

**Do Whitebark Pine – Lichen Ecosystems of West
Central British Columbia Display Tipping Point
Behaviour in Response to Cumulative Stress?**

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Introduction

British Columbia is renowned for the outstanding diversity of its forest and rangeland ecosystems. The rugged topography and turbulent geological history of this province have created an exceptionally varied template of climate, soils, plant and animal life. Disturbances such as wildfires, storms, geomorphic activity, and insect and disease outbreaks act upon this template to modify the pattern of ecosystems across a landscape both in the short term (successional dynamics within an ecosystem) and over longer time periods (state shifts from one type of ecosystem to another).

Scientific research shows that the response of ecosystems to changes in environmental conditions is typically non-linear (Scheffer et al. 2001; Schneider 2004). Instead of shifting incrementally, ecosystems often display threshold-type behaviour whereby significant events serve as tipping points, precipitating a sudden switch from one state to another. The massive outbreak of mountain pine beetle (*Dendroctonus ponderosae*, hereafter MPB) that spread through British Columbia in the early 2000s provided an unparalleled opportunity to investigate such tipping point behaviour in forest ecosystems because tree mortality freed up site resources across an exceptionally wide range of spatial scales, creating a resource pulse (i.e., temporary increase in resource availability; Ostfeld and Keesing 2000, Yang et al. 2008) that could act as the impetus for ecosystem reorganization.

British Columbia's climate has warmed rapidly since the beginning of the 20th Century and it is understood that climatic warming has and will have profound effects on forest ecosystems (Taylor and Taylor 1997; Hebda 1998; Hamman and Wang 2006). It is difficult to observe the direct effects of a warming climate because they are confounded by smaller scale sources of climatic variability such as El Niño/La Niña cycles and the Pacific Decadal Oscillation (PDO). Responses to climate variability are also often non-linear with indirect or delayed effects on ecosystem dynamics (Schneider 2004; Dale et al. 2001). Most British Columbia forest ecosystems display considerable resilience or inertia and are able to recover from or adapt to many types of environmental change. Ecological resilience theory suggests that ecosystems most likely to display tipping point behaviour are those that (a) are situated near a climatic threshold, and (b) are simultaneously exposed to a variety of other stressors (Scheffer et al. 2001).

Whitebark pine (*Pinus albicaulis*) – reindeer lichen (*Cladina* spp.) ecosystems of west central British Columbia are a perfect test case for studying ecosystem resilience to cumulative change. Whitebark pine is considered a keystone species in the subalpine forests of western North America because the pine's large, oil-rich seeds (pine nuts) form the base of a complex subalpine food-web that supports grizzly bears and many smaller species, including red squirrels and Clark's nutcrackers that harvest, cache and disperse the seed (Tomback et al. 2002). Unfortunately, whitebark pine is dying throughout its range from the double-barreled threat of the indigenous MPB, which attacks large trees, and the alien white pine blister rust fungus (*Cronartium ribicola*, hereafter WPBR) which kills both small and large trees (Campbell and Antos 2000, Zeglen 2002). Climatic warming increases the risk from these agents at high elevations (Logan and Powell 2001). Since whitebark pine regenerates and grows best in open conditions following wildfires, it is also vulnerable to environmental changes such as fire suppression that reduce wildfire frequency in subalpine forests. In response to these multiple threats, the B.C. Conservation Data Centre recently blue-listed both the whitebark pine tree species and all whitebark pine-dominated ecological communities throughout British Columbia (CDC 2008; Charleson and Campbell 2008).

The whitebark pine-dominated ecosystems of west central British Columbia lie at the northwest limit of the tree's range on the remote, unroaded eastern slopes and foothills of the Coast Mountain Range south of the Skeena River. These dry, open forests have distinctive white carpets of *Cladina* (reindeer) lichens and are hotspots of biodiversity and biocomplexity within a forest landscape that is dominated by dense, often monospecific stands of subalpine fir with shaded mossy understories (Fig 1). Reindeer lichen-dominated forest understories are

a characteristic feature of boreal forests, but rarely occur at temperate latitudes, making them a potential bellwether of global warming. Thus, the peripheral nature of both the whitebark pine overstory and the lichen understory as well as the multiple stresses they face, makes these Whitebark pine – *Cladina* lichen ecosystems ideal candidates for studying tipping point behaviour in forest ecosystems, while also permitting us to gather basic information on an understudied, but highly threatened ecosystem.

Our recent research in MPB-affected lodgepole pine-*Cladina* lichen ecosystems of central BC indicates that MPB mortality releases a pulse of resources to the understory plant community that results in losses of reindeer lichens and increases in understory tree, shrub and moss growth (Cichowski et al. 2008). These lodgepole pine forest studies had a 6 year time frame. In the current study, we were interested to see how a similar phenomenon might play out over a longer (30 yr) time period in more vulnerable whitebark pine ecosystems exposed to additional stresses and situated closer to a climatic threshold.

This report presents the results of a preliminary analysis of our 2007 study. A more in-depth study is currently underway with results being prepared for submission to a refereed scientific journal, thus we do not present detailed statistical, dendrochronological or vegetation analyses here.

Objectives and Hypotheses

Our objective was to use low elevation, peripheral occurrences of a blue-listed Whitebark pine - *Cladina* lichen-dominated ecological community in the moist cool Engelmann Spruce-Subalpine Fir biogeoclimatic subzone (ESSFmk/02 and /03 site series, Banner et al. 1993) of west central British Columbia as a model system to study how non-linear ecosystem shifts may occur in response to cumulative stress associated with insects, diseases, wildfire and climate and to demonstrate that such shifts can result in a loss of ecosystem diversity.

