

The Date Creek Experiment: Ecology and Management of Northern Temperate Forests of British Columbia

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Location and objective: The Date Creek Research Forest (55°22'N, 127°50'W; 370-665 m elevation) is in the transitional coast-interior forests (the Interior Cedar-Hemlock zone) of northwestern British Columbia approximately 21 km north of Hazelton and west of the Kispiox River. The overall goals of the project, initiated in 1990, and its component studies were to understand ecosystem processes and functions in interior cedar-hemlock forests and to identify and promote management practices that achieve sustainability.

Background: Research sites are located in mature stands that originated from a fire in 1855 and in old-growth stands (300 yrs+ since fire). Understories in these forests are typified by sparse shrub and herb development with a continuous layer of moss, dominated by red-stemmed feather moss (*Pleurozium schreberi*), step moss (*Hylocomium splendens*), knight's plume (*Ptilium crista-castrensis*) and electrified cat's tail moss (*Rhytidiadelphus triquetrus*). Soils on mesic sites are typically Eluviated or Orthic Dystric Brunisols developed on morainal parent materials, ranging in texture from loamy sand to clay loam with 5-10 cm thick Hemimor or Mormoder forest floors. Hybridization of spruce in the study area is complex with individual trees rarely identified to species. Spruce trees are collectively called "hybrid spruce" and can be crosses of white spruce (*Picea glauca*), Sitka spruce (*P. sitchensis*) and occasionally, at higher elevations, Engelmann spruce (*P. engelmannii*). Mature stands in the study area are a stratified mixture of coniferous and deciduous tree species. Western hemlock (*Tsuga heterophylla*) dominates, with western redcedar (*Thuja plicata*), hybrid spruce, subalpine fir (*Abies lasiocarpa*), Amabilis fir (*Abies amabilis*), lodgepole pine (*Pinus contorta* var *latifolia*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and black cottonwood (*Populus balsamifera* ssp. *trichocarpa*). In the old-growth stands western hemlock dominates with minor components of western redcedar, subalpine fir and amabilis fir.

The overall experimental design has four stand structure treatments; each replicated four times, in a randomized block design (each treatment unit being about 20 ha in size). The blocking factor was a combination of stand age and ecological site type. Two levels of partial cutting were used and compared with both undisturbed forests and clearcuts. Logging took place in 1992. The intent was to create four differently structured treatments that would provide a wide variety of environmental conditions both between and within treatments. In the light partial cutting, about 30% of the stand volume was removed by cutting either single stems or small gaps (3 - 10 trees). In the heavy partial cutting, about 60% of stand volume was removed. Here, the cutting pattern used both large gaps (500 - 5000 m² in size), evenly distributed across the treatment units, and either single-tree or small gaps in the forest matrix between the larger gaps. In the clearcut treatment all stems were removed except for scattered residual deciduous trees, mostly trembling aspen and paper birch. Individual experiments were designed to operate at one or more of three scales: stand (or treatment unit); gap (from 10 to 5000 m² in size); and microsites.

In order to assess the long-term implications of both natural and human disturbance on tree community dynamics, we have parameterized the spatially-explicit mixed-species simulation model SORTIE-ND for conditions at Date Creek. We believe managed forest stands will become increasingly complex in terms of structure and tree species. There are many questions regarding stand responses to differing silvicultural strategies and interventions. The modeling component of our research program will examine the consequences of a wide range of silvicultural strategies, at different spatial scales and over different time periods, an impossible undertaking for the field-based research program.

Web Sites: Click on Date Creek at <http://www.for.gov.bc.ca/rni/research/>.

Date Creek Publications

Note: Publications are listed by year from the most recent to earliest. Many of these publications are available on line from the listed journals. Extension notes and unpublished file reports are listed at the end as well as some information about ongoing studies. Copies of all publications can be obtained from the contacts listed on page 1.

Kranabetter, J.M., S.W. Simard, R.D. Guy, K.D. Coates. 2009. *Species patterns in foliar nitrogen concentration, nitrogen content and $\delta^{13}C$ abundance for understory saplings across light gradients*. Plant Soil, in press.

Abstract: Soil nitrogen (N) supply and uptake by regenerating trees is an important ecosystem attribute but difficult to quantify in partial-cut forests where light availability varies. The foliar attributes of N concentration (N%) and N per unit area (Na) may help characterize the influence of soil nutrition, but ideally the relationship between soils and foliage would be tested separately by species across well-defined light gradients. To do this, we examined foliar attributes of four tree species across gradients of light availability in 12 year-old partially-cut forests in northwest British Columbia, Canada. There were no differences in forest floor or mineral soil N mineralization rates across the light gradients, and for western hemlock (*Tsuga heterophylla*) and hybrid white spruce (*Picea glauca* x *sitchensis*), this consistent level of soil N supply corresponded with unchanging foliar N%. In contrast, foliar N% of *Betula papyrifera* (paper birch) and *Thuja plicata* (western redcedar) declined with shading, perhaps due to shifts in root-shoot biomass allocation for *B. papyrifera*, and climatic constraints on shade tolerance for *T. plicata*. Leaf $\delta^{13}C$ approached an asymptote at approx. 40% full light for the coniferous species, but increased linearly with light for *B. papyrifera*. Foliar Na was linearly correlated with leaf $\delta^{13}C$ for three species, reflecting the dual effect of light and nutrition on photosynthesis processes, and suggesting that foliar Na may be a simple parameter to integrate both resource constraints on regenerating saplings. These results demonstrate both support for and limits to foliar attributes among species in isolating soil N effects against light constraints in partial-cut forests.

