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ALTITUDINAL VARIATION OF CHLOROPHYLL CONCENTRATION AND REFLECTANCE OF THE BARK OF *POPULUS TREMULOIDES*¹

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Abstract. Although quaking aspen (*Populus tremuloides* Michx.) bark appears greener at higher elevations in the Sangre de Cristo mountain range of New Mexico, chlorophyll concentrations are inversely correlated ($p = .001$) with altitude. The higher concentration of chlorophyll at lower elevations is effectively masked by a white bloom of dead periderm cells which is also characteristic of exposed site trees. At higher elevations the bloom is yellow-brown and more translucent, thus allowing the chlorophyll layers beneath to show through. Therefore, trees at higher elevations appear greener even though they have lower cortical chlorophyll concentrations.

The altitudinal gradient in bark reflectance characteristics may be of adaptive value. If cortical photosynthesis is more important at higher elevations, the translucent bloom would be advantageous in making more light available for photosynthesis. Increased light absorption might also be important in raising bark temperatures for physiological activity during the winter months. At lower elevations where air temperatures are higher, the highly reflective bloom may protect the trees from high bark temperatures and sunscald.

Key words: Altitudinal gradient; aspen; bark photosynthesis; chlorophyll; *Populus tremuloides*; reflectance.

INTRODUCTION

In the Sangre de Cristo Mountains of New Mexico quaking aspen (*Populus tremuloides* Michx.) exhibits an altitudinal cline in bark color with bark greenness increasing with altitude. Cottam's (1954) observations indicated a similar cline in aspen bark color in northern Utah. Pearson and Lawrence (1958b) demonstrated that bark greenness in aspen is caused by the presence of chlorophyll in cortical tissues.

Photosynthesis in quaking aspen bark has been demonstrated by various authors (Pearson and Lawrence 1958a, b, Strain and Johnson 1963, Strain 1964, Schaedle and Foote 1971) and shown to be sufficient to contribute to growth by Strain and Johnson (1963). Parker (1953) suggested that branches of deciduous trees which contain cortical chlorophyll might carry on photosynthesis throughout the winter. Furthermore, Pearson and Lawrence (1958a) established that winter season photosynthesis occurs in the bark of quaking aspen even at air temperatures well below 0°C. Perry (1971) demonstrated that dormant twigs of *Platanus occidentalis* L., *Carya illinoensis* (Wangenh.) K. Koch, and *Quercus phellos* L. were capable of photosynthesis during winter. In addition he found that *Liquidamber styraciflua* L. seedlings increased in dry weight by 42% during the

leafless period. Cortical photosynthesis may also be important in providing metabolic energy for localized biochemical events within woody tissues (Kriedemann and Buttrose 1971).

Schaedle et al. (1968) estimated that the bark provides up to 15% of the photosynthetic surface of quaking aspen trees. Also, leaves are present for only 3-4 mo, but the bark provides a year-round photosynthetic surface.

Strain and Johnson (1963) suggested that quaking aspen's ability to carry on cortical photosynthesis might partially account for its extreme latitudinal and altitudinal distribution. Pearson and Lawrence (1958a) proposed that this might explain why aspen can survive in regions of long and severe winters which are generally thought to be more suitable for evergreen conifer species.

Quaking aspen exhibits tremendous ecotypic and ecophenic variation (Vaartaja 1960, Graham et al. 1963, Strain 1964). Several authors (Baker 1921, Marr 1947, Cottam 1954, Egeberg 1963, Strain 1964) have reported differences in bark color among quaking aspen. Variations in date of leafing out have also been reported (Cottam 1954, Vaartaja 1960, Egeberg 1963). Although there is evidence for ecotypic differences in date of leafing out, the general trend is ecophenic, with earlier leafing out and later senescence in aspen at lower elevations.

