Notes on the *Populus* "Dripzone Effect" on Lichens in Well-ventilated Stands in East-central British Columbia.

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The "dripzone effect" involves the above-ground transfer of nutrients — presumably in the form of leachates — from the upper crown of one tree species to the lower crown of another. In humid, poorly ventilated *Picea* stands, nutrient enrichment associated with *Populus* dripzones has been shown to promote the development of cyanolichens belonging to the *Lobarion*. Here we examine the same phenomenon in well-ventilated stands, in which members of the more xerophytic *Xanthorion* are favoured, while some species of the alectorioid lichen genus *Bryoria* are excluded. The latter phenomenon may partly account for the often discontinuous occurrence of *Bryoria* in many mixed conifer stands at lower elevations.

Key Words: Hair lichens, dripzone, *Populus*, *Xanthorion*, Wells Gray Park, British Columbia.

The microscale organization of epiphytic lichens in space and time reflects, in addition to chance, a complex interplay of environmental factors. Among the most important of these are diaspore availability, insolation, ventilation, humidity relations, chemical and textural properties of tree bark and wood, and nutrient input from extraneous sources (see James et al. 1977). Regarding the last factor, enrichment, several forms of extraneous nutrient input have been identified, including animal waste, atmospheric dust, long-range transport of industrial emissions in rain and snow, and precipitates from ocean spray, waterfalls, and fog (see Barkman 1958).

One enrichment phenomenon that has received little attention to date is the "dripzone effect"; i.e., the above-ground transfer of leachates from the upper canopy of one tree or shrub species to the lower canopy of another tree or shrub species growing nearby. Recently Goward and Arsenault (2000) documented a striking instance of the dripzone effect in the humid low-elevation forests of south-central British Columbia. Here the occurrence of neutrophytic cyanolichens (e.g., *Lobaria pulmonaria*, *Pseudocyphellaria anomala*, *Sticta fuliginosa*) was shown to be highest on *Picea* branches subject to calcium from the upper canopies of nearby *Populus* trees.

Our earlier study was conducted entirely in humid and poorly ventilated stands. A *Populus* dripzone effect, however, can also be discerned in stands that are both drier and well-ventilated. The primary objectives of this paper are to examine the impact of the dripzone effect on epiphytic lichen community structure in such stands, and to compare the resulting patterns with the earlier results of Goward and Arsenault (2000). Potential ecological implications inherent in our findings will also be briefly discussed.

Study Area

Our study was confined to *Picea* trees growing along the north bank of the Murtle River in Wells Gray Provincial Park, south-central British Columbia (51°58'N, 120°07'W). In its lower reaches, at about 800 m elevation, the Murtle River traverses the "Murtle Plateau", a flat-lying basaltic lava flow dating from the early Pleistocene overlaid by a mantle of weakly acidic glacial till and fluvioglacial deposits (Goward and Hickson 1996). The Murtle Plateau is located in a relatively humid region in which summer precipitation (May through September) averages roughly 260 mm (Environment Canada 1975a). Mean monthly temperatures range from -10°C in January to 15°C in July (Environment Canada 1975b). Air quality in this region is high (Anonymous 1990).

Vegetationally, our study area is representative of the moist-warm subzone of the Interior Cedar-Hemlock Zone (ICHmw: Lloyd et al. 1990), as well as the humid province of the Lower Oroboreal Subzone (Tuhkanen 1984; Goward and Ahti 1992). The tree layer consists primarily of *Abies lasiocarpa*, *Betula papyrifera*, *Picea engelmannii × glauca*, *Pinus contorta*, *Populus trichocarpa*, *P. tremuloides*, *Pseudotsuga menziesii*, and *Thuja plicata*. The forest cover is unmodified by human activity, and dates from an intense wildfire that swept southern Wells Gray Park in 1926 (Edwards 1954). For a more complete description, see Hämet-Ahti (1965) and Goward and Hickson (1996).

Material and Methods
Sampling

Field work was carried out in September and October 1999, and was restricted to the branches of *Picea engelmannii × glauca* aged 50 to 70 years

growing along a 1.5 km stretch of river judged to be relatively homogeneous for aspect, insolation, ventilation, humidity, and fire history. A major advantage of the study site is that *Populus* is restricted here to the immediate river margin, where the likelihood of nutrient "contamination" from *Populus* trees growing nearby is negligible.

Only ten trees could be found that met all of the above criteria. Of these, five were located within the dripzone of *Populus trichocarpa*; the others occurred at a distance of at least 15 to 20 m from the nearest *P. trichocarpa* canopy. Sampling was further restricted to *Picea* branches exposed to at least moderate ventilation. Only branches within 2 m of the ground were examined.