Coates K. David, Charles D. Canham, Philip T. LePage. 2009. *Above versus Belowground Competitive Effects and Responses of a Guild of Temperate Tree Species*. J. Ecol. 97:118-130.

Abstract: The neutral theory debate has highlighted the scarcity of robust empirical estimates of the magnitude of competitive effects and responses within guilds of co-occurring tree species. Our analysis quantifies the relative magnitude of all possible pairwise competitive interactions within a guild of nine co-occurring tree species in temperate forests of northern, interior British Columbia, and explicitly partitions the competitive effects of neighbours into the effects of shading versus the residual effects of “crowding”, assumed to reflect belowground competition. Models that treated neighbours as equivalent in their competitive effects were the most parsimonious for the 5 species with the smallest sample sizes. For the remaining species (samples sizes of ≥ 150 individuals), the best models estimated separate competition coefficients for all 9 species of neighbours. We take this as evidence that species do indeed differ in their competitive effects, but that there can be a minimum sample size required to discriminate between them. There was a strong size-dependency in potential growth. Six species showed an optimal growth at a size between 5 and 20 cm diameter. Potential growth declined moderately-strongly as diameter increased. Sensitivity to crowding varied as a function of tree size for 5 of the 9 species. This response was not consistent by tree size. The magnitude of reduction in growth due to crowding was greater on average than the reduction in growth due to shading, except for the two least shade tolerant conifers. Sensitivity to shading among the conifer species was correlated with their shade tolerance. The per capita effects of crowding by different species of neighbours varied widely. A large number of the estimated pairwise per capita competition coefficients were very low. The relative magnitude of the strength of intra- versus interspecific competition also varied widely among the tree species. Model selection techniques effectively separated above- and belowground competition in complex forests, and allowed us to assess differences among species in competitive effects and responses. While belowground effects were strong, they were due to proximity of neighbours from a very specific (and small) subset of strong competitors within the guild. Response to crowding varied with tree size but the nature of the relationship varied widely among the species.

Mahon, C. Lisa, Kathy Martin, Valerie LeMay. 2008. *Do cross-scale correlations confound analysis of nest selection for Chestnut-backed Chickadees? The Condor* 110(3):563–568.

Abstract: Multiscale models of nest site selection often ignore cross-scale correlations (correlations between predictor variables at different scales). We reexamined nest site selection of Chestnut-backed Chickadees (*Poecile rufescens*) at two scales within territories to isolate: (1) variation associated purely with variables measured at the patch (0.031 ha) and tree scales, and (2) variation shared by variables measured at the patch and tree scales. We used conditional (fixed-effect) logistic regression to build a patch, tree, and full model, and subtracted pure and shared components of variation from the deviance explained by the full model. Tree scale and patch scale variables accounted for 85% and 9% of the total explained variation, respectively. Only 6% of explained variation in nest site locations was due to cross-scale correlations. We suggest that multiscale habitat selection studies incorporate a diagnostic tool like variance decomposition to avoid spurious results caused by lack of independence of habitat relationships.

Mahon, C. Lisa, J. Douglas Steventon, Kathy Martin 2008. *Cavity and bark nesting bird response to partial cutting in Northern conifer forests. For. Ecol. Manage.* Vol 256 (12):2145–2153.

Abstract: We investigated whether partial cutting used to mimic small-scale natural disturbances could maintain cavity and bark nesting breeding birds. We assessed changes in the relative abundance of cavity nesting birds in two intensities of partial cutting, compared to uncut and clearcut stands, 9 years post-treatment. We then examined the relationship between forest structure and nesting abundance (stand scale) and compared characteristics of used nest and forage trees to unused trees (tree scale). The relative abundance of most species was highest in either heavy removal or light removal treatments 9 years postharvest. Brown creepers were most abundant in uncut, and red-breasted sapsuckers were most abundant in clearcut and heavy removal treatments. The proportion of deciduous trees and the density of dead trees were the best predictors of nest abundance. Individual nest tree use was predicted by the presence of large deciduous trees with broken tops and early to advanced stages of decay. Forage tree use was predicted by the presence of large conifer trees in advanced stages of decay. To maintain breeding habitat for cavity nesters, we suggest that forest managers retain the specific structural attributes required for nesting, but also the diverse forest conditions required for foraging.