If cortical photosynthesis is important in allowing quaking aspen to grow beyond the altitudinal limits of other deciduous trees, one would expect natural selection to favor phenotypes with a high potential

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TABLE 1. Average cortical chlorophyll content, SE, and sample size for aspen at various elevations. N = number of trees sampled at each site

Elevation (m)	Chlorophyll content (mg/m ²)	SE	N	Sampling date (1971)
3,261	374	17.60	5	8 Sept.
3,246	345	8.87	3	21 July
3,237	460	18.06	4	25 Aug.
3,231	357	13.89	5	1 Sept.
3,200	404	35.72	3	20 Aug.
3,124	503	29.83	5	8 Sept.
3,118	414	17.61	5	1 Sept.
3,115	432	38.33	4	25 Aug.
3,054	479	10.06	3	20 Aug.
3,054	450	10.60	5	1 Sept.
3,045	393	31.29	3	21 July
2,987	443	14.22	5	8 Sept.
2,896	511	74.97	3	20 Aug.
2,893	479	36.58	4	25 Aug.
2,880	521	46.27	5	8 Sept.
2,880	591	45.02	3	21 July
2,853	523	29.91	3	21 July
2,844	400	7.99	5	1 Sept.
2,703	387	33.00	3	20 Aug.
2,697	564	20.26	4	25 Aug.

for this supplemental photosynthesis, especially at high altitudes with short growing seasons. The cline in bark greenness suggests a similar cline in chlorophyll concentration and photosynthesis. The purpose of this research is to examine the altitudinal gradient in bark color and chlorophyll concentration. Since bark color is not solely dependent upon chlorophyll content, reflectance of the bark is also studied.

MATERIALS AND METHODS

This study was conducted in the Tesuque Watershed Study area of the Sangre de Cristo Mountains northeast of Santa Fe, New Mexico. A complete site description can be found in Gosz (1975). Sampling sites were selected at random along an elevational gradient ranging from 2,695 m (8,850 ft) to 3,260 m (10,700 ft). On each sampling date (21 July–18 September 1971) sites were chosen randomly from each of four altitudinal zones (2,690–2,880, 2,880–3,050, 3,050–3,150, 3,150–3,300). At each site three to five trees were randomly sampled. Increment cores showed that tree age ranged from a minimum of 50 to a maximum of 81 yr.

Chlorophyll samples

I collected bark samples for chlorophyll determinations by stamping out discs with a steel die of 16 mm diam (Pearson and Lawrence 1958b). Four such discs (8 cm² total) were taken from the south side of each tree sampled. The discs were placed immediately in cold 80% acetone with 0.5 g CaCO₃ to retard chlorophyll breakdown (Smith and Benitez 1955). The sample bottles were stored in the dark

in an ice chest for transport to the laboratory. Chlorophyll determinations were made spectrophotometrically on an 80% acetone extract of the bark sample (MacKinney 1941).

Reflectance samples

A knife was used to cut bark samples approximately 64 cm² to be used in reflectance measurements. The bark was pried away with a chisel and care was taken to avoid damage to the surface area to be used in the reflectance measurements. Samples were kept in plastic bags in an ice chest for transport to the laboratory. The Bausch and Lomb Spectronic 600 with the visible light reflectance attachment was used to measure bark reflectance from 400 to 700 nm as compared to a MgCO₃ block as the 100% reflecting surface. The illuminant was a tungsten lamp. After the initial measurements the bloom of dead periderm cells (Kaufert 1937) was rubbed off with Kimwipes®, and measurements were taken again to estimate the contribution of the bloom to total reflectance.

Calculations

I used the equation of MacKinney (1941) to calculate chlorophyll concentration:

$$C = 8.02(663E) + 20.2(645E)$$

where C is total chlorophyll concentration in mg/liter and 663E and 645E are the absorbance measurements at 663 nm and 645 nm.

