

Bark reflectance spectra of conifers and angiosperms: implications for host discrimination by coniferophagous bark and timber beetles

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The spectral reflectance of phytophagous insects' host plants is usually quantified between 300–350 nm (ultraviolet, UV) and 700 nm (far-red to infrared), and the shape and magnitude of the distribution of reflected light determine the hue, saturation, and intensity perceived by insects (Moericke 1969). Host perception also depends on the distribution of environmental light (Endler 1993) and on the constraints of the insects' visual system, which is usually described as dichromatic, with one type of photoreceptor responding maximally to blue light ($\lambda_{\text{max}} = \text{ca. } 400\text{--}470 \text{ nm}$) and another to green light ($\lambda_{\text{max}} = \text{ca. } 500\text{--}530 \text{ nm}$). UV receptors also appear to be common, if not ubiquitous (Briscoe and Chittka 2001; Mazza *et al.* 2002). Several phytophagous insects have been shown to use visual cues, including UV reflectance, to locate and (or) discriminate among plants (Prokopy and Owens 1983).

Bark- and wood-boring beetles (Coleoptera: Scolytidae, Cerambycidae) that colonize coniferous tree boles are apparently attracted to dark hues that may match their hosts (*e.g.*, Dubbell *et al.* 1985), and they also use chemical cues in host location (Wood 1982). In addition to differing in chemical profile (*e.g.*, Huber *et al.* 2000), non-host angiosperms (*e.g.*, aspens, birches) may appear white in comparison with host conifers. We analysed the spectral reflectance of the bark of the coniferous hosts and angiosperm non-hosts of several bark and timber beetles in western North America, as well as that of black and white multiple-funnel traps (Lindgren 1983) used to assess how these

beetles integrate visual and olfactory tree cues (Campbell 2004).

We sampled the following conifers in southern British Columbia in 2003: Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco (Pinaceae); lodgepole pine, *Pinus contorta* var. *latifolia* Engelm. *ex* S. Wats. (Pinaceae); ponderosa pine, *Pinus ponderosa* P. & C. Lawson; and "interior" fir, *Abies bifolia* A. Murray \times *A. lasiocarpa* (Hook.) Nutt. (Pinaceae). We also sampled three sympatric non-host angiosperms: trembling aspen, *Populus tremuloides* Michx. (Salicaceae); paper birch, *Betula papyrifera* Marsh. (Betulaceae); and red alder, *Alnus rubra* Bong. (Betulaceae). We selected eight trees (six ponderosa pine), $\geq 100 \text{ m}$ apart and $\geq 25 \text{ cm}$ in diameter at breast height (130 cm), and removed a small square of bark from the north aspect of the bole at a height of 170–200 cm. Samples were wrapped in wax paper and stored at 6–15 °C until analysed.

The spectral quality of reflected light was measured in 10-nm increments relative to an internal MgO standard on a Cary 17 spectrophotometer (Varian, Inc., Palo Alto, California) with an integrating sphere (scanning speed, $2 \text{ nm}\cdot\text{s}^{-1}$). Intensity was calculated relative to the difference between black and white external standards. Reflectance was measured from UV (300–350 nm) to red (670 nm), although instrument sensitivity was lower at the limits of this range. We analysed data in the 400–580-nm range using MANOVA (PROC GLM, SAS version 8.02, SAS Institute Inc., Cary, North Carolina) with Pillai's trace as the multivariate statistic (Zar 1999), spanning the known sensitivity maxima for bark beetles (Groberman and Borden 1982). We tested for differences in intensity at each 10-nm increment by univariate ANOVA (PROC GLM) followed by the REGWQ multiple-range test (Day and Quinn 1989).

Except for ponderosa pine, which exhibited a sharp transition over approximately 620–660 nm,