Mahon, C. Lisa, Kathy Martin, J. Douglas Steventon. 2007. *Habitat attributes and Chestnut-backed Chickadee nest site selection in uncut and partial-cut forests.* Can. J. For. Res. 37:1272–1285.

Abstract: We examined the relationship between habitat attributes and nest-site selection by chestnut-backed chickadees (*Poecile rufescens* (Townsend, 1837); hereinafter chickadees) in uncut and partial-cut forests in northwest British Columbia. We described the characteristics of uncut sites and compared them with structurally modified partial-cut sites (mature and old forests). We then compared the use and selection of habitat by chickadees at uncut and partial-cut sites at three spatial scales: (1) the stand (19–24 ha uncut or partial-cut stand), (2) the nest patch (a 0.031 ha patch centered on nest trees), and (3) the nest tree. At the stand scale, we found no correlation between the density of breeding chickadees and the characteristics of uncut and partial-cut sites. At the nest-patch scale, chickadees in uncut and old partial-cut sites selected nest patches with higher densities of broken-top trees compared with available habitat within territories. At the nest-tree scale, chickadees selected nest trees with boring insects and broken tops in uncut and mature partial-cut sites and large trees with boring insects in old partial-cut sites. Our results suggest that chickadees exhibited flexibility in resource selection but also selected resources with similar attributes at the nest-patch and nest-tree scales. Managed stands that maintain a range of tree species and conditions, including live trees with areas of disease, insect attack, and damage, will provide the specific structural attributes used for nesting by weak cavity excavators such as the chickadee.

Mahon, C. Lisa & Kathy Martin. 2006. *Nest Survival of Chickadees in Managed Forests: Habitat, Predator, and Year Effects.* J. Wildlife Manage. 70(5):1257–1265

Abstract: We examined the influence of year, habitat, and predators on nest survival by monitoring 69 natural cavity nests of the chestnut-backed chickadee (*Poecile rufescens*) across a range of uncut and partial cut stands in northwest British Columbia during 2000–2003. We considered 3 spatial scales of habitat: 1) the stand (19–24 ha of uncut and partial cut stands), 2) the nest patch (a 0.03-ha patch centered on nest trees), and 3) the nest tree. At each scale we

hypothesized that nest survival time of chickadees differed among years, as a result of harvest treatment, habitat characteristics, and predator activity. Nest predation rates fluctuated among years: 56% in 2000, 64% in 2001, 10% in 2002, and 12% in 2003. We identified the red squirrel (*Tamiasciurus hudsonicus*) as the dominant nest predator. At the stand and nest patch scales, only the covariate year reliably predicted survival time: Risk $\frac{1}{4}$ 1.81 (Year 2001) for both models. At the nest tree scale, we found the most support for a model with year and nest height: Risk $\frac{1}{4}$ 1.67 (Year 2001) – 0.08 (Nest Height). All models indicated that for chickadees nesting in 2001, the probability of nest failure increased by more than 5 times. We found no effect of harvest treatment in the stand, nest patch, and nest tree models. Since squirrel density, space use, and activity near nest areas did not differ among years, we suggest that squirrels undergo a functional response and consume food items like eggs and nestlings following low mast years and cones following high mast years. Resource fluctuations that alter the availability and quality of food for red squirrels may result in strong variability in chickadee nest survival. Studies that do not consider such temporal variation may conclude that sites with low nest survival are sink habitats. Managers and researchers may need to consider longer term and/or multitrophic level studies to examine interactions among birds, their predators, and the environment.

Temesgen, H & A. R. Weiskittel. 2006. *Leaf mass per area relationships across light gradients in hybrid spruce crowns*. *Trees* 20: 522–530.

Abstract: This study examined the distribution and variation of mass to projected area ratio of foliage (LMA, g/m²) within hybrid spruce (*Picea engelmannii* Parry × *Picea glauca* (Moench) Voss × *Picea sitchensis* (Bong.) Carr) crowns across three stages of stand development (20, 60, and 140 years). Variability of LMA was assessed at different heights and branch positions. LMA decreased with distance from top of tree ($p < 0.0001$) at rates that varied among stand development stages ($p < 0.0001$). A multi-level mixed effect analysis indicated that distance from the tip of the first-order branch ($p = 0.0002$) had a significant influence on LMA. In general, LMAs decreased towards the base of the tree and increased towards tree apex. LMA differed significantly across stand development stages. Older trees (140 years) showed the highest LMA, while younger trees (20 years) showed the lowest LMA values. LMA also increased with foliage age, suggesting a developmental change in leaf area and mass with increasing foliage age. Multiple linear regression (MLR) relationships were developed to predict LMA at various positions within tree crowns. The precision of the models was slightly greater when branch position (from the apex of the tree) was described relative to tree height, rather than relative to crown length. The MLR function resulted in precise representations of LMA within tree crowns.