Hypotheses:

- (1) We hypothesized that a generally warmer, milder and wetter climate has prevailed in the ESSFmk subzone of west central British Columbia since the mid-1970s as a combined result of global warming (Murdock 2007) and the 1976/1977 shift in the PDO (Mantua et al. 1997, Gedalof and Smith 2001) from a dominantly negative (cool) phase (1947 to 1976) to a dominantly positive (warm) phase (1977 to 2000+).
- (2) Reindeer lichen-dominated forest plant communities are associated with cold, dry soil conditions in northern and central B.C. and are rare to the west and to the south of the study area where climates are wetter and/or warmer (Meidinger and Pojar 1991). We hypothesized that changes in climatic conditions in the study area since the mid-1970s (Hypothesis 1) have caused dry Whitebark pine - *Cladina* lichen-dominated ecological communities (ESSFmk/02 and /03) to shift to a more common submesic to mesic Subalpine fir-(Mountain hemlock)-Moss ecological community (ESSFmk/01), resulting in reduced ecosystem diversity in the ESSFmk landscape.
- (3) We anticipate that in old-growth ESSFmk forests, the shift in ecosystem states to a more mesic condition (Hypothesis 2) was precipitated by cumulative whitebark pine mortality from WPBR and MPB that freed up light, water and soil nutrients to shade-tolerant subcanopy trees and understory plants. We therefore hypothesized that the shift will be more evident on old growth forest sites that experienced one or more localized MPB outbreaks between 1977 and 2000 (i.e., several resource pulses) than on sites subject to MPB attack only after 2000 (i.e., a single, recent resource pulse).
- (4) A stand-destroying wildfire can be expected to produce a more intense pulse of nutrient, water and light availability than an MPB outbreak (cf. Wan et al. 2001 to Lovett et al. 2002). We therefore hypothesized that in young ESSFmk forests burned by wildfires since the mid-1970s, drier than mesic sites will have regenerated directly to a Subalpine fir-Mountain hemlock-Moss (ESSFmk/01) ecological community rather than to a Whitebark pine-*Cladina* Lichen (ESSFmk/02 or /03) ecological community due to the combined effects of the post-fire resource pulse, a warmer, wetter climate (Hypothesis 1), poor whitebark pine seed crops and high levels of blister rust-induced tree death.



Figure 1. Open whitebark pine woodlands(dashed outline) with their white carpets of reindeer lichen (inset photo) are a striking feature of the ESSFmk landscape. These rare ecosystems are not found west (CWHws/MHmm subzones) or south (ESSFmw) of the ESSFmk, and are therefore believed to be vulnerable to climate change, especially when combined with changes in the disturbance regime.

Methods

Old Growth and Young Wildfire Study Sites

We assembled ecosystem description data on old growth Whitebark pine-dominated ecosystems within the moist cool subzone of the Engelmann Spruce – Subalpine Fir biogeoclimatic zone (ESSFmk; Meidinger and Pojar 1991) that were collected in west central British Columbia as part of the biogeoclimatic ecosystem classification (BEC) sampling program in the late 1970s and early 1980s. From this dataset, we selected two BEC plots representing old growth ESSFmk/02 site series and two representing old growth ESSFmk/03 site series for resampling (Table 1(a)).

Table 1. Study site description (site series from Banner et al. 1993)

| Site | Sample Yr | Latitude (N) | Longitude (W) | Elev. (m) | Site Series | Parent Material |
|---------------------------------------|-----------------|--------------|---------------|-----------|-------------|-----------------|
| (a) Old Growth Whitebark Pine Stands: | | | | | | |
| Burnie | 1978, 2007 | 54° 09' 54" | 127° 48' 43" | 831 | ESSFmk/02b | glacio-fluvial |
| Kidprice | 1985, 2007 | 53° 54' 44" | 127° 29' 35" | 987 | ESSFmk/02b | glacio-fluvial |
| Laventie | 1980, 2007 | 53° 37' 06" | 127° 31' 34" | 1026 | ESSFmk/03 | morainal |
| Bergeland | 1978, 2007 | 53° 48' 57" | 127° 31' 55" | 1017 | ESSFmk/03 | morainal |
| (b) Young Wildfire-Origin Stands: | | | | | | |
| Clore (33 yr) | 2007 | 54° 09' 03" | 127° 49' 25" | 855 | ESSFmk/03 | morainal |
| McKendrick (40 yr) | 1996-2000, 2007 | 54° 45' | 126° 45' | 1100 | ESSFmc/03 | morainal |

Two wildfire-origin stands less than 40 years of age were located in the Clore Canyon wildfire, 1.75 km south of the Burnie old growth site, and at McKendrick Pass, 30 km east of Smithers (Table 1(b)). Clore (ESSFmk/03) was an unreported wildfire that had never before been sampled, but which had large whitebark pine snags, evident from the air. McKendrick was located on an /03 site series in the ESSFmc subzone, 100-150 km northeast of the ESSFmk study sites in a juvenile stand that established following a ~1966 wildfire as a mixture of subalpine fir, whitebark pine, lodgepole pine and hybrid white x Engelmann spruce (*Picea glauca* x *engelmannii*). This wildfire site was of interest because a WPBR monitoring study was established there in 1996.

Field Methods

Using aerial and ground photos, we attempted to relocate the original sample plots and soil pits. In each relocated plot, we described site, soil, and organic layer characteristics and recorded vegetation percent cover by species and layer, tree mensuration data and noted wildlife activity using the standard provincial methodology (Province of British Columbia 1998), which conforms closely to the methods used in the original 1978-1985 BEC inventory.

One sample of each mineral soil horizon and the FH organic layer was collected for analysis. Mensuration data were collected on two circular prism plots. The location of the soil pit and the two prism plot centres were recorded using GPS and metal stakes. Vertical and oblique ground photos were taken at each plot stake.

At the Burnie River old growth stand (Burnie, Table 1), we established three side-by-side stand reconstruction plots. Metal stakes were located at the point of commencement (POC) and point of termination (POT) of three 100 m transects located in the centre of each 10 m x 100 m plot. Locations were recorded using GPS and oblique and vertical photos were taken as above. Vegetation and coarse woody debris percent cover by species was recorded along each 100 m transect using the line intercept method (Habitat Monitoring Committee 1996).

