Reflectance of Alaskan black spruce and white spruce foliage in relation to elevation and latitude

ANDREW D. RICHARDSON,1,2 GRAEME P. BERLYN1 and SHANE P. DUIGAN1
1 School of Forestry and Environmental Studies, Yale University, 370 Prospect Street, New Haven, CT 06511, USA
2 Author to whom correspondence should be addressed (andrew.richardson@yale.edu)

Received June 14, 2002; accepted November 2, 2002; published online May 1, 2003

Summary Leaf reflectance at visible and near-infrared wavelengths (400–1000 nm) is related primarily to pigmentation, leaf structure and water content, and is an important tool for studying stress physiology and relationships between plants and their growth environment. We studied reflectance of two co-occurring Alaskan conifers, black spruce (Picea mariana (Mill.) BSP) and white spruce (Picea glauca (Moench) Voss), at elevations from 60 to 930 m a.s.l. along a latitudinal gradient from 61° to 68° N. Black spruce samples were collected from 24 sites and white spruce from 30 sites. Overall, reflectance spectra of the two species were similar, but from 400 to 700 nm, needle reflectance was consistently higher in black spruce than in white spruce (all P ≤ 0.05). This difference is probably related to differences in epicuticular wax morphology or amount, and may represent a photoprotective mechanism in black spruce. Reflectance at visible wavelengths generally increased with elevation and latitude in both species, consistent with a general stress response. However, in a multiple regression, latitude and elevation explained only 25–45% of the total variation in the indices studied. Reflectance indices suggested that needle yellowness increased, whereas chlorophyll content and photochemical efficiency decreased with both elevation and latitude. These trends were consistent between species, but white spruce generally showed a much smaller (and insignificant) reflectance response to latitude compared with black spruce. Differences between species could be related to black spruce’s ability to colonize more stressful sites and white spruce’s greater competitiveness on less stressful sites, coupled with the effects of drainage and microtopography (which may vary less predictably with latitude than elevation) on species distribution. The black spruce results suggest that a 1000-m increase in elevation is roughly comparable with a 6° increase in latitude.

Keywords: boreal, chlorophyll, Picea, spectral reflectance, stress, subarctic, treeline.

Introduction

Air temperature generally decreases with increasing elevation and increasing latitude (Young 1989), and in this respect, latitude “compensates” for altitude (Billings 1973). The fact that high-latitude and high-elevation systems are inherently low energy systems has direct biological consequences. For example, the elevation at which the treeline occurs typically decreases with increasing latitude from the equator to the Arctic; this pattern was noted in 1817 and is known as Humboldt’s Law (Salisbury and Ross 1992).

With increasing elevation, air temperatures decrease by about 6 °C km−1 as a result of adiabatic cooling (Körner 1999). In contrast, low temperatures at high latitudes are the product of reduced inputs of solar energy. Thus, although the tilt of the earth’s axis results in long summer days in the Arctic and Subarctic, the low angle of the sun in the sky means that (1) solar radiation must pass through a thicker portion of the atmosphere (which absorbs, scatters and reflects incoming radiation); and (2) the sun’s rays are spread out across a larger ground area than at lower latitudes. As a result, the total amount (integrated over the day) of solar radiation reaching the earth’s surface decreases with increasing latitude above about 30° N, even on the summer solstice (Ahrens 1994).

Although air temperature heat sums (daily means above 10 °C) differ between Arctic (temperature sum of 600–700 °C) and alpine (200–300 °C) timberlines, leaf temperature heat sums are similar (800 °C) at both high-latitude and high-elevation timberlines (Davitaja and Melnik 1962, cited in Tranquillini 1979). Temperature is not the only factor determining tree line position, but it is a major factor. Other important environmental factors, such as precipitation, wind, cloudiness, peak total and UV solar irradiance, atmospheric pressure, CO2 partial pressure, length of the growing season, snow-free period, and diurnal and seasonal temperature amplitude, may show opposite trends in relation to increasing elevation and latitude, or there may be no clear trend (Billings 1973, Körner 1999). Thus, in many respects, elevation and latitude are not direct analogs. Additionally, the elevational gradient is often considered “steeper” (Billings 1973) than the latitudinal gradient because environmental conditions change more rapidly over a short distance up the side of a mountain than over a short distance northward.