For each tree, we recorded diameter at breast height (dbh) and determined age using an increment borer. We also documented lichen frequency and abundance using a five-point scale (see Goward and Arsenault 1997), as follows: *1* = 2 or fewer colonies per tree; *2* = 3-5 colonies per tree; *3* = 6 colonies per tree, or up to 20% branch cover (under optimum conditions); *4* = 21% to 50% branch cover (under optimum conditions); and *5* = 51% branch cover or more (under optimum conditions). For ease of sampling, only those lichen species readily identified in the field were assessed; other species were collected

and subsequently examined in the laboratory, but are not discussed here. Lichen taxonomy and nomenclature follow Esslinger and Egan (1995).

From each of the ten *Picea* trees examined, we collected dead corticate branches for assessment of bark pH. Sampling was restricted to the exposed, distal portions of branches on which a diverse assemblage of macrolichens was present. Branch segments supporting leprose lichens were assumed to signal microsites sheltered from precipitation (Tnsberg 1992), and therefore sheltered from canopy leachates; such branches were avoided.

All branch segments were later carefully stripped of bark and the bark was then air-dried, ground using a mechanical mill, and placed overnight in de-ionized water. pH readings were taken using a Fisher pH meter calibrated using buffers at pH 4.0 and pH 7.0. For a more detailed description of our methods, see Goward and Arsenault (2000).

Analysis

Epiphytic lichen community structure was examined using PCA and Spearman rank correlations between factor scores and the original vegetation matrix (for further details, see Goward and Arsenault 2000). Lichen frequency and abundance data are presented in Table 1, in which the species are

TABLE 1. Frequency and abundance of epiphytic macrolichens associated with *Picea* branches growing within (N = 5) and outside (N = 5) the *Populus* dripzone. Also shown are bark pH and Spearman rank correlation between frequency and abundance data and the scores of the first PCA axis. * = $P<0.05$, ** = $P<0.01$.

	Sampled trees										
	Within *Populus* Dripzone					Outside *Populus* Dripzone					
Lichen species	1	2	3	4	5	6	7	8	9	10	
Parmelia sulcata		1	2	3	1	1	3	2	2	3	0.14
Parmeliopsis hyperopta										1	0.17
Hypogymnia occidentalis								2			0.29
Hypogymnia austerodes	1	1	1			1		1	1	1	0.34
Alectoria sarmentosa		1			1	3	1		1	1	0.38
Bryoria fuscescens			1			1	3	3	1		0.44
Hypogymnia physodes		1	1	1		1		3	2	3	0.50
Hypogymnia imshaugii									1		0.52
Parmeliopsis ambigua						1		1			0.52
Tuckermannopsis chlorophylla						1	2		1	1	0.64*
Ramalina thrausta	1			2	1	3	3	1	2	3	0.66*
Platismatia glauca							1		2	1	0.67*
Bryoria capillaris	1			1		3	3	3	4	1	0.92**
Hypogymnia tubulosa		1	1	1		1	1	1			-0.14
Usnea lapponica	1	2		1			1	1	1		-0.21
Nephroma resupinatum					1						-0.41
Parmelia hygrophila					1						-0.41
Leptogium saturninum			1								-0.52
Physcia aipolia			2	1							-0.54
Lobaria pulmonaria			1		1						-0.70*
Melanelia subaurifera	3	3	3	3	2		1	1	1	1	-0.81**
Caloplaca holocarpa		1	1	1	1						-0.85**
Bark pH	4.54	5.3	5.76	5.22	5.5	4.84	4.69	4.73	4.67	4.98	0.79**

arranged across a similarity gradient to assist in interpretation. Differences in the frequency and abundance of species were further assessed using a Kruskall Wallis test. In addition, we included species occurring on *Picea* branches in the low ventilation sites discussed earlier by Goward and Arsenault (2000) for comparison.

The mean and standard deviations of bark pH were calculated for five branch samples occurring within the *Populus* dripzone and for five samples occurring outside the dripzone. Differences were assessed using a t-test.

Results and Discussion

Phorophytes

The *Picea* trees sampled varied from 50 to 70 years old, with an average age of 62 years. Their trunk diameters at breast height varied from 20 cm to 63 cm, with a mean of 36 cm. When trees occurring within and outside the *Populus* dripzone were compared, no significant difference could be noted for either tree age or diameter.

Bark pH

In an earlier study of 80 branch samples, *Picea* branches growing within the dripzone of *Populus* had a mean pH of 5.8, whereas similar branches growing at distance from *Populus* had a pH of 4.9 (Goward and Arsenault 2000). pH readings followed a similar trend in the present study. With the exception of a single outlier (see Table 1), bark pH was consistently higher within the *Populus* dripzone (mean pH = 5.2, 5.4 when outlier is excluded) than outside the dripzone (mean pH = 4.8). The outlier had a pH of 4.5, and possibly signaled a recent lowering of enrichment levels not yet reflected in the lichen flora. Bark is a dynamic substrate influenced by multiple factors; a certain amount of variation in bark pH is to be expected over time. When the outlier is excluded, the difference in bark pH between the two sets of branches changes from merely significant ($P < 0.05$) to highly significant ($P < 0.001$).