Walters, M.B., Lajzerowicz, C., Coates, K.D. 2006. *Soil resources and the growth and nutrition of tree seedlings near harvest gaps – forest edges in interior cedar-hemlock forests of British Columbia*. *Can. J. For. Res.* 36:62–76

Abstract: Observations of tree seedlings with chlorotic foliage and stunted growth near harvest gap-forest edges in interior cedar-hemlock forests inspired a study addressing the following questions: Near gap-forest edges: 1) do seedling foliage chemistry, foliage nitrogen (N) vs. growth relationships, and fertilizer responses suggest N limited seedling growth? 2) are patterns in soil characteristics consistent with N limitation, and can interrelationships among these characteristics infer causality? Our results suggest that seedling growth near gap-forest edges was co-limited by N and light availability. Soil mineral N and organic N (DON) concentrations, in situ net N mineralization, and water generally increased from forest to gap, whereas N mineralization from a laboratory incubation, and total N and carbon did not vary with gap-forest position. Interrelations among variables and path analysis suggest that soil water and total soil N positively affect DON concentration and N mineralization, and proximity to mature gap-edge trees negatively impacts mineral N concentration and water. Collectively, our results suggest that seedling growth-limiting soil N levels near gap edges can be partially explained by gap edge trees direct negative impacts on mineral N concentrations and their indirect impacts on N cycling via soil water, and not via effects on substrate chemistry.

Kranabetter, J.M. 2005. *Understory conifer seedling response to a gradient of root and ectomycorrhizal fungal contact*. *Can. J. Bot.* 83:638-646.

Abstract: The possible benefit of common mycorrhizal network (CMN) linkages to seedling growth was tested in a low light partial-cut forest understory. Naturally-regenerated western hemlock (*Tsuga heterophylla*) and hybrid spruce

(*Picea glauca* x *Picea sitchensis*) seedlings were transplanted directly into soil or within bags of different pore sizes to restrict the amounts of root and ectomycorrhizal contact. The 5 year study included 'full contact' (no bag), 'moderate contact' (250 μ m openings) and 'low contact' (4 μ m openings) treatments. Height increment was lowest for full contact seedlings over most of the experiment, and highest for low contact seedlings by years 4 and 5. Full contact seedlings also had slightly lower foliar N content than moderate and low contact seedlings. There were no significant interactions in growth detected between tree species and treatments, despite the higher potential for CMN linkages between a western hemlock understory and canopy. Fifty-eight ectomycorrhizal fungal morphotypes were identified on the seedlings, including many with smooth mantles or with only sparse emanating hyphae, which likely reduced the potential for CMN linkages. These results would support the more traditional concepts of competition for scarce resources by isolated seedlings as the primary interaction for the understory of these mature forests.

Canham, C.D., LePage, P., Coates, K.D. 2004. *A neighbourhood analysis of canopy tree competition: effects of shading versus crowding*. Can. J. For. Res., 34:778-787.

Abstract: Partial harvesting and all-aged management require consideration of an almost infinite variety of spatial configurations of the level of removal of different species and tree sizes within a stand, and an almost infinite variety of permutations of residual stand conditions. We have developed an extension of traditional distance-dependent, spatial competition models that allows independent estimates of (1) the potential maximum tree growth for a given set of climatic and edaphic conditions, as a function of tree species and size, and (2) the magnitude of the competitive effects of neighboring trees on target tree growth as a function of the species, size, and distance to neighboring trees. The analyses provide empirical estimates of inter- and intraspecific competition coefficients, and explicitly partition the competitive effects of neighbors into the effects of shading *versus* the residual effects of "crowding". We developed and tested the method using data from forests of northern, interior British Columbia dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* (Donn ex D. Don in Lamb). We used maximum likelihood estimation to test a suite of alternate models. For both species, the most parsimonious models included terms for (1) the effects of tree size, (2) crowding, (3) shading, and (4) separate competitive effects of 4 different groups of competing species. The models explained 33-59% of the variation in radial growth of the 2 species. Potential radial growth peaked at 34 – 40 cm DBH for the two species. For both species, growth declined more steeply as a function of crowding than shading, particularly in redcedar. There was a striking asymmetry in the strength of interspecific competition between hemlock and redcedar, with crowding by hemlock having a very strong *per capita* effect on redcedar, while crowding by redcedar had relatively little effect on the radial growth of hemlock.

Greene, David F., Charles D. Canham, K. David Coates, Philip T. LePage. 2004. *An evaluation of alternative dispersal functions for trees*. J. Ecology, 92:758-766.