Plants with wide ecological ranges typically respond to different environments through a combination of physiological...
acclimation and morphological plasticity. Such flexibility enables species to remain competitive even in sub-optimal growth environments. However, we have previously found that the capacity for adjustment to increasing elevation may be limited, and stress responses to elevation (such as changes in leaf pigmentation) can be exhibited even many hundreds of vertical meters below the alpine tree line (Richardson et al. 2001, Richardson and Berlyn 2002a). The purpose of the present study was to investigate whether the two dominant and co-occurring conifers in boreal Alaska, black spruce (Picea mariana (Mill.) BSP) and white spruce (Picea glauca (Moench) Voss), show parallel stress responses to increases in latitude and in elevation, and whether these patterns are similar in these congeneric species. We collected samples across a latitudinal range of 7° and an elevational range of 900 m. Samples were collected from sites at the limits of tree growth wherever possible.

To quantify stress physiology, we measured the reflectance of individual needles across a spectrum of visible and near-infrared wavelengths (400–1000 nm). Reflectance across this range is determined largely by pigment content, leaf structure, and water content (Carter 1991, Peñuelas and Filella 1998, Gamon and Surfus 1999, Richardson et al. 2002, Sims and Gamon 2002), and is known to be altered by environmental stress (Jackson 1986, Carter 1993, 1994). Previously, we found that a variety of reflectance indices show a strong and consistent response to increasing elevation in the conifers, red spruce (Picea rubens Sarg.) and balsam fir (Abies balsamea (L.) Mill.), as well as the angiosperm, paper birch (Betula papyrifera var. cordifolia (Regel) Fern.) (Richardson et al. 2001, Richardson and Berlyn 2002a).

Methods

Black spruce and white spruce were selected for study because they are the two conifers with the greatest latitudinal range in Alaska: from south of 60° to north of the Arctic circle. Both species have similar transcontinental distributions, ranging from northern Alaska and Yukon to New England and the Canadian Maritime provinces. In the southern Rocky Mountains of British Columbia and Alberta, white spruce grows to an elevation of 1520 m; in northern Alberta, black spruce grows to an elevation of 1830 m (Burns and Honkala 1990).

In early June 2001, foliage samples were collected from sites close to the Parks Highway, Richardson Highway and Dalton Highway (Figure 1). Across the study area, mean daily temperatures range from about –20 to –30 °C in January to 10 to 13 °C in July (Burns and Honkala 1990), although because of extreme continentality, seasonal temperature variation is generally more exaggerated in the central interior of Alaska than at either end of the latitudinal transect. For example, in Fairbanks (64.82° N, 147.87° W, 130 m a.s.l.), mean July temperature is about 16 °C. Total precipitation in interior Alaska is typically low (<50 cm per year), and decreases slightly from south to north (1961–1990 data, available at http://lwf.ncdc.noaa.gov/oa/documentlibrary/clim81supp3/clim81.html), but is likely enhanced at local scales by the orographic effects of the Coastal, Alaska and Brooks Ranges.

Samples were collected at intervals of about 50–100 km. Where possible, samples of both species were collected at the same site, or at two closely located sites. Site locations were recorded with a hand-held Global Positioning System (GPS) (Magellan 315, Thales Navigation, San Dimas, CA); elevations measured by GPS were checked against an analog pocket altimeter (TX-22, Revue Thommen AG, Waldenburg, Switzerland). Site elevations ranged from 60 to 930 m a.s.l., along a latitudinal gradient from 61° to 68° N. Black spruce samples were collected from 24 sites, and white spruce from 30 sites (Figure 1). There was no correlation in either species between site latitude and elevation (r ≤ 0.05, P ≥ 0.95). Collections were made only on flat or moderately sloping sites with southeast to southwest aspects. Because there can be reflectance
differences between sun and shade foliage (Richardson 2003), samples were collected only from the south-facing outer canopy of trees growing in full sun.