At Clore, we found two uniform areas of subxeric to submesic ESSFmk/03 with a high concentration of whitebark pine snags and coarse woody debris on rapidly drained ridge crests. We located one 10 m x 100 m stand reconstruction plot on a ridge, and two side-by-side plots on a second ridge 50 m north of the first plot. Linear transects were staked, photographed and sampled as above.

Within all old growth and young wildfire stand reconstruction plots, we tagged, numbered and took two increment cores, close to ground level, on all live and dead whitebark pine, lodgepole pine and western hemlock trees (plus all mountain hemlock and black cottonwood at Clore) with diameter at breast height (DBH) greater than 5 cm. For subalpine fir (plus mountain hemlock at Burnie), we tagged and numbered every tree and cored every fourth tree within 2 randomly selected 10 m x 20 m subplots within each plot. At Burnie, we also sampled sound, fallen logs rooted within the plot with DBH > 5 cm.

We mapped the location of each tagged tree and recorded its diameter, height and condition following the Whitebark Pine Ecosystem Foundation guidelines (Tomback et al. 2005). Seedlings and saplings < 5 cm dbh were subdivided into 5 height classes (< 10 cm, 10 – 30 cm, 30 – 70 cm, 70 – 130 cm, > 130 cm). In each 10 m x 20 m subplot (see above) we counted the number of trees within each height class and destructively sampled 2 trees per height class per species to obtain a stem cross-section at the root collar for dendrochronological analysis. For uncommon species, we searched the entire plot to obtain 2 trees per height class.

At Burnie, we located, cored and recorded mensuration data from 9 live dominant whitebark pine trees, 3 live lodgepole pine trees and one co-dominant subalpine fir tree outside the plots but within the same ecosystem and stand for cross-dating purposes. At Clore, we located, cored and recorded mensuration data from all live whitebark pine stems within a 3.5 ha area surrounding the sample plots.

For whitebark pine saplings and seedlings that grew within a well defined clump (i.e., from a single cone or cache), we sampled just one core or basal disk per clump and assigned the same age to all trees within the clump.

Tree cores and basal disks were mounted and sanded following Stokes and Smiley (1996). Of the two cores taken from each tree, the core with the most easily datable tree rings was used for dendrochronological analyses. Tree rings were measured and assigned dates and statistical crossdating methods (COFECHA, Grissino-Mayer 2001) were used to verify tree ring dates. For cores that missed the pith, Duncan's (1989) method was used to estimate the number of missing rings.

At McKendrick, 119 whitebark pine trees were tagged and numbered in 1996 and tree height, diameter and health were monitored annually until 2000. Active WPBR cankers were manually removed from 1996 to 2006. The site was re-inventoried in June 2007 but no blister rust canker removal has been carried out since 2000. McKendrick has a colder, more continental climate than the ESSFmk and lacks hemlock. It also has a dominantly mesic to submesic moisture regime on moderately textured glacial till parent materials and is succeeding directly to a *Vaccinium* and feathermoss-dominated understory community without going through an

extended *Cladina* lichen-dominated stage. Thus the site is not directly comparable to our ESSFmk study sites but was included to provide information on WPBR mortality rates in young stands.

Data Analysis

We used the ClimateBC ver. 3.1 model (Wang et al. 2006) to estimate climatic data for the four old growth stands from 1947 to 2000. ClimateBC interpolates data for sites without climatic records using data from long- and short-term climatic stations to 2000 only. We compared the mean annual value of each estimated climatic variable during the 1947-to-1976 cool PDO phase interval to that for the 1977-to-2000 warm PDO phase interval at each site, and calculated the mean and standard deviation for all four sites combined.

We tested for significant differences in basal area or percent cover for major plant species and functional group (e.g., shade tolerant conifers, Ericaceous species, terricolous lichens, forest floor bryophytes) and tested the hypothesis that the original value was greater than or less than the 2007 value using a one-sided paired t-test.

The root collar age of trees cored or cut above the root collar was estimated by developing a regression equation that predicts age by species from height and diameter data for all trees that were sampled at the root collar ($r^2 = 0.74$). For the simplified stand dynamics diagrams presented in this research report, we used core height ages rather than root collar ages since both methods introduce a source of error (Niklasson 2002).

Results

Climatic Changes at Old Growth Study Sites

Differences in climatic regimes before and after the 1976/1977 PDO phase shift were similar at all four old growth sites and are summarized together (Table 2). Since 1977, the winters have been markedly warmer with 10% less precipitation while the summers have been milder with a 26 % longer frost free period and 2 % more precipitation than during the 1947-1976 cold PDO interval. The increases in temperature were substantial and consistent, whereas changes in precipitation were of lesser magnitude with greater interannual variability.

Table 2. Climatic conditions at the old growth study sites before and after the 1976/77 PDO regime shift as estimated by ClimateBC v. 3.1 (Wang et al. 2006). Values are the mean (\pm 1 standard deviation) of the four study sites.

| Time Period | Mean Annual Temperature (°C) | Mean Degree Days <0°C | Mean Degree Days >5°C | Frost Free Period (days) | Mean Annual Precipitation (mm) | Mean Summer Precipitation (mm) | Precipitation as Snow (mm) |
|----------------|------------------------------|-----------------------|-----------------------|--------------------------|--------------------------------|--------------------------------|----------------------------|
| 1947 – 1976 | 1.5 (0.5) | 995 (64) | 634 (101) | 54 (12) | 1639 (436) | 394 (59) | 825 (244) |
| 1977 - 2000 | 2.3 (0.5) | 832 (63) | 713 (111) | 68 (11) | 1613 (412) | 402 (57) | 745 (214) |
| Difference | 0.8 | -163 | 79 | 14 | -26 | 8 | -80 |
| Percent change | - | -16% | 12% | 26% | -2% | 2% | -10% |

Forest Health in Old-Growth Stands

At Bergeland and Laventie we located the 1978/1985 BEC plots to within 1-5 meters. The 1978 soil pit was still clearly visible at Bergeland. At Burnie and Kidprice we were unable to relocate the soil pits and vegetation plots because the terrain and vegetation on these large glacio-fluvial landforms was very homogeneous. However, because of the high degree of homogeneity, we are comfortable that the resampled soil and vegetation plots provide close approximations of the ecosystem that was originally sampled.