Average reflectance was calculated for each bark sample both before and after removal of the bloom. The equation of Wright (1969) was used:

$$\text{Average reflectance} = \sum(\beta_{\lambda} P_{\lambda} \bar{y}_{\lambda})$$

where β is the spectral luminance factor read from the spectrophotometrically determined reflectance curve for each sample, P is the spectral composition of the illuminant, \bar{y} is the distribution coefficient for the illuminant, and λ is the wavelength in 5 nm increments.

The mean reflectance curve for each stand sampled was calculated from the formula

$$\bar{\beta}_{\lambda} = \sum \beta_{\lambda} / 5$$

where $\bar{\beta}_{\lambda}$ is the mean spectral luminance factor for the stand and $\sum \beta_{\lambda}$ equals the sum of the individual spectral luminance factors as read from the reflectance curves for each of the five trees sampled from each stand.

RESULTS

Although I observed some clonal differences in date of leafing out among clones at the same elevation, the dominant trend was an earlier leafing out

TABLE 2. Reflectance characteristics of individual aspen bark samples from four representative elevations

Elevation (m)	Average reflectance (%)		Average reflectance ^b (%)
	Before	After ^a	
3,231	18.79	13.19	5.60
3,231	18.56	12.61	5.95
3,231	20.74	17.07	3.67
3,231	18.36	13.98	4.38
3,231	19.62	13.76	5.86
3,124	24.28	20.00	4.28
3,124	20.94	15.73	5.21
3,124	23.41	17.35	6.06
3,124	22.54	17.05	5.49
3,124	21.92	15.51	6.41
2,987	29.72	18.69	11.03
2,987	30.32	21.24	9.08
2,987	36.67	20.79	15.88
2,987	29.68	18.09	11.59
2,987	29.47	17.75	11.72
2,880	42.07	18.20	23.87
2,880	41.36	18.47	22.62
2,880	39.42	17.68	21.74
2,880	32.36	18.00	14.36
2,880	32.90	19.62	13.28

^a Before and after removal of the bloom of dead periderm cells.

^b This is the reflectance attributed to the bloom.

and a later senescence at lower altitudes. Trees at the highest elevations (3,260 m) leafed out as much as 5 wk later than trees at the lowest elevations (2,440 m). The latter were isolated groups of aspen occurring along stream bottoms and represent the lower altitudinal limits of aspen in the Tesuque Watershed Study area. A similar difference in date of leaf senescence occurred, with trees at the highest elevations senescing approximately 3–5 wk earlier than those at the lowest elevations.

The stands at 3,054 m and 2,880 m elevation were sampled twice for chlorophyll concentration (Table 1) to test for a treatment effect due to sampling date. Analysis of variance failed to demonstrate significant differences in chlorophyll concentrations between sampling dates at these two elevations because of excessive variation within sampling dates. Therefore, the measurements from all dates were combined and analyzed for a correlation between elevation and chlorophyll concentration in the bark. Contrary to what I expected, correlation analysis gave a highly significant ($P = .001$) negative correlation coefficient (-0.447). The inverse relationship between chlorophyll concentration and altitude is illustrated in Fig. 1.

In an attempt to explain why bark greenness was inversely related to chlorophyll content, bark was collected from trees at four representative elevations for reflectance measurements (Table 2). The mean reflectance curves before and after removal of the bloom are presented in Fig. 2. While rubbing off the bloom I noticed that the lowest elevation trees

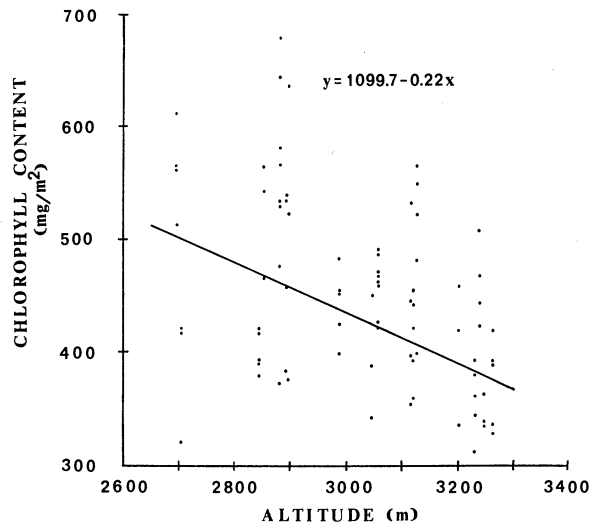


FIG. 1. Chlorophyll concentration in the bark of *Populus tremuloides* vs. altitude.

had a white bloom in comparison to the yellow-brown bloom of higher elevations.