At each site, branches were collected from five trees; reflectance spectra were measured on six individual needles per tree. Thus, a total of 1620 individual needles were analyzed. Cut branches were generally 15–20 cm in length, but measurements were made only on previous-year (summer 2000 flush) foliage, representing approximately the last 5 cm of growth. Immediately after cutting, samples were sealed in plastic bags and then placed on snow or ice in a Styrofoam cooler. The delay between branch cutting and reflectance measurements was always less than 72 h. Richardson and Berlyn (2002b) demonstrated that, for spruce foliage, the reflectance indices on which we focus here changed little, if at all, in the first 3 days following branch cutting.

Spectral reflectance at wavelengths from 306 to 1138 nm was measured with a UniSpec spectral analysis system (PP Systems, Haverhill, MA) with a 1.0-mm diameter mini-foreoptic and an internal 6.8-W halogen lamp. Instrument details are given in Richardson and Berlyn (2002b). The reflectance spectrum (%) for each scan was calculated as $R_n = \frac{\text{(leaf radiance at wavelength $\lambda$)}(\text{reflectance standard radiance at wavelength $\lambda$})100. We transformed the mean raw reflectance spectrum for each leaf to a first-difference spectrum (%)/nm), calculated as $D_n = \frac{R_n - R_{n-1}}{(\text{reflectance standard radiance between 1 and 256. The first-difference spectrum is an approximation of the slope, or first derivative of the raw spectrum.}

A variety of indices were used to characterize the complex spectra and make comparisons possible among different elevations. These indices have been derived by other authors based on knowledge of the reflectance properties of pigments and biochemical components.

We used two indices well-correlated with total chlorophyll (chl) content: a revised version of the normalized difference vegetation index, which we call Chl NDI, and the red edge position, denoted ARE. A standard index in remote sensing work (Gamon and Qiu 1999), the normalized difference vegetation index is usually calculated as NDVI = $\frac{R_{750} - R_{675}}{R_{750} + R_{675}}$. The revised version, which is better correlated with leaf chl content and more sensitive to a wider range of chl contents (Richardson et al. 2002), was calculated as Chl NDI = $\frac{R_{750} - R_{675}}{R_{750} + R_{675}}$ (Gitelson and Merzlyak 1994).

Total chl content is also correlated with λRE (Curran et al. 1990), which is the wavelength $\lambda$ (nm) of the maximum slope of the reflectance spectrum at wavelengths between 690 and 740 nm. We calculated λRE based on the first-difference spectra described above. Although past work (Richardson et al. 2002) has suggested that the root mean square error of λRE as a predictor of leaf chl is twice as high (23.8%) as that for Chl NDI (12.1%), it may be a better indicator in some cases, because first-differencing yields a spectrum that is less influenced by confounding external factors (Wessman et al. 1988).

The yellowness index (YI) was formulated to indicate chlorosis in stressed leaves by measuring changes in the shape or concavity of reflectance spectra around 600 nm (Adams et al. 1999). We calculated the index as a finite approximation to the second derivative of the reflectance spectrum between 580 and 668 nm: $YI = -0.1(R_{580} - 2R_{590} + R_{600})/\Delta \lambda^2$, with $\lambda_0 = 580$ nm, $\lambda_1 = 624$ nm, $\lambda_2 = 668$ nm and $\Delta \lambda = 44$ nm. The scaling factor of –0.1 was included to indicate increasing yellowness within increasingly positive values (Adams et al. 1999).

The photochemical reflectance index (PRI) was calculated as $\frac{(R_{531} - R_{730})(R_{531} + R_{730})}{(Gamon et al. 1997). Over short time spans (e.g., diurnally), PRI is correlated with both the epoxidation state of xanthophyll cycle pigments and photosynthetic radiation use efficiency (PRUE): PRUE = $\frac{\text{(net photosynthesis)}(\text{incident photosynthetically active radiation (PAR)})}{(Gamon et al. 1992, Peñuelas et al. 1995, Filella et al. 1996). Over longer time spans, or across species or sites, PRI is positively correlated with photosystem (PS) II efficiency as measured by chlorophyll fluorescence and the chl:carotenoids ratio, which may itself be an indicator of photosynthetic efficiency (Sims and Gamon 2002, Stylinski et al. 2002).