Most large whitebark pine trees were dead. Mortality averaged 81% of total whitebark pine basal area and ranged from 56 % at Kidprice where the stand was highly irregular, to 100 % at Laventie where there had been a single overstory cohort of large pine (Table 3a). At Laventie, all pines died in the recent MPB epidemic, whereas at Burnie most mortality occurred during a localized MPB outbreak between 1988 and 1994, with a few large trees dying in the 1950s and 1960s of non-MPB causes (Table 3a, Figs. 2-3). Bergeland and Kidprice were intermediate. The few remaining large trees at Burnie were in the green attack stage in 2007, whereas the other sites were attacked earlier (est. 2004 – 2006) and were mostly in the red attack stage in 2007. We discovered that whitebark pine snags shed their bark and deteriorate very slowly. It wasn't possible to visually differentiate trees killed in the 1990s from those that died in the 1950s and 1960s.

White pine blister rust was abundant on whitebark trees, saplings and seedlings, and most trees were also scarred from small mammal chewing on the WPBR cankers. At Burnie, 75 % of live trees had visible WPBR cankers and 33 % of dead trees were deemed to have died as a result of WPBR infection.

Other major tree species present included lodgepole pine (13 ± 13 % of total basal area), subalpine fir (7 ± 6 %) and mountain hemlock (9 ± 8 %). These trees were also mostly unhealthy (Table 3b). Lodgepole pine had heavy MPB mortality (85 % of basal area). Many subalpine fir were dead from balsam bark beetle (*Dryocoetes confusus*) and stem decay (46% of basal area), and most live firs were in poor health (chlorotic foliage, dead tops and branches). Mountain hemlock had healthy green foliage, but were small-statured (≤ 6 m tall

at 50-100 years breast height age) and formed krummholz-like thickets through layering, rather than growing upward into the tree canopy. Dying mountain hemlock trees were rare at all sites. Western hemlock (*Tsuga heterophylla*) saplings were scattered at Burnie and Bergeland but did not appear in the tree layer. Spruce (*Picea*) were absent.

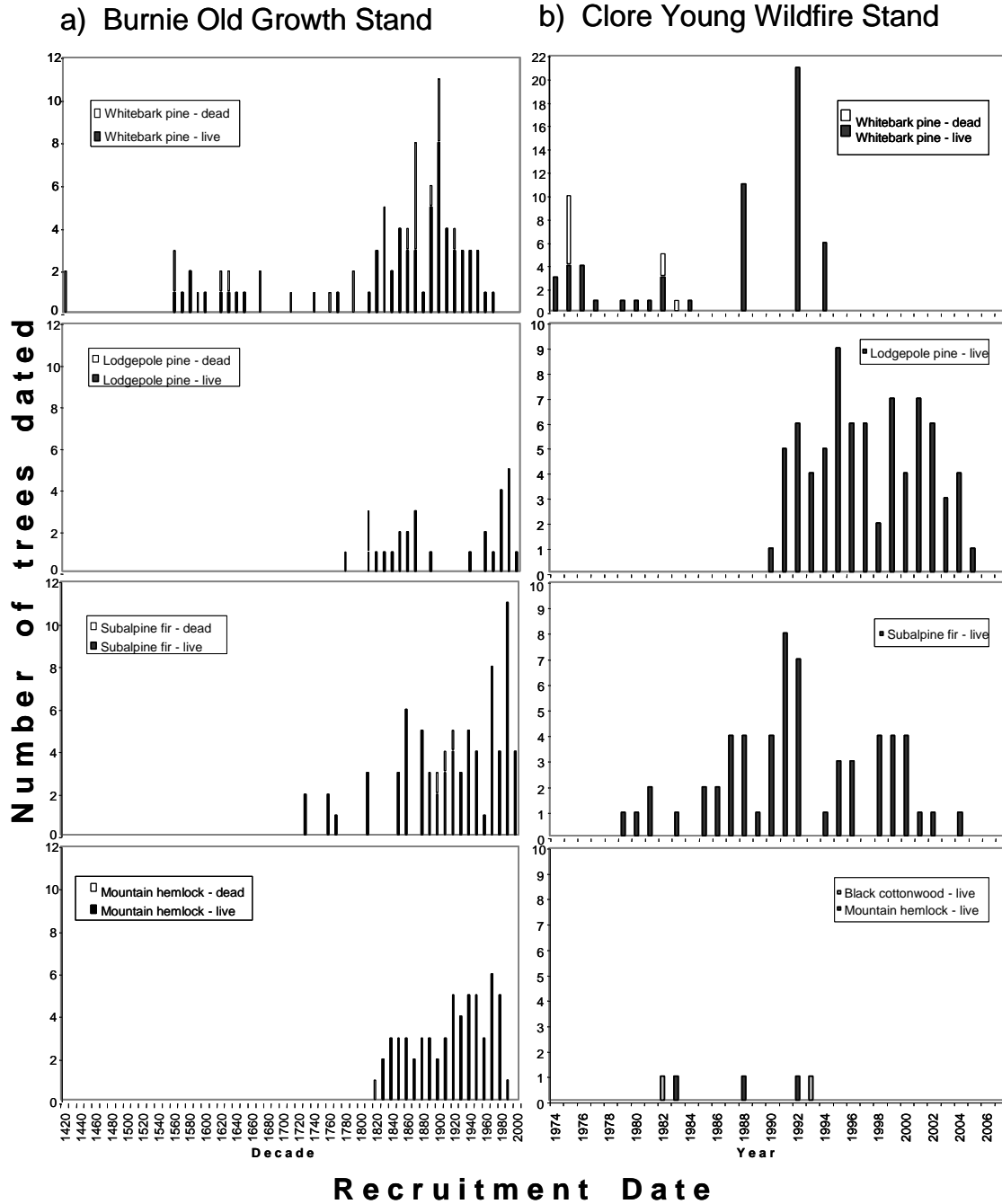


Figure 2. Recruitment dates by species for cored trees at (a) Burnie old growth stand and (b) Clore wildfire stand.