Analysis of the data from Table 2 shows that bark reflectance is inversely correlated with altitude ($P = .001$). A t -test demonstrates that average reflectance after removal of the bloom is significantly lower ($P = .001$) than reflectance before removal for all four stands studied. The amount of reflectance attributed to the bloom is inversely correlated with altitude ($P = .001$).

Generally the bark at lower elevations has a higher average reflectance than the bark of trees at higher elevations in the Tesuque watersheds. Also, it is apparent from Fig. 2 and the results reported above that much more of the total light reflected is attributed to the bloom at lower elevations than at higher elevations. An exception is that at intermediate elevations (about 3,045–3,150 m) trees exposed to higher insolation, as along a road cut, develop a white bloom, more characteristic of lower elevations. Members of the same clone that were under closed canopy retain the green bark. I did not observe any trees at the lowest elevations that could compare in greenness to those of the highest elevations nor did I find trees at the highest elevations which exhibited a white bloom.

DISCUSSION

The appearance of greener barked aspen at higher elevations is due to differences in the reflectance characteristics of the bloom of dead periderm cells and not to higher chlorophyll concentrations. I found, in fact, that chlorophyll concentrations were inversely correlated with altitude.

Cottam (1954) attributed the bole color difference

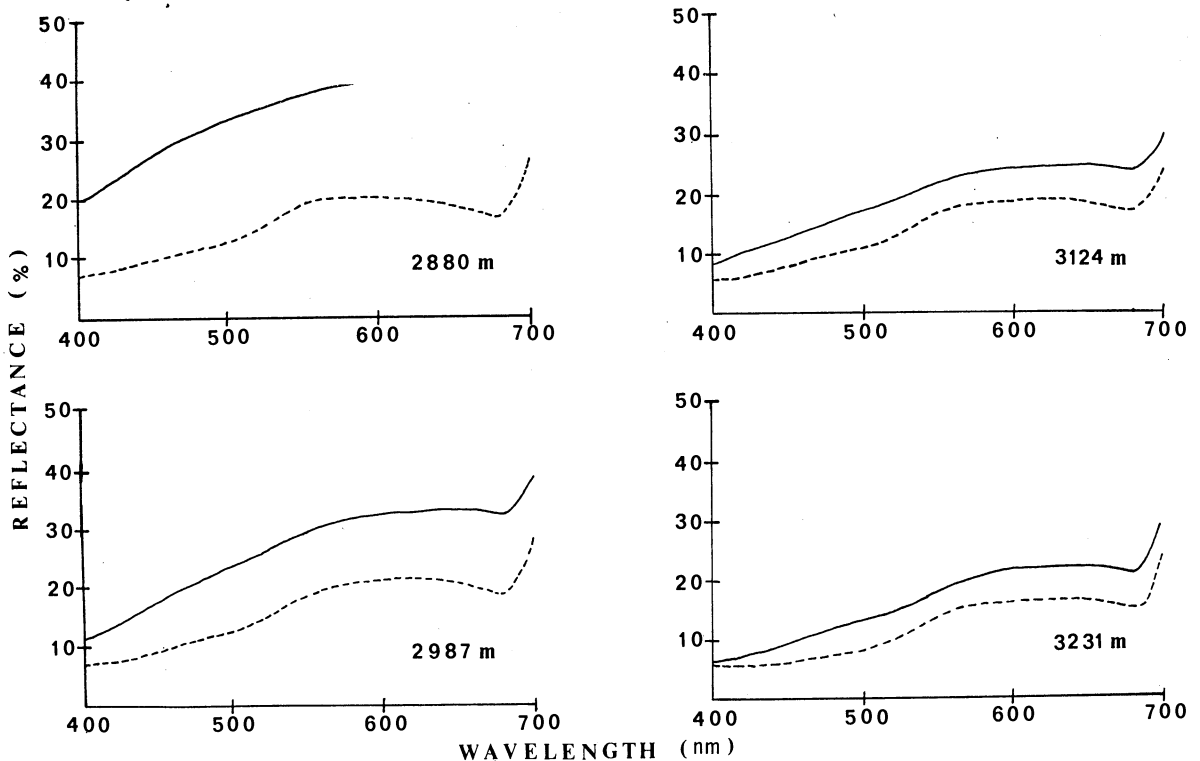


FIG. 2. Mean reflectance curves from aspen bark for a sample of five trees from each of four elevations before (solid line) and after (broken line) removal of the bloom.

that he observed to the failure of the greener barked trees to produce the copious bloom of the whiter barked trees. I suggest that this color difference is due not to the quantity but to the quality of the bloom produced, which I found to be profuse at high as well as low elevations. At lower elevations this bloom is white and effectively masks the high chlorophyll concentrations that are present. At higher elevations where chlorophyll concentrations are less, the bloom is yellow-brown and more translucent, thus allowing the green of the chlorophyllous layers to show through more readily. These results are in agreement with those of Strain (1964), who found that higher bark reflectance in aspen was correlated with the characteristics of the bloom rather than with bark chlorophyll content. Barber and Jackson (1957) noted a similar masking of chlorophyll and anthocyanin pigments by bloom whiteness in *Eucalyptus* trees in Tasmania.