**Results**

The mean reflectance spectra of the two species were generally similar, and exhibited the familiar green peak (550 nm), red trough (680 nm), red edge (700 nm) and near-infrared plateau (750–1000 nm) characteristic of most terrestrial plants (Figure 2A). Reflectance was consistently higher across the range from 400 to 700 nm for black spruce than for white spruce, and although the absolute difference was slight (above 1.0% only for the range 500–667 nm), it was consistently significant ($P \leq 0.05$ for each wavelength). Above 700 nm, there were no significant differences in reflectance between species ($P > 0.05$ for all wavelengths). Although first-difference spectra have been helpful in identifying subtle differences between untransformed spectra that are otherwise similar (e.g., Richardson and Berlyn 2002a), we found that the mean first-difference spectra were almost identical for black and white spruce (Figure 2B).

To examine the effects of latitude or elevation on reflectance at individual wavelengths, while controlling for the effect of the other factor, we used Pearson’s partial correlation. Analyses were conducted separately for each species, and then again for the pooled data from both species (Figure 3A). For black spruce ($n = 24$), a correlation coefficient greater than $r = 0.41$ was significant at $P \leq 0.05$; for white spruce ($n = 30$) and the pooled data ($n = 54$), the $r$ values were 0.36 and 0.27, respectively. With elevation held constant, wavelengths from 429 to 725 nm were correlated significantly (all $P \leq 0.05$) with latitude for black spruce; the highest correlation ($r = 0.65$) occurred at 700 nm. In white spruce, no wavelengths were correlated significantly with latitude (all $P > 0.05$); all correlations were lower for white spruce than for black spruce. For the pooled data, results were more or less intermediate between the species considered separately.

With latitude held constant, reflectance at individual wavelengths had a higher correlation with elevation in white spruce
than in black spruce (Figure 3B). From 535 to 665 nm and from 688 to 712 nm, reflectances of both white spruce samples and pooled samples were significantly correlated with elevation (all $P \leq 0.05$). The peak correlation was around 600 nm ($r = 0.51$ for white spruce, $r = 0.44$ for pooled data). For black spruce, no individual wavelengths were significantly correlated with elevation (all $P > 0.05$).

Because three-dimensional scatter plots are visually difficult to interpret, we have included them here for only one variable, PRI (Figure 4). There was a general trend toward decreasing PRI with increasing elevation and increasing latitude in both species. To quantify these trends, reflectance indices were analyzed by multiple regression. Within each species, the indices were modeled as linear functions of elevation and latitude. The results of these regressions are shown in Table 1. Model fits were somewhat better for black spruce than for white spruce, as indicated by the higher $R^2$ values for three of the four indices.

To depict relationships between species, and across the elevational and latitudinal gradients, we plotted the regression equations from Table 1 separately for each independent vari-

able (Figure 5). We used a standard elevation of 500 m when calculating values for the latitude plots, and a standard latitude of 65° N when calculating values for the elevation plots. The coefficients on the independent variables in the multiple regressions are equal to the slopes of the lines plotted in Figure 5, and hence represent rates of change in index values per degree of latitude or per km of elevation.

For both species, the coefficients suggest that chl content decreases (which likely implies a corresponding shift in the relative ratio of chl:carotenoids), needle yellowness increases (likely related to reduced chl content) and photochemical efficiency decreases, with increases in both latitude and elevation. The response to latitude was steeper for black spruce than for white spruce for every reflectance index (Figure 5). In general, white spruce showed only a weak response to latitude, especially for $\lambda$RE. Thus, the latitude response was significant (all $P \leq 0.10$) for all black spruce indices, whereas it was not significant (all $P \geq 0.10$) for any white spruce index. The absence of significant responses in white spruce can be attributed to the smaller latitude coefficients rather than increased variability, because the standard errors of the latitude coefficients were similar for both species (Table 1).
The response to elevation was similar in both species for all indices except PRI, with a response twice as steep in black spruce as in white spruce (Figure 5). For all indices, responses to elevation were significant in both species (all $P \leq 0.01$ in white spruce; all $P \leq 0.10$ in black spruce).