Abstract: We compared three commonly-used empirical seed/seedling dispersal functions for trees (lognormal, 2Dt, and two-parameter Weibull) by analysis of published studies where the location of the source is known, as well as by inverse modeling within an old growth hardwood forest in southern Quebec. Almost all the species were wind-dispersed. For the discrete source studies, the lognormal was clearly superior, while for the inverse modelling the performance of the three dispersal functions was somewhat more even. We speculate that collisions with boles spuriously enhanced the likelihood of the 2Dt and the Weibull with inverse modeling, as both these functions assume that the greatest seed/seedling density will occur at the base of the maternal parent bole. We conclude that the lognormal function is to be preferred because, as well as providing a framework for mechanistic interpretation, it tends to provide a closer approximation to observed dispersal curves. We also argue that mean distances traveled by seed crops are far more extensive than indicated by previous studies that used the Weibull function.

Kranabetter, J.M. 2004. *Ectomycorrhizal community effects on hybrid spruce seedling growth and nutrition in clearcuts*. Can. J. Bot. 82: 983-991.

Abstract: A diverse community of ectomycorrhizal fungi is generally considered beneficial to forest ecosystems, but the function of ectomycorrhizal communities should be considered within an ecological context. The growth of hybrid spruce (*Picea glauca* x *sitchensis*) seedlings were compared after transplanting into recent clearcuts, where soil moisture and nitrogen are typically readily available. The seedlings had either a 'forest' ectomycorrhizal community

(taken from forest gap edges) or a 'pioneer' ectomycorrhizal community (taken from disturbed road edges) and were planted at wide and close spacing. After three years, there was considerable overlap in morphotype distribution and abundance (64% community similarity between 'forest' and 'pioneer' seedlings), but height growth was 25% greater for the 'pioneer' seedlings. There was a reduction in diameter at close spacing, with little difference in competition effects between ectomycorrhizal communities. There were no differences detected in foliar nitrogen concentrations, and no evidence of nitrogen or phosphorus deficiencies. The advantage of fungi such as *Amphinema byssoides*, *Thelephora terrestris* and *Laccaria laccata* might be the proliferation of fine roots that allows for the fullest utilization of abundant soil resources. The results suggest that the ectomycorrhizal communities arising after clearcut disturbances are well adapted to these initial soil conditions.

Kranabetter, J.M. & Coates, K.D. 2004. *Soil resource availability and conifer nutrition across canopy removal treatments in a northern temperate forest*. Can. J. For. Res. 34:800-809.

Abstract: Soil resource availability, especially nitrogen, was compared across canopy removal treatments created by silviculture systems (clearcut, partial-cut and unharvested forest) 9 - 10 years after harvesting in temperate western hemlock forests of northwestern British Columbia. Differences in soil properties across the canopy removal treatments were most apparent in the forest floor. Depth and C:N ratio of the forest floor had decreased slightly in clearcuts, and forest floor moisture was highest under partial-cuts. Despite these differences in soil chemistry and soil moisture, no differences were detected in mineralizable nitrogen (anaerobic incubation) nor in situ net nitrogen mineralization between treatments. Height growth and foliar mass were reduced under the low light conditions of the partial-cut, but there were no differences in foliar nitrogen concentrations of hybrid white spruce, western redcedar and western hemlock saplings. Mature western hemlock trees in the partial-cut also had concentrations of foliar nitrogen equal to mature trees in the unharvested forest. Overall, we found consistently moderate levels of nitrogen availability and comparable levels of below-ground competition for nitrogen across silviculture systems in this early stage of stand development. We conclude that light availability is the most important resource affecting tree growth across canopy openings.

Coates, K.D., Canham, C.D., Beaudet, M. Sachs, D.L., Messier, C. 2003. *Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests*. For. Ecol. Manage. Vol 186, Issue 1-3:297-310

Abstract: The discipline of silviculture is evolving rapidly, moving from an agricultural model that emphasized simple stand structures toward a natural disturbance- or ecosystem-based model where stands are managed for multiple species and complex structures. Predicting stand dynamics and future yields in mixed-species complex structured stands can not be easily accomplished with traditional field experiments. We outline the development and structure of SORTIE/BC, a descendent of the SORTIE model. SORTIE/BC is a light-mediated, spatially explicit, mixed-species forest model that makes population dynamic forecasts for juvenile and adult trees. We use the model to simulate partial cutting prescriptions in temperate deciduous, boreal and temperate coniferous mixed-species forests. The species, amount and spatial pattern of canopy tree removal had a major influence on understory light environments. Low and uniform removal of canopy trees were less successful in favouring the growth and survival of regenerating trees of intermediate to shade intolerant species and the growth of retained canopy trees than patch removal. In the boreal mixedwood, strip cutting can maintain mixed stands but careful attention must be paid to buffer and strip management to optimise stand growth. We conclude that SORTIE/BC can be very useful to explore and explain the silvicultural implications of complex silvicultural prescriptions for which there are no existing long-term experiments.

