet Links

- <http://www.arl.noaa.gov/research/programs/uv.html>
- <http://www.cmc.ec.gc.ca/cmc/htmls/A-ozone.html>
- <http://www.cmdl.noaa.gov/star/arcticuv2.html>
- http://www.cpc.ncep.noaa.gov/products/stratosphere/uv_index/uv_information.html
- http://www.ecoinfo.org/env_ind/region/ozone/ozone.htm
- <http://www.epa.gov/ozone/index.html>
- <http://www.gcric.esto.or.jp/UNEP1998/>
- <http://www.msc-smc.ec.gc.ca/woudc/>
- <http://www.srrb.noaa.gov/UV/>
- <http://www.unepie.org/ozonaction.html>
- <http://cc.joensuu.fi/~aphalo/photobio.html>
- <http://sedac.ciesin.org/ozone/>
- <http://www.iai.int/ozone.htm>