Figure 5 shows that $\lambda_{RE}$, Chl NDI and PRI were generally higher in white spruce than in black spruce, whereas YI was higher in black spruce than in white spruce. Thus, white spruce foliage appears to have a higher chl content and less yellowness than black spruce foliage, across the entire range of latitudes and elevations studied. Differences in PRI suggest that white spruce has higher photochemical efficiency than black spruce, although gas exchange or fluorescence data would be required to verify this suggestion.

**Discussion**

**Differences in reflectance spectra**

Needle reflectance was higher in black spruce than in white spruce (Figure 2), especially at the green peak (550 nm). Integrated across the range of visible wavelengths (400–700 nm), black spruce needles reflected 21% more than white spruce needles ($P \leq 0.01$). Although this may be a thermo- or photoprotective mechanism, the differences in reflectance are almost certainly a manifestation of differences in needle color between species. Black spruce needles are described as pale bluish-green with a whitish bloom, whereas white spruce needles are blue-green (Hultén 1968). The difference in needle color is probably related to differences in either the quantity or morphology of epicuticular wax. Cape and Percy (1993) found that black spruce had between 15 and 60% more wax than white spruce when the two species were grown together in five different environments.

**Comparison with other species**

Reduced pigment content and a lower chl/carotenoid ratio are common plant responses to a variety of stress factors, and generally result in a shift in foliage color from green to yellow (Peñuelas and Filella 1998). Konopka et al. (1996) found that

<table>
<thead>
<tr>
<th>Type of spruce</th>
<th>Multiple regression model results</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black spruce</td>
<td>$\lambda_{RE} = 722.87(12.18) - 0.390(0.189) \times L - 2.499(1.275) \times E$</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>Chl NDI = 1.405(0.404) - 0.018(0.006) \times L - 0.090(0.042) \times E</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>YI = $-11.535(3.510) + 0.183(0.055) \times L + 0.925(0.367) \times E$</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td>PRI = $0.462(0.180) - 0.007(0.003) \times L - 0.051(0.019) \times E$</td>
<td>0.40</td>
</tr>
<tr>
<td>White spruce</td>
<td>$\lambda_{RE} = 699.82(7.89) - 0.008(0.123) \times L - 3.281(0.941) \times E$</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>Chl NDI = 0.601(0.303) - 0.004(0.005) \times L - 0.117(0.036) \times E</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>YI = $-1.977(2.463) + 0.027(0.038) \times L + 1.003(0.294) \times E$</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>PRI = $0.289(0.227) - 0.004(0.004) \times L - 0.098(0.027) \times E$</td>
<td>0.35</td>
</tr>
</tbody>
</table>
yellowed foliage of declining *Picea* (L.) Karst in Germany has impaired PSII function (as indicated by changes in the chlorophyll fluorescence parameter $F_v/F_m$) as well as enhanced degradation of the D1 protein. Increasing yellowness and the apparent reductions in chl content (indicated by the trend in Chl NDI) and photosynthetic efficiency (suggested by the trend in PRI) with increasing elevation and latitude are consistent with the general pattern observed in numerous species along an elevational gradient (reviewed by Tranquillini 1979). This is at least partially a phenotypic stress response, as demonstrated by Benecke (cited in Tranquillini 1979), who planted seedlings from the same provenance at three elevations and observed photosynthetic declines of between 25% (in *Alnus*) and 76% (in *Nothofagus*) between mid- (1300 m) and high-elevation (1950 m) sites. In contrast, Oleksyn et al. (1998) found that *Picea abies* trees from high elevations had higher chl, nitrogen and maximal rates of photosynthesis than trees from low elevations, when the different provenances were grown in a common garden. Together, these results suggest that responses to the elevation gradient (and presumably the latitudinal gradient as well) reflect a combination of both genotypic and phenotypic effects.