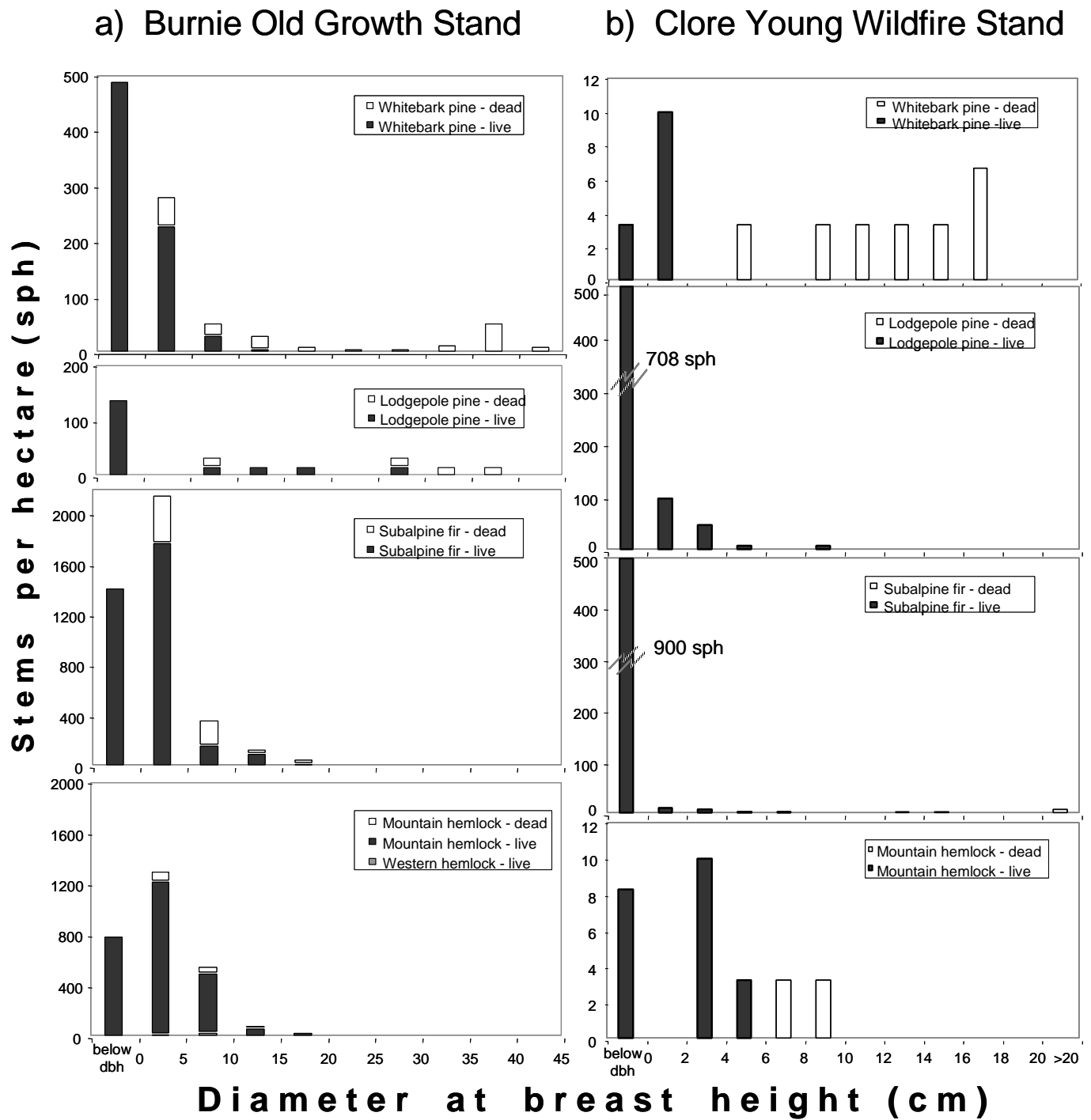


Figure 3. Diameter distributions by tree species at (a) Burnie old growth stand and (b) Clore wildfire stand.

Vegetation Changes in Old-Growth Stands

Although all old growth stands experienced a substantial biomass reallocation from overstory pine to subcanopy and understory vegetation layers between the original inventory and 2007, there was no unidirectional, statistically significant shift towards a mesic or zonal Subalpine fir – Mountain hemlock – Moss plant community (Table 4).

Percent cover of shade tolerant subalpine fir and hemlock increased by 27 – 31 % at Burnie and Bergeland, but decreased by 2 – 32 % at Kidprice and Laventie. Black huckleberry (*Vaccinium membranaceum*) and other Ericaceous species characteristic of mesic sites (*V. ovalifolium*, *Menziesia ferruginea*) increased 9 % ($p = 0.032$), but some sites had higher cover of non-mesophytic dwarf Ericaceous species in 2007 than previously while others had lower cover. Mesic herbs such as *Cornus canadensis*, *Rubus pedatus* and *Orthilia secunda* were essentially absent at all sites.

Contrary to expectations, there was no across-the-board increase in feathermosses or bryophytes (mosses + liverworts) at the expense of lichens ($p > 0.50$). Laventie and Bergeland (both ESSFmk/03 site series with predominantly recent MPB mortality) experienced 5 – 13 % increases in feathermosses and 30 % declines in lichens, whereas Burnie and Kidprice (both ESSFmk/02 site series with greater pre-2000 pine mortality) experienced a near-doubling of lichen cover and no increase in feathermosses or total bryophytes (Table 4).