My observations regarding altitudinal variations in aspen phenology are in close agreement with Hopkins's bioclimatic law, i.e., that the date of occurrence of a given phenological event is approximately 4 days later per 400 ft (120 m) increase in altitude in the spring and early summer and earlier in the late summer and autumn (Hopkins 1918). In the Tesuque watersheds the leafless period is as much

as 8–10 wk longer at the highest elevations. This seems to indicate that cortical photosynthesis is more important at higher elevations.

Though my results discount the notion that chlorophyll concentrations are higher in the green-barked trees, they do not preclude the possibility of higher rates of photosynthesis at higher elevations. The reflectance measurements (Table 2) illustrate that considerably more of the incident radiation is absorbed by the bark of trees at higher elevations. Also rates of insolation generally increase with altitude. Thus, the light available for cortical photosynthesis is probably greater at the higher elevations. It is possible, therefore, that high-elevation stands have greater rates of cortical photosynthesis even though they have lower chlorophyll contents than the trees at low elevations.

Differences in bark color are probably both ecotypic and ecophenic. Evidence for the former comes from observations of green-barked clones growing contiguous to and seemingly under identical environmental conditions with white-barked clones (Baker 1921, Cottam 1954, Egeberg 1963).

My observations give evidence for an environmentally induced variation in aspen bark color. In the Tesuque watersheds the trees of the lower elevations have a white bloom even under closed canopy.

At intermediate elevations clones whose members have green bark under closed canopy exhibit a white bloom if they are exposed to higher insolation as along a road cut (Results). More evidence for an insolation-induced whiteness comes from my observation that the bark is generally whiter on the south side of the trees—the side receiving the highest rates of insolation. Strain (1964) also found that exposed-site aspen had higher bark reflectance than non-exposed-site aspen.

The development of this white bloom on exposed-site aspen might be attributed either to the direct effect of increased insolation or to its indirect effect of increased bark temperatures. The former is suspect because of the appearance of white-barked aspen at lower elevations even under closed canopy and by the lack of white-barked aspen at higher elevations even on fully exposed sites. At higher elevations the decrease in atmospheric screening should further enhance the development of a white bloom if increased insolation were the direct cause.