Bartemucci, Paula, Coates, K. Dave, Harper, Karen A., Wright, Elaine F. 2002. *Gap disturbances in northern old-growth forests of British Columbia, Canada*. J. Veg. Sci., 13:685-696.

Abstract. We characterized the abundance, size and spatial patterning of canopy gaps, as well as gap-forming processes and light availability in boreal, sub-boreal, northern temperate, and subalpine old-growth forests of northwestern British Columbia. The proportion of area in canopy gaps ranged from 32 % in northern temperate forests to 73 % in subalpine forests. Evenly distributed developmental gaps were dominant but permanent openings created by edaphic components and by shrub communities were also common, particularly in sub-boreal forests. Abundant gaps,

large gap sizes, high numbers of gap makers per gap, and frequent gap expansion events suggest that gaps have long tenure in these forests. Snapped stems and standing dead mortality were the most common modes of mortality in all forest types resulting in little forest floor disturbance, creating few germination sites for seedling establishment. We found high mean light levels (16-27 % full sun), and little difference between non-gap and gap light environments. Our results suggest that gap dynamics in these forests differ fundamentally from those in temperate and tropical forest ecosystems.

Coates, K.D. 2002. *Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada*. For. Ecol. Manage. 155:387-398.

Abstract: Tree seedling recruitment was monitored after various types of logging in mixed conifer and deciduous forests of northern British Columbia, Canada. Predicting tree seedling recruitment after disturbance is fundamental to understanding forest dynamics and succession and is vital for forest management purposes. Seedling recruitment success in multi-species northern latitude forests varied as a function of mature tree canopy cover, gap size and position in a gap. Recruitment was abundant within canopy gaps across a wide range of gap sizes (20 to 5000 m²), but recruit numbers dropped rapidly under the closed forest canopy and in the open conditions of clearcuts. Inside canopy gaps, recruitment was similar by gap position in small gaps (<300 m²) but, in these northern latitude forests, exhibited a trend of increasing density from the sunny north to shady south end of larger gaps. This was true for all tree species regardless of their shade tolerance ranking. There was no evidence of gap partitioning by any of the tree species during the regeneration phase, suggesting that adaptation to the subtleties of gap size during early recruitment are not well developed in these tree species. Favourable locations for emergence and early establishment of germinants were less favourable for growth and survival of established seedlings, that is, the regeneration niches in these forests were discordant. Tree abundance and species diversity appears to be controlled more by differentiation among growth and survival niches than by the regeneration niches. From the perspective of forest management, abundant natural regeneration of all the dominant tree species of these mixed-species forests can be obtained after partial cutting.

Kranabetter, J.M. & Friesen, J. 2002. *Ectomycorrhizal community structure on western hemlock seedlings transplanted from forests into openings*. Can. J. Bot., 80:861-868.

Abstract: This study tested whether mature-forest ectomycorrhizal (ECM) communities could be maintained in forest openings on seedlings. Naturally-regenerated western hemlock (*Tsuga heterophylla*) seedlings were transplanted from mature forests into openings and compared the ECM fungal community after two years with similar seedlings planted back into the forests, or seedlings from openings planted back into openings. Fewer ECM morphotypes, lower average richness per seedling, and a steeper, less even species distribution curve were found, all of which suggest the mature-forest ECM fungal community changed after transplanting forest seedlings into the openings. The increased abundance of pioneer fungi such as *Thelephora terrestris* suggested many of the mature-forest ECM fungi were unable to maintain or continue root colonization in openings. Results suggest many mature-forest ectomycorrhizal fungi require further stand development to maintain enough rooting density and hyphal contact to persist.

Kranabetter, J. M. & Kroeger, P. 2001. *Ectomycorrhizal mushroom response to partial cutting in a western hemlock-western redcedar forest*. Can. J. For. Res. 31:978-987.

Abstract: We examined epigeous ectomycorrhizal mushroom richness and productivity five years after partial cutting in a western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) - western redcedar (*Thuja plicata* Donn ex D. Don in Lamb) forest of northwestern British Columbia. Mushrooms were collected throughout the fruiting season (July to October) for three years from plots with mesic soil conditions and residual basal areas ranging from 23 m²/ha to 69 m²/ha for western hemlock, and 0 m²/ha to 26 m²/ha for western redcedar. Partial cutting had no apparent effect on mushroom phenology over the three years. Significant block interactions demonstrated that reductions in basal area of western hemlock could lead to positive, neutral and negative responses in mushroom richness, biomass and number of fruiting bodies. These responses were related to stand structure and the potential differences in tree vigour after partial cutting. In addition, there was weak evidence that western redcedar, a host for vesicular-arbuscular mycorrhiza, had a negative effect on average taxa richness. The study demonstrated that partial cutting systems could allow some timber removal without necessarily reducing ectomycorrhizal mushroom communities.