Epiphytic Lichen Community Structure

Principal Components Analysis performed on epiphyte abundance data separated the sampled trees into two distinct clusters along the first axis. These clusters correlate both with bark pH and with distance class from *Populus* (Figure 1). The first cluster is negatively correlated with the first axis, and incorporates lichens more or less restricted, on *Picea*, to the *Populus* dripzone. Predominating here are members of the *Xanthorion* alliance (i.e., *Caloplaca holocarpa, Physcia aipolia*, and *Melanelia subaurifera*) and, to a lesser extent, the *Lobarion* (i.e., *Leptogium saturninum, Lobaria pulmonaria*, and *Nephroma resupinatum*). Both the *Xanthorion* and the *Lobarion* are epiphytic alliances strongly associated with nutrient-rich substrates, though they differ in their moisture requirements (James et al. 1977).
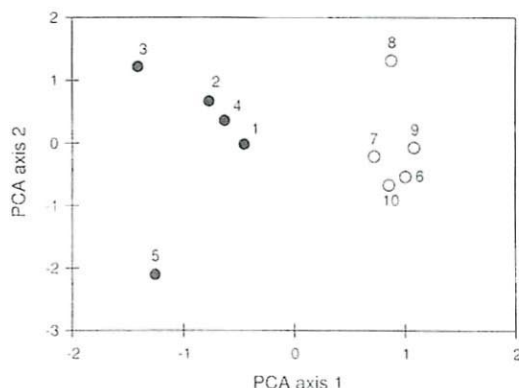

Figure 1. PCA ordination of epiphytic lichens occurring on branches of 10 *Picea* trees in Wells Gray Park. Numbers correspond with the tree numbers given in Table 1. Filled circles indicate trees occurring within *Populus* dripzone. Open circles indicate trees occurring outside the *Populus* dripzone.

The second species cluster is positively correlated with the first axis (Figure 1), and is associated predominantly with *Picea* branches growing outside the *Populus* dripzone. Those species denoted by an asterisk show significant correlation: *Alectoria sarmentosa, Bryoria capillaris*, B. fuscescens, Hypogymnia physodes, Parmeliopsis ambigua, Platismatia glauca*, Ramalina thrausta**, and *Tuckermannopsis chlorophylla**. All these species can be assigned to the *Pseudevernion* — an epiphytic alliance characteristic of acidic substrates (James et al. 1977). The general trend exhibited by the acidophytes accords well with the earlier findings of Goward and Arsenault (2000) (see also Table 2). One prominent exception is *Ramalina thrausta*, which would be classified as strongly acidophytic in this study, versus weakly neutrophytic in the earlier study. This species, however, appears to be rather ventilation-dependent (Wirth 1995); its distribution in the poorly ventilated stands of Goward and Arsenault (2000) probably reflects random litterfall events from conifer branches higher in the canopy.

During the course of field work, we repeatedly observed strong spatial variation in lichen community structure along the axis of most *Picea* branches. Neutrophytic lichens, if present at all, were generally restricted to the distal portions of the branches, whereas *Bryoria* and other acidophytic species occurred on the proximal portions of the same branches. We infer from this that nutrient enrichment increases in the direction of the branch tips, an observation in agreement with the "centrifugal" architecture of *Picea* (and most other conifers), in which canopy leachates should tend to be shed outwards from the trunk. In practice, however, probably only those branch segments exposed to weather are significantly enriched.

TABLE 2. Epiphytic lichens occurring on *Picea* branches, and significantly affected by the *Populus* dripzone effect in stands subject to high and low ventilation (present study and Goward and Arsenault 2000, respectively). "0" = species not present in study area; ns = no significant difference in abundance between species found within and outside the dripzone; + = abundance positively affected by the *Populus* dripzone; - = abundance negatively affected by the *Populus* dripzone; * = P<0.05, ** = P<0.01, as determined by Kruskall Wallis tests.