The evidence that higher bark temperatures cause the development of the white bloom is much stronger. Strain (1964) observed that bark reflectance increased during the growing season as air temperatures increased. It is possible that air temperatures at the lower elevations are high enough to induce the formation of the white bloom even under closed canopy. At the highest elevations the air temperatures may be cool enough to keep bark temperatures below the critical level by convective heat transfer. At intermediate elevations the amount of insolation may be critical in raising bark temperatures to that point at which the white bloom results.

Since reflectance characteristics are important in determining the heat budget of most organisms (Gates et al. 1965), variations in aspen bark color may function to control bark temperatures. If cortical photosynthesis is more important at higher elevations, the more translucent bloom might be advantageous to the aspen in that more insolation would be absorbed and hence available for photosynthesis and for raising the bark temperatures for physiological activity during the winter months.

Higher bark temperatures may be disadvantageous in some instances. Quaking aspen is susceptible to sunscald (Hartley and Hahn 1920), which subjects the damaged bark to fungal infection (Graham et al. 1963). At higher elevations the bark temperatures are most apt to be ameliorated by lower air temperatures but at lower elevations and exposed sites the higher reflectance of the bloom may be important in protecting the bark from high temperatures and sunscald. In this regard Peace (1962) noted that many trees develop a paler bark when growing in hotter climates and suggested that this may function

to protect such trees from injuriously high bark temperatures.

Winter sunscald, better termed frost damage, may also occur in aspen when the bark thaws during the day and then freezes during the night. Barber (1955) suggested that bloom whiteness in *Eucalyptus* is related to frost activity, the white-bloomed individuals being more frost resistant. This might be because the higher reflectance prevents bark tissues from thawing during the winter months. In contrast with this hypothesis for *Eucalyptus*, Marr (1947) found that the green-barked aspen were more winter hardy than were the white-barked aspen. Whether aspen and eucalypts are subjected to the same mechanisms of selection for bloom whiteness is uncertain.

My results concerning altitudinal variations in bloom characteristics of aspen are in apparent contrast to the results of similar studies of castor bean (*Ricinus communis* L.) by Harland (1947) and *Eucalyptus* trees by Barber (1955) and Barber and Jackson (1957). Working in Peru, Harland found that white-bloomed individuals of *Ricinus communis* occurred more frequently at higher elevations, with practically none at lower elevations. He presented evidence that the bloom characteristics of *Ricinus* are genetically controlled and suggested that temperature alone could not explain the altitudinal distribution of bloom types that he observed. He hypothesized that reproductive failure of white-bloomed individuals is associated with a fog belt occurring at lower elevations in his study area and that this failure was due to the absence of sun or the presence of fog or both. He offered no mechanism to explain these environmental effects.

Studies of *Eucalyptus* species in Tasmania (Barber 1955, Barber and Jackson 1957) revealed an altitudinal variation in stem and leaf whiteness, with bloom whiteness increasing continuously along increasing altitude. Barber (1955) suggested that these clines in glaucousness are genetically controlled and are associated with frost activity, which might favor those genotypes capable of developing the white bloom. However, his observations have firmly established that phenotypic variation in *Eucalyptus* also occurs. In agreement with my results for aspen, Barber and Jackson (1957) noted that white-bloomed eucalypts occur predominantly on exposed sites.

From this discussion two points regarding future research emerge. First, since reflectance characteristics must control to a large extent a plant's photosynthetic capacity and heat budget and hence its success or failure in a given habitat, variations in reflectance both within and among species merits further research. Second, research should be conducted into the ecological significance of variations in cortical chlorophyll and non-leaf photosynthesis.

The occurrence of this supplemental photosynthesizing surface seems widespread and may be important in explaining why some deciduous trees such as aspen can survive in areas with extremely long leafless periods.

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