Coates, K.D. 2000. *Conifer seedling response to northern temperate forest gaps*. Forest Ecol. Manage. 127:1-3, 249-269.

Abstract: Studies of gap dynamics have contributed significantly to our understanding of the role of small-scale disturbance in forest ecosystems, but have been little used by foresters for predicting tree responses to partial cutting. Fifth year growth and survival of five commonly planted tree species were contrasted in canopy gaps (single-tree to 5000 m²), in the forest understory and in the open conditions of a clear-cut. There were strong and consistent trends in growth response among the tree species as gap size increased. Growth of all species increased rapidly from small single-tree gaps to about 1000 m² gaps, but thereafter showed little change up to 5000 m². Tree size and current growth rates for all species were highest in full open conditions. Performance of lodgepole pine (*Pinus contorta*), the most light-demanding species, exceeded that of all other species in large gaps (1001-5000 m²) and clearcuts. In large and medium gaps (301-1000 m²), the largest trees of all species were found in the middle gap position and there was little difference between the sunny north and shady south positions, except for lodgepole pine which clearly grew poorly in the south position. Total size and growth rates of all species were nearly identical in small gaps (10-300 m²) and again in the forest understory. The light advantage expected off the north end of high latitude gaps was not a benefit for tree growth, suggesting that below-ground effects of canopy edge trees have an important influence on seedling growth in these forests. Differences in mortality among the tree species were evident, with the most light demanding species having the greatest early mortality in shaded areas of medium gaps, in small gaps and in the forest understory. Careful matching of tree species to gap size and gap position can minimize early mortality and maximize growth rates. Opening sizes need not be very large (0.1-0.2 ha or larger) in order for most tree species to achieve growth rates similar to those found in the open conditions of clearcuts.

LePage, P., Canham, C.D., Coates, K.D., Bartemucci, P. 2000. *Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia*. Can. J. For. Res. 30:415-427.

Abstract: We examine the influence of (1) the spatial distribution and abundance of parent trees (as seed sources) and (2) the abundance and favourability of seedbed substrates, on seedling recruitment for the major tree species in northwestern interior cedar-hemlock forests of British Columbia, under 4 levels of canopy openness (full canopy, partial canopy, large gap, and clearcut). Substrate distribution varied with canopy openness, and substrate favourability was a function of both canopy openness and seedling species. Lack of suitable substrates was the predominant factor limiting seedling density under full canopies. Partial canopy and gap sites provided a broad range of favourable substrates in close proximity to parent trees, resulting in the highest observed seedling densities. There was much higher effective dispersion of seedlings away from parent trees in gaps than in the partially cut stands. Seedling dispersion to clearcut sites was poor with seedlings being tightly restricted to a narrow band along the forest edge. Thus, seedling recruitment in these forests was a reflection of the interaction between the abundance of seed and substrate favourability, and the relative importance of these factors varied significantly with canopy structure.

Prescott, C.E., Blevins, L.L., Staley, C.L. 2000. *Effects of clear-cutting on decomposition rates of litter and forest floor in forests of British Columbia*. Can. J. For. Res. 30(11):1751-1757.

Abstract: The rate of mass loss of three standard substrates (pine needle litter, aspen leaf litter, and forest floor material) was measured in forests and adjacent clearcuts at 21 sites throughout British Columbia, to test the hypotheses that (i) rates of mass loss are greater in clearcuts than in forests and (ii) clear-cutting would stimulate decomposition most in colder zones. Mass loss ranged from 53 to 75% after four years in pine needles, 49 to 70% after 3 years in aspen leaves, and 11 to 20% after 4 years in forest floor material. Mass loss from pine needles was significantly slower in clearcuts throughout the 4-year incubation. Aspen leaf litter and forest floor material lost mass at similar rates in forests and clearcuts. The effect of clear-cutting did not vary between relatively cold and warm sites. The effect of clear-cutting was not related to the size of the clearcuts, which ranged from 1 to 97 ha.

Richardson, A.D., Berlyn, G.P., Ashton, P.M.S., Thadani, R., Cameron, I.R.. 2000. *Foliar plasticity of hybrid spruce in relation to crown position and stand age*. Can J. Bot. 78(3): 305-317.

Abstract: This study examined the foliar response of putative hybrid Engelmann \times white \times Sitka spruce (*Picea engelmannii* Parry \times *Picea glauca* (Moench) Voss \times *Picea sitchensis* (Bong.) Carr) needles in relation to crown position and across three stages of development (15, 55, and 145 years). We focused on the morphological and anatomical response, and used physiological measures (photosynthesis and stomatal conductance) to emphasize the important relationship between structure and function. We found that needles from the upper outer crown position were adapted to reduce stress from evapotranspiration. Trees from the 15- and 55-year-old stands generally responded the most, and trees from the 145-year-old stand responded the least. As they mature, these spruce trees may have reduced ability to adapt to their environment. Some of our results contradict what the literature considers "typical" for sun-shade dimorphism in temperate forests. For example, in all stands, sun needles were broader than shade needles and, in the two younger stands, sun needles were larger in area, not smaller, than shade needles. Also, in the youngest stand, stomatal pores were longer on sun needles than on shade needles. There were no definite patterns in stomatal spacing with regard to crown position. Our results are indicative of the strategies adopted to increase competitiveness in a resource-limited environment. We suggest that, in the 15-year-old stand, neither water nor light is limiting; in the 55-year-old stand, both water and light are highly limiting; and in the 145-year-old stand, water is most limiting.