Species	Ventilation	
	Low	High
Bryoria capillaris	ns	-**
Bryoria fuscescens	ns	-*
Caloplaca holocarpa	0	+*
Hypogymnia austerodes	+*	ns
Hypogymnia occidentalis	-**	ns
Leptogium saturninum	+**	ns
Lobaria hallii	+*	0
Lobaria pulmonaria	+**	ns
Melanelia subaurifera	ns	+**
Nephroma resupinatum	+**	ns
Parmeliopsis ambigua	-**	ns
Parmeliopsis hyperopta	-**	ns
Platismatia glauca	-**	-**
Ramalina thrausta	ns	-*
Tuckermannopsis chlorophylla	ns	-*
Tuckermannopsis ciliaris	-**	0
Vulpicida pinastri	-*	0

The *Lobarion* versus the *Xanthorion*

When the results of this study are compared with data from the earlier study of Goward and Arsenault (2000), *Platismatia glauca* emerges as the only species shared by both studies that exhibits a significant (in this case negative) correlation with the *Populus* dripzone (Table 2). Nevertheless, a broad consistency in species response does exist. For example, members of the *Lobarion* (i.e., *Leptogium*, *Lobaria*, and *Nephroma*) associate with the dripzone in both studies, though they are much more frequent in the humid, poorly ventilated stands of the earlier study; presumably the drier, more ventilated conditions captured in the present study are somewhat inimical to them. Members of the *Xanthorion* (i.e., *Caloplaca*, *Melanelia*, and *Physcia*) are also favoured by the *Populus* dripzone in more xeric stands. Here it can be noted that the *Xanthorion* alliance is associated with rather dry habitats, being optimally developed, for example, in Mediterranean regions of Europe (James et al. 1977). The *Lobarion* alliance, by contrast, is restricted to moist localities, and is characteristic of rather oceanic or at least montane regions (Rose 1988; Goward and Arsenault, in preparation). Given the very different moisture requirements of these two alliances, the results reported were expected.

Alectorioid lichens

Goward (1998) has recently suggested that the microsite occurrence of *Bryoria* in high-elevation forests is controlled largely by sensitivity to prolonged wetting. Consistent with this hypothesis, *Bryoria* is poorly developed on sheltered conifer branches subject to heavy snow cover, but can be abundant on branches exposed to wind. Similar patterns are discernible also in low-elevation forests, though the microsite occurrence of *Bryoria* here is much less predictable on microclimatic grounds alone; presumably it is controlled by other environmental factors as well (Goward and Arsenault, in preparation). The present study points to a sensitivity to nutrient enrichment as an important ecological factor for at least some members of this genus.

As a rule, the bark of conifers is much more acidic than that of most hardwood trees (Barkman 1958). In this connection, it is probably not coincidental that alectorioid lichens show a strong preference for conifer bark (Brodo and Hawksworth 1977). The strong negative correlation between alectorioid abundance and nutrient-enriched *Picea* bark (Spearman rank correlation = -0.78) would seem to support this view — a conclusion further supported by the generally depauperate appearance of alectorioid thalli on nutrient-enriched *Picea* branches. *Bryoria*, for example, was repeatedly observed to be attached from the lower side of the supporting branch, having apparently lost through decay the initial point of contact on the opposing, upper side.

The negative correlation of *Alectoria sarmentosa*, *Bryoria capillaris*, and *B. fuscescens* with nutrient enrichment supports the earlier results of Goward and Arsenault (2000). In that study, however, both *A. sarmentosa* and *B. fuscescens* were significantly correlated with enrichment, whereas the only alectorioid species significantly correlated here is *B. capillaris*. Whether this reflects an actual physiological difference in the sensitivity of these species to enrichment, or whether it is an artifact of our present (rather meagre) data set is difficult to determine. In favour of the latter interpretation, both *A. sarmentosa* and *B. fuscescens* are much more abundant outside the *Populus* dripzone than within it (Table 1); nevertheless, they are simply too scarce in the present study to be included among the statistically significant species.

This study provides evidence in support of the hypothesis that the *Populus* dripzone effect can limit the small-scale occurrence of at least some alectorioid lichens. It remains to be determined whether the same phenomenon is capable of influencing alectorioid distribution at larger spatial scales as well. Here at least three questions should be explored: (1) does a *Populus* dripzone effect manifest itself on other tree species besides *Picea*; (2) might the presence of *Populus* act as a chemical barrier to alectorioid

dispersal from one conifer stand to another; and (3) could the *Populus* dripzone be partly responsible (in concert with the dripzones of other tree species!) for the patchy distribution characteristic of alectorioid lichens at lower elevations? The answers to these questions may be of some assistance in shaping future management policies pertaining to Flying Squirrels, Mountain Caribou, and other animal species dependent on a high biomass of alectorioid lichens.

Conclusions

When the results of this study are pooled with those of Goward and Arsenault (2000), at least three broad conclusions seem justified. First, depending on ambient moisture levels, the *Populus* dripzone effect promotes the colonization of *Picea* branches by members of either the *Lobarion* (humid conditions) or the *Xanthorion* (drier conditions). Second, at least some alectorioid lichens appear to be excluded by the dripzone effect. And third, the dripzone effect as a whole has potential to shed light on various critical, but often occult and therefore generally overlooked, chemical processes at work in mixed stands.

Acknowledgments

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