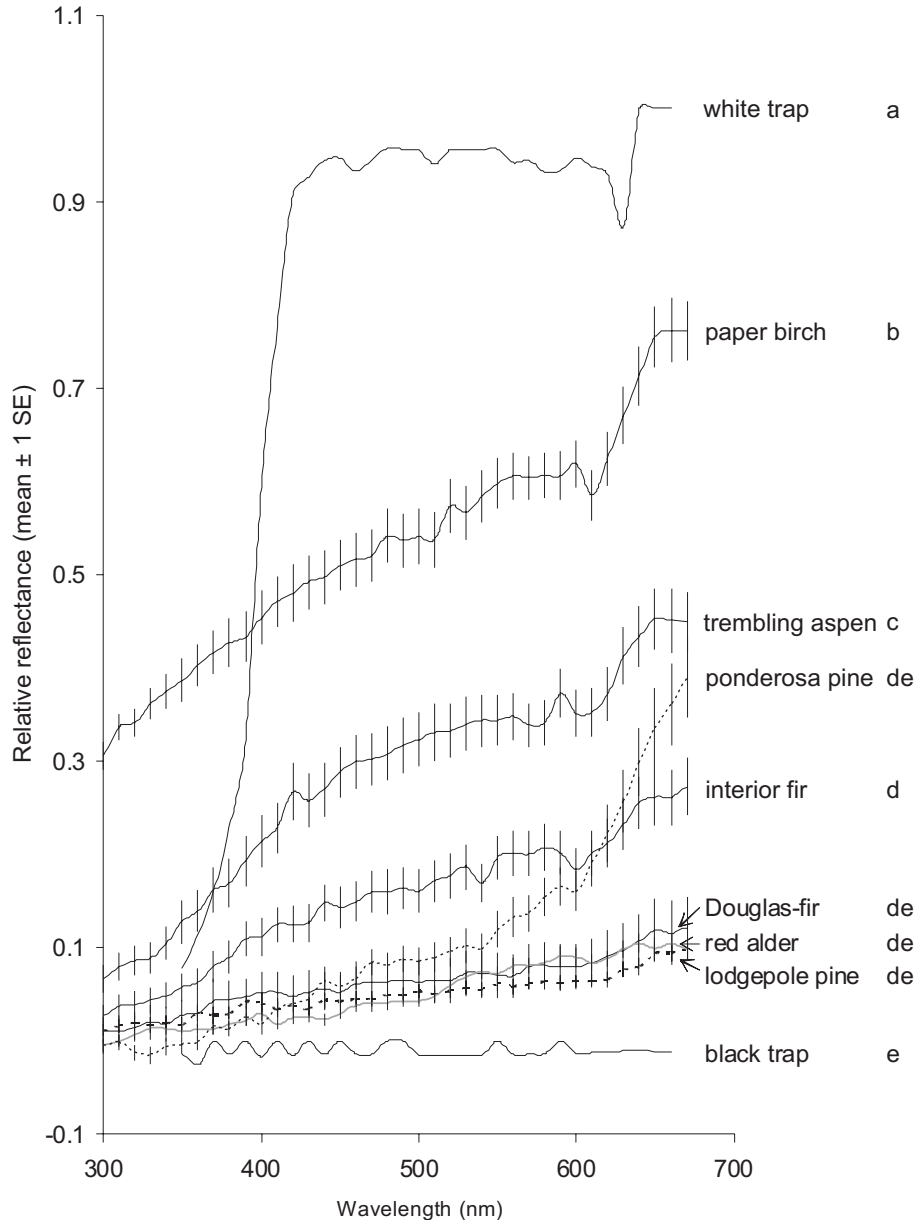
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Fig. 1. Reflectance spectra of conifers, angiosperms, and experimental traps. Traces comprise relative reflectance means \pm 1 SE for 10-nm increments over 300–670 nm. Spectra followed by the same letter are not significantly different for all increments over 400–580 nm (REGWQ multiple-range test).



there were few qualitative differences in reflectance among tree species and between tree barks and trap plastics (Fig. 1). Tree species differed in intensity (MANOVA: Pillai trace = 4.2878; $F_{114,140} = 4.48$; $P < 0.0001$), and trees and traps differed at every 10-nm increment (univariate analyses, $P < 0.0001$); significant differences among species and traps (Fig. 1) were the same for every univariate REGWQ

test across 400–580 nm. Paper birch had the highest reflectance over most wavelengths, followed by trembling aspen. For most visible wavelengths, interior fir, ponderosa pine, Douglas-fir, red alder, and lodgepole pine were not different from each other, and the last four were not different from the black trap. When traps were excluded from analysis, reflectance of interior fir was significantly greater than that

of red alder and the other conifers. Paper birch and, to a lesser extent, trembling aspen reflected UV light more intensely than the white trap for wavelengths <400 nm and <370 nm, respectively.

Our results are similar to those of Lang *et al.* (2002), who assessed the reflectance of sunlight ($\lambda = 400\text{--}2400$ nm) in the field from the bark of Scots pine, *Pinus sylvestris* L., and silver birch, *Betula pendula* Roth. For ponderosa pine, the peak reflectance at approximately 650–670 nm is consistent with its reddish brown appearance and with the reflectance spectrum of the related loblolly pine, *P. taeda* L. (Strom *et al.* 1999). All other species appear dark to light grey or brown to the human eye, consistent with these spectral profiles. Examination of the known sensitivity maxima of bark beetles and many insects (Groberman and Borden 1981, 1982; Briscoe and Chittka 2001) reveals that to blue (450 nm) and green (510–530 nm) photoreceptors, respectively, trembling aspen should appear 7.3 and 6.6 times brighter, and paper birch 12.8 and 11.4 times brighter, than lodgepole pine. These quantitative differences in reflectance intensity could complement odours used to discriminate between host conifers and non-host angiosperms. Supporting this hypothesis, five species of coniferophagous bark beetles, three large wood-boring beetles, and a wood-boring wasp all avoided white attractant-baited traps relative to black baited traps (Strom *et al.* 1999, 2001; Campbell 2004). Conversely, there were no differences that would suggest reflectance might guide discrimination among conifers.

Paper birch strongly reflected short-blue and UV light (*i.e.*, 300–400 nm), as also found by Mazokhin-Porshnyakov (1969). This could be the result of bark surface reflectance. In addition, birches have thin bark, and UV-reflecting pigments within cortical cells may have evolved to prevent sunlight from damaging subcortical photosynthetic or vascular tissues (Vogelmann 1993), complementing a capacity to produce UV-absorbing phenolics in response to high UV radiation (Tegelberg *et al.* 2002). UV–blue–green trichromacy appears to be ancestral in pterygote insects (Briscoe and Chittka 2001), and it is likely that UV light detection occurs in bole-colonizing insects (Droska *et al.* 1983; Briscoe and Chittka 2001; Mazza *et al.* 2002), which might also utilize UV cues from these non-hosts.

Because black traps were not statistically different in reflectance from either Douglas-fir or

lodgepole pine bark, they would provide good reflectance models for bole-colonizing insects that attack these species. Small imperfections in the bark (*e.g.*, lenticels in birch) would have lowered the reflectance intensity detected by the spectrophotometer, but would become difficult to resolve with increased distance from the tree. Thus, white traps may appear even more similar to trembling aspen and paper birch in the field, and could be used to evaluate the responses of coniferophagous insects to non-host visual cues (Strom *et al.* 2001).

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