Wright, E.F., Canham, C.D., Coates, K.D. 2000. *Effects of suppression and release on sapling growth for eleven tree species of northern, interior British Columbia*. Can. J. For. Res. 30:1571-1580.

Abstract: Saplings of canopy tree species frequently undergo alternating periods of suppression and release before reaching canopy size. In this study, we document the effects of periods of suppression and release on current responses to variation in light by saplings of the 11 major tree species of northwestern, interior British Columbia. We were specifically interested in the degree to which increasing length of suppression had long-term effects on subsequent response to release in gaps or following partial cutting, and the degree to which the effects of suppression were ameliorated with time following release. At least some saplings of all 11 species had undergone alternating periods of suppression and release. The most shade tolerant species generally did not show either a decline in growth over time during suppression, or a gradual increase in growth at a given light level over time during release. The least shade tolerant species exhibited significant declines in growth rate during suppression; however, in all of the species except trembling aspen (*Populus tremuloides*), the effects of suppression disappeared over time during release. Failure to account for the effects of past suppression and release leads to significant overestimates of the initial responses of shade intolerant species to release. Our results suggest that competitive balances between species shift substantially over time as a result of growth history, and that these shifts have significant effects on successional patterns.

Canham, C.D., Coates, K.D., Bartemucci, P., Quaglia, S. 1999. *Measurement and Modeling of Spatially-explicit Variation in Light Transmission Through Interior Cedar-Hemlock Forests of British Columbia*. Can. J. For. Res. 29:1775-1783.

Abstract: We have characterized canopy geometry and light transmission by the nine dominant conifer and hardwood tree species of the interior cedar-hemlock (ICH) forests of northern British Columbia. Our field data were used to parameterize a spatially-explicit model of light transmission through mixed-species forests. That model, a component of the forest dynamics simulator SORTIE, was developed for eastern deciduous forests, and this paper presents a test of that model in a very different ecosystem. Our results show that individual crowns of the ICH forests generally intercepted much more light than species of eastern deciduous forests, but that the canopy as a whole allowed much greater light penetration, largely because of openings between the relatively narrow, conical crowns of the western conifers. Light transmission by individual crowns was correlated with shade tolerance among the conifers (as in eastern deciduous species), but crown depth was not (in contrast to eastern species). Despite the fundamental differences in the nature of light transmission in the two ecosystems, the SORTIE light model developed for eastern deciduous forests was very effective at predicting spatial variation in understory light levels in these western coniferous forests. The goodness of fit of such a simple model suggests that the most important factors regulating spatial variation in understory light levels in forests are simply the sizes and distribution of nearby trees, and the local sky

brightness distribution. Discrete canopy gaps represent a special case in which a region of the canopy is not occupied by crowns.

Coates, K.D. & Burton, P.J. 1999. *Growth of planted tree seedlings in response to ambient light levels in northwestern interior cedar - hemlock forests of British Columbia*. Can. J. For. Res. 29:1374-1382.

Abstract: Insights into field-planted conifer seedling growth were gained by fitting height and diameter growth to relative irradiance over the growing season using Michaelis-Menton functions. There was little difference among tree species (*Abies lasiocarpa*, *Picea glauca* x *sitchensis*, *Pinus contorta*, *Thuja plicata*, *Tsuga heterophylla*) in response to ambient light. No meaningful variation in whole-plant compensation points was observed among species but the ranking of species' compensation points was consistent with their shade tolerance ranking. Five years after planting, total size and recent growth rates varied little among species from low to high light, implying an absence of trade-offs in low- and high-light growth strategies. *Thuja plicata* had the greatest response to increased light under deep shade (<20% relative irradiance). All species increased growth above 40% relative irradiance, with no clear whole-plant light saturation point evident under field conditions. Growth rates at high light were broadly overlapping and varied considerably within species. As expected, *Pinus contorta* growth exceeded that of other species above 70% relative irradiance, but it also exhibited high growth rates at low light. Greatest variability among species was at intermediate light levels (30-70% relative irradiance) where careful matching of tree species to light environment can maximize growth rates.

Durall, D.M., Jones, M.D., Wright, E.F., Krueger, P., Coates, K.D. 1999. *Species richness of ectomycorrhizal fungi in