We were unable to show that the shift towards mesic site vegetation was correlated with the amount of MPB mortality prior to 2000 (Hypothesis 3). The best correlations were with the total basal area of dead pine (whitebark + lodgepole). The total cover of mesophytic vegetation and total cover of non-pine vegetation were significantly positively correlated with the amount of dead pine ($p \leq 0.04$), but no individual plant functional group was positively correlated with the degree or timing of MPB (Table 4).

Table 3. Old growth stand composition in 2007 and at the time of the original BEC inventory, expressed as the basal area (m²/ha or %) of live and dead trees.

| Site | 2007 inventory | | | | Original (1978-1985) inventory | | | |
|-----------|---------------------------------|---------------------|----------------------|--------------------------------------|---------------------------------|---------------------|----------------------|--------------------------------------|
| | basal area (m ² /ha) | | | % of total whitebark pine basal area | basal area (m ² /ha) | | | % of total whitebark pine basal area |
| | Live Whitebark pine | Dead Whitebark pine | Total Whitebark pine | | Live Whitebark pine | Dead Whitebark pine | Total Whitebark pine | |
| Burnie | 0 | 10 | 10 | 97 | 0 | 97 | 3 | |
| Kidprice | 8 | 10 | 18 | 11 | 44 | 56 | 44 | |
| Laventie | 0 | 4 | 4 | 0 | 100 | 100 | 0 | |
| Bergeland | 6 | 16 | 22 | 27 | 45 | 73 | 27 | no data |
| Mean | 4 | 10 | 13 | 34 | 47 | 81 | 19 | 0 |
| Std dev | 4 | 5 | 8 | 43 | 41 | 21 | 21 | 0 |

| Site | 2007 inventory | | | | Original (1978-1985) inventory | | | |
|-----------|---------------------------------|--------------------|-----------------------|-------------------------------------|---------------------------------|---------------------|--------------------|--------------------------------|
| | basal area (m ² /ha) | | | % of total standing tree basal area | basal area (m ² /ha) | | | % of total standing basal area |
| | Live Lodgepole pine | Live Subalpine fir | Live Mountain hemlock | | Live Lodgepole pine | Dead Lodgepole pine | Live Subalpine fir | |
| Burnie | 1 | 8 | 11 | 3 | 14 | 8 | 5 | 11 |
| Kidprice | 2 | 0 | 2 | 7 | 21 | 0 | 0 | 2 |
| Laventie | 0 | 0 | 20 | 0 | 0 | 0 | 4 | 20 |
| Bergeland | 0 | 10 | 0 | 0 | 6 | 10 | 0 | 0 |
| Mean | 1 | 5 | 8 | 3 | 10 | 5 | 2 | 8 |
| Std dev | 1 | 5 | 9 | 3 | 9 | 5 | 3 | 9 |

*includes total whitebark pine basal area from (a).

Table 4. Old growth vegetation composition. P-values are for paired, one-sided t-tests based on the hypothesized change in vegetation to mesophytic conditions. Statistically significant mean differences, correlation coefficients (r) and p-values are highlighted.

| Species or Species Group | Percent Cover by Species or Species Group | | | | | | | | Change in % Cover | | | Correlation with basal area of dead pine | |
|--------------------------------------|---|------|----------|------|----------|------|-----------|------|-------------------|-----------|-------------------|--|--------------|
| | Burnie | | Kidprice | | Laventie | | Bergeland | | Mean | Std. Dev. | p-value | r | p-value |
| | 2007 | 1978 | 2007 | 1985 | 2007 | 1980 | 2007 | 1978 | | | | | |
| Whitebark pine | 3 | 29 | 17 | 25 | 0 | 16 | 17 | 37 | -18 | 8 | 0.009 | -0.15 | 0.85 |
| Lodgepole pine | 18 | 6 | 12 | 20 | 0 | 0 | 0 | 0* | 1 | 8 | 0.59 | 0.05 | 0.95 |
| All pine | 21 | 35 | 29 | 45 | 0 | 16 | 17 | 37 | -17 | 3 | < 0.001 | -0.28 | 0.72 |
| Subalpine fir | 27 | 22 | 18 | 27 | 2 | 33 | 41 | 13 | -2 | 25 | 0.55 | 0.86 | 0.14 |
| Mountain hemlock | 27 | 9 | 10 | 3 | 78 | 79 | 5 | 2 | 7 | 8 | 0.099 | 0.53 | 0.47 |
| All shade tolerant conifers | 59 | 32 | 28 | 30 | 80 | 112 | 46 | 15 | 6 | 29 | 0.36 | 0.90 | 0.11 |
| Black huckleberry | 20 | 15 | 25 | 8 | 20 | 12 | 35 | 12 | 13 | 8 | 0.025 | 0.53 | 0.47 |
| All mesophytic Ericaceous species | 20 | 16 | 25 | 8 | 23 | 15 | 47 | 42 | 9 | 6 | 0.032 | 0.00 | 1.00 |
| All Ericaceous (tall + dwarf shrubs) | 25 | 35 | 38 | 29 | 23 | 15 | 50 | 44 | 3 | 9 | 0.26 | -0.29 | 0.72 |
| All mesophytic Vascular plants | 79 | 48 | 53 | 38 | 103 | 127 | 93 | 57 | 15 | 27 | 0.18 | 0.964 | 0.031 |
| All non-pine vascular plants | 84 | 67 | 67 | 63 | 103 | 126 | 96 | 60 | 9 | 25 | 0.27 | 0.91 | 0.09 |
| Feathermosses | 41 | 51 | 10 | 26 | 50 | 45 | 35 | 22 | -2 | 13 | 0.61 | -0.21 | 0.80 |
| All bryophytes | 55 | 54 | 28 | 41 | 57 | 66 | 50 | 29 | 0 | 15 | 0.50 | 0.52 | 0.48 |
| Lichens | 44 | 23 | 62 | 36 | 10 | 15 | 29 | 42 | 7 | 19 | 0.75 | 0.28 | 0.72 |
| Bryophytes + Lichens | 99 | 76 | 90 | 77 | 67 | 81 | 79 | 71 | 8 | 16 | 0.20 | 0.86 | 0.15 |
| All shrubs, bryophytes & lichens | 124 | 111 | 128 | 106 | 90 | 96 | 129 | 115 | 11 | 12 | 0.084 | 0.91 | 0.09 |
| All non-pine vegetation | 183 | 143 | 157 | 140 | 170 | 207 | 175 | 131 | 16 | 37 | 0.23 | 0.963 | 0.037 |