We are unaware of previous studies on changes in reflectance along latitudinal gradients. However, we can compare the elevation coefficients with our previous studies on balsam fir, red spruce and mountain paper birch (Richardson et al. 2001, Richardson and Berlyn 2002a). For Chl NDI, rates of change in index values of white spruce ($-0.117 \text{ km}^{-1}$) and black spruce ($-0.090 \text{ km}^{-1}$) were intermediate between those of red spruce ($-0.066 \text{ km}^{-1}$) and paper birch ($-0.135 \text{ km}^{-1}$). Of the five species, balsam fir ($-0.049 \text{ km}^{-1}$) was the least sensitive to increases in elevation. For PRI, black spruce ($-0.098 \text{ km}^{-1}$) was more sensitive to increases in elevation than either paper birch ($-0.063 \text{ km}^{-1}$) or white spruce ($-0.051 \text{ km}^{-1}$); both red spruce ($-0.031 \text{ km}^{-1}$) and balsam fir ($-0.030 \text{ km}^{-1}$) were only one-third as sensitive to elevation as black spruce. Black, white and red spruce are generally considered to be closely related members of the genus *Picea* (but see discussion in Weng and Jackson 2000). Both black spruce and red spruce (Manley and Ledig 1979, Berlyn et al. 1990) hybridize with other spruces and have similar foliar characteristics (Weng and Jackson 2000). Hybridization of black spruce and white spruce, although reported, has been questioned (see Parker and McLachlan 1978). Our results provide further evidence that there are distinct ecophysiological differences among these three *Picea* species.

**Relationships between elevation and latitude**

Latitude–elevation relationships have frequently been derived on the basis of changes in tree-line elevation with increasing latitude. According to Daubenmire (1954), the tree line in North America between 35° and 70° N decreases at a rate of 110 m elevation per degree latitude. Across the entire Northern Hemisphere, Körner (1999) calculated a rate of 130 m per degree from 30° to 50° N, and 75 m per degree from 45° to 70° N. Cogbill and White (1991) estimated a rate of 83 m per degree in the northern Appalachians of the eastern USA (44° to 55° N). We are unaware of similar estimates for Alaska; however, across the range of latitudes studied, mean annual temperature drops steadily with increasing latitude, from about $-1 ^\circ C$ at 61° N to about $-9 ^\circ C$ at 68° N (data interpolated from mean annual air temperature map 1961–1990, available at [http://lwf.ncdc.noaa.gov/oa/documentlibrary/clim81supp3/clim81.html](http://lwf.ncdc.noaa.gov/oa/documentlibrary/clim81supp3/clim81.html)). Thus, mean annual temperature decreases by about 1.15 °C per degree of latitude. Assuming a mean adia-

---

**Figure 5.** Changes in reflectance indices of black spruce ($n = 24$) and white spruce ($n = 30$) collected at different latitudes and elevations in Alaska. Plotted lines are best-fit lines calculated from multiple linear regressions (Index value = $\alpha + \beta L + \phi E + \epsilon$, where $L =$ latitude and $E =$ elevation) conducted separately for each species. For “latitude” plots, a standard elevation of 500 m was used; for “elevation” plots, a standard latitude of 65° N was used. Asterisks adjacent to each graph indicate slope coefficients significantly different from zero according to the $t$-test: * $= P \leq 0.10$; ** $= P \leq 0.05$; and *** $= P \leq 0.01$. Abbreviations: Chl NDI = chlorophyll normalized difference index; and PRI = photochemical reflectance index.
batic lapse rate of $-6 \, ^\circ C \, km^{-1}$ (Körner 1999), we calculate a slope of 192 m per degree. The slope would likely be lower if based on mean summer instead of mean annual temperatures (Cogbill and White 1991).