*Lodgepole pine in this plot (recently dead in 2007) were apparently mistaken for whitebark pine in 1978

Old Growth Stand Dynamics

Burnie and Kidprice had charred basal scars on some of the largest, oldest pine trees (400-500+ years old), while Laventie had several scarred mountain hemlock trees (ca. 300-350 years old), indicating that these sites had experienced a partial fire. No fire scarred veterans were found at Bergeland, where the oldest trees were 320 years old, but charcoal was present.

The stand reconstruction at Burnie (Figs. 2a, 3a) shows a wave of tree regeneration beginning around 1810, which suggests a wildfire. All four major tree species had irregular age distributions with saplings and seedlings present in the understory of the stand, although lodgepole pine had a distinctly bimodal age distribution and the lowest seedling density (138 sph, compared to 500 – 1400 sph for the other species). The 'seedlings' ranged in age from 2 to 173 years old. Subalpine fir and mountain hemlock had small diameters (< 20 cm dbh) and were not found in the upper tree canopy, despite their advanced age.

Young Wildfire Stand Dynamics

The Clore wildfire was a severe, stand-destroying wildfire that exposed much bedrock and left behind few live trees (none within our study area) (Fig 4). There was no record of the fire on the BC provincial wildfire database, but we determined that it may have occurred in 1974, a year with an active fire season in west central B.C. (John Parminter, BC Ministry of Forest and Range fire ecologist, pers. comm., Oct. 2007), which is close to the age of the oldest live tree found (Fig. 2b). Based on the composition of standing snags (Fig. 3b) and fallen logs (data not shown), pre-fire stand composition of the study plot was similar to that of Burnie in 1978 (Table 3), with abundant large and smaller whitebark pine, scattered lodgepole pine, and frequent subalpine fir and mountain hemlock in smaller diameter classes. Several very large whitebark pine snags had basal fire scars (Fig. 4 inset), indicating that this stand also had a prior history of lower severity wildfire.



Figure 4. The Clore wildfire with inset photo showing giant whitebark pine snag with a basal fire scar showing that the tree had survived an earlier wildfire. (Large photo credit S. Curtis-McLane)

Post-fire regeneration in the study plot, located approximately 300 m from the wildfire edge, occurred gradually (Fig. 2b). Whitebark pine seedlings were the first to establish, in groups of 3 to 20 seedlings derived from seed caches. Densities were extremely low, with just 3 clumps and 19 total stems per hectare. Of these stems, 50 % had active WPBR cankers, 22 % had inactive cankers and 27 % were rust-free. No whitebark pine seedlings established after 1995, but a few of the largest saplings in the stand (5 – 7 m tall) bore cones in 2007 and Clark's Nutcrackers were actively harvesting whitebark pine seeds during September fieldwork.

Subalpine fir and lodgepole pine were the most abundant trees at Clore, with 937 and 892 stems per hectare, respectively, although 96 % and 79 % of these stems were less than 1.3 m tall (Fig. 3b). Much of the subalpine fir, and all of the cored lodgepole pine (Fig 2b) apparently became established as a second cohort in the 1990s, after the sparse, initial post-fire cohort began to produce seed. The subalpine fir, unlike those in the old growth stands, appeared healthy, although slow-growing. Mountain hemlock (21 sph), black cottonwood (9 sph) and western hemlock (3 sph) averaged 2-4 m in height and 12-30 years of age.

Rate of WPBR Mortality in Young Wildfire-Origin Stands

At the 40-year old McKendrick wildfire, 49 % of the 119 live trees flagged in 1996 were either dead or missing by 2007, and 11 % were healthy and rust-free. Forty-nine percent of the remaining live trees had active blister rust cankers while 30 % had small mammal damage, inactive cankers and various other insect and disease symptoms. The rate of tree mortality gave an almost perfect fit to a quadratic function which estimates that in the first year of the study, the mortality rate was 10 % per year, but thereafter the rate of mortality fell by 0.44% per year ($r^2 = 0.998$, Fig. 4).

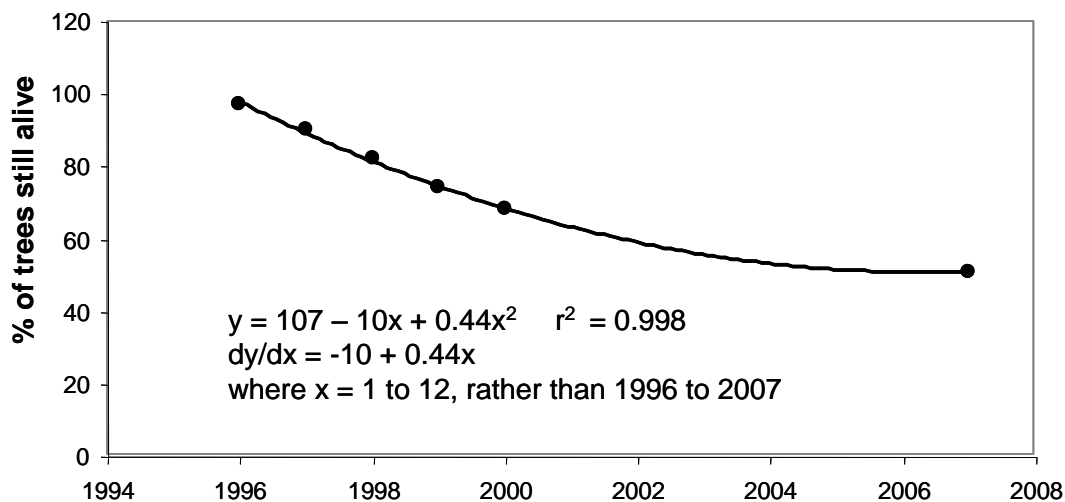


Figure 5. Whitebark pine mortality at McKendrick (1996 – 2007).

The first cone-bearing whitebark pine trees at McKendrick were observed in 2000. In 2007 one 6 m-tall, rust-resistant tree produced approximately 20 cones.

Discussion

Our first hypothesis, that the climate at our ESSFmk study sites was substantially warmer and wetter from 1977 to 2007 (PDO positive/warm phase) than from 1947 to 1976 (PDO negative/cold phase) was at least partly correct. Temperatures were substantially higher, with warmer winters and much longer frost-free periods; however, there was no clear evidence that the climate was wetter. Anecdotal information and climate data from surrounding communities such as Smithers, Terrace and Kitimat and river peak flow records suggest that post-1977 had lower and less variable snowpacks in winter and more cool, cloudy weather with fewer heat waves in summer than pre-1977. We will need to do month-by-month analyses using updated model estimates and other climatic records to assess whether the post-1977 precipitation and evapo-transpirative regime would favor the growth of mountain hemlock and subalpine fir over the more drought-tolerant pines, and favor huckleberries and moss over lichens. Detailed tree ring analysis can also be used to correlate tree growth rates at our site with the ClimateBC estimates.

Our second and third hypotheses, that we would observe a shift from a dry Pine-Lichen dominated ecological community towards a mesic Subalpine fir – Mountain hemlock – Huckleberry – Moss dominated ecological community, and that this shift would be most evident on sites that had experienced the greatest pre-2000s MPB mortality were not supported by the data. Although overstory pine died at all four sites, there was no universal understory response and differences in the response were not clearly correlated with the degree or timing of MPB attack.

There are four possible explanations for the lack of a unilateral statistically significant vegetation response: (1) Large sampling error due to our small sample size ($n = 4$) and imperfect relocation of plots could either mask trends or create spurious trends. (2) Short-term or cyclic fluctuations in shrub, moss and lichen cover may have obscured longer-term directional trends. For example, Sedia and Ehrenfeld (2003) and Frego (2007) have indicated that large interannual variability in understory vegetation cover can occur even when vegetation is undisturbed. Moreover, short-term responses to the recent MPB outbreak can be large and unsynchronized (Cichowski et al. 2008) and could be masking longer term climatically-driven trends. (3) Perhaps there is no long-term directional change in the vegetation and the data correctly show a wide variability in response due to variability in micro- to macro-scale site factors. (4) It appears possible that the xeric to subxeric glacio-fluvial ESSFmc/02 sites (Burnie and Kidprice) are responding in a fundamentally different way from the submesic morainal ESSFmc/03 sites (Laventie and Kidprice) to the same environmental changes. A larger sample with increased sub-sampling per site that includes all existing ESSFmk/02, ESSFmk/03, ESSFmc/02 and ESSFmc/03 BEC plots with whitebark pine (Banner et al. 1993), and longer term monitoring of the understory response to the recent MPB mortality would address these possibilities.

Stand establishment data from the Clore wildfire supports our fourth hypothesis. It seems that the Clore site will develop into a low productivity subalpine fir (and mountain hemlock) - dominated forest by way of a lodgepole pine-dominated seral stage rather than becoming dominated by whitebark pine. After more than 30 years, whitebark pine stem densities are too low for this species to gain dominance of the site, and any second cohort will face competition from lodgepole pine and subalpine fir. In southern B.C., Campbell and Antos (2003) determined that where lodgepole pine established abundantly after fire, it dominated stands and limited the abundance of whitebark pine, even after the postfire lodgepole pine had largely died. Where few or no lodgepole pine established, whitebark pine dominated stands throughout most of the successional sequence. Furthermore, if the McKendrick WPBR mortality rates are representative of mortality rates at Clore, there will be a continuing loss of those few whitebark pine seedlings that have already established. The Clore vegetation transect data (not included in preliminary analysis) will provide additional support for a switch to a mesic Subalpine fir – Hemlock – Moss plant community if they show a positive spatial correlation between subalpine fir trees and *Vaccinium* and moss understories.

Conclusions and Recommendations

- There has been massive MPB mortality of mature whitebark pine in low elevation ESSFmk forests (800-1100 m) of west central BC amounting to 80-85% of whitebark pine basal area at these elevations.
- At this time, we have no evidence that blue-listed Whitebark Pine – Cladina lichen ecological communities (ESSFmk/02 & /03 site series) have reached a tipping point whereby a state shift to the much more common Subalpine fir – Mountain hemlock – Moss ecological community (ESSFmk/01) has taken place.
- We now believe that submesic ESSFmk/03 sites are shifting gradually into the zonal ESSFmk/01 stability domain whereas xeric to subxeric ESSFmk/02 sites are more resilient and are retaining distinctive vegetation and soil characteristics, albeit with much less whitebark and lodgepole pine. However, a larger sample size and additional vegetation monitoring and soils analyses are needed to confirm this.
- Low intensity wildfires appear to create and maintain the open canopies of Whitebark Pine – Lichen ecological communities and should be reintroduced to these ecosystems through prescribed fire and/or a let-burn policy to maintain subalpine biodiversity and biocomplexity.
- Wildfire alone is unlikely to restore Whitebark pine – lichen ecosystems that have been heavily affected by MPB and WPBR. Seed collections from apparently rust-resistant whitebark pine trees should begin immediately to allow restoration planting.

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