The elevation and latitude coefficients from the multiple regressions can be used to derive latitude–elevation relationships for black spruce and white spruce. The black spruce results suggest that a one degree increase in latitude is roughly comparable with an increase of between 140 m (based on PRI) and 199 m (based on Chl NDI) in elevation. These figures correspond well with the latitude–elevation relationship based on mean annual temperature, and indicate that a 1000 m increase in elevation can be equated with a 6° increase in latitude. However, when the same analysis was performed with the white spruce results, one degree of latitude equated to an increase of less than 40 m elevation (based on ARE, Chl NDI and Y1) or more than 400 m elevation (based on PRI). Thus, although there was a clear latitude–elevation relationship for black spruce, it is more difficult to establish such a pattern for white spruce. It should be noted that, in the multiple regressions (Table 1), elevation and latitude accounted for roughly 25–50% of the total variability in index values. Thus, there are other factors, which we did not quantify, that account for between 50–75% of the total variability in index values.

How might ecological differences between species explain why black spruce showed a clear response to latitude, whereas white spruce did not? Black spruce populations from Ontario exhibit genetic variation for traits such as height growth and timing of bud break that has been related to climatic variables including temperature and precipitation (Parker et al. 1994). On the other hand, common garden experiments with white spruce show mixed results. For example, frost tolerance or hardening capacity of white spruce does not vary with latitude for eastern Canadian provenances (Coursolle et al. 1998); but white spruce from high latitudes or high elevations in interior British Columbia were found to have improved frost hardiness (Hawkins and Shewan 2000). In an experiment with 22 white spruce seed sources, height growth of northern and western provenances was lowest, although corresponding patterns in allozyme data could not be detected (Furnier et al. 1991).

The explanation may lie in differences in species ecology and the types of sites that black and white spruce occupy. The factors controlling white spruce distribution at the northern edge of its range are not yet fully understood (Burns and Honkala 1990). However, at higher latitudes, where it can tolerate only a limited range of sites, white spruce usually grows best on well-drained south-facing slopes and moist alluvial soils alongside lakes and rivers (Burns and Honkala 1990). White spruce typically demands better quality sites than black spruce, which can be found in wet bogs and swamps and organic soils, and is much better adapted to growing on permafrost than white spruce, because it has a shallower rooting habit (Burns and Honkala 1990). Therefore, local topography and drainage control the distribution of these two Picea species; white spruce is more competitive and occupies richer, more productive sites, whereas black spruce is more tolerant and occupies poor quality, wet sites.

Along latitudinal gradients (and to a lesser degree, elevational gradients), there are what Billings (1973) referred to as “mesotopographic gradients” related to ridge/valley position and driven by water availability. Ridge tops are generally exposed to strong winds, have lower snow cover, have a longer growing season and are more xeric than valley bottoms, which are cooler but more sheltered, accumulate more snow and are mesic or possibly even hydric. Environmental differences between a ridge and valley, which may be separated by only tens or hundreds of meters, can be tremendous despite the spatial proximity (Billings 1973). Thus, one explanation for the absence of a white spruce latitude response may be that, at high latitudes, white spruce is able to exploit these microsite differences to a greater degree than black spruce. We hypothesize that by selectively occupying only the best sites (warmer, drier and more sheltered) at the northern limits of its range (or by being out-competed by other vegetation types on all but the best sites), white spruce shows little or no stress response to the latitudinal gradient. Additional support for this hypothesis comes from Cooper (1986), who found white spruce trees growing on protected, south-facing slopes in the Brooks Range, at 1465 m (some 700 m above the tree line) and well beyond the Arctic circle—these are among the highest elevation trees in Alaska. Cooper found no black spruce growing beyond the tree line, even though it is thought to be considerably more frost-tolerant than white spruce (Bigras and Margolis 1996). Thus, different environmental factors control the distribution of black spruce and white spruce, and this may offer an explanation for the differences in their latitude–elevation responses.

Acknowledgments

We thank the School of Forestry and Environmental Studies, Yale University for financial support, and Alexander Evans for producing the maps in Figure 1. Andy Friedland, John Gamon and Ellen Denny kindly reviewed the manuscript prior to submission.

References


TREE PHYSIOLOGY ONLINE at http://heronpublishing.com

544 RICHARDSON, BERLYN AND DUIGAN

TREE PHYSIOLOGY VOLUME 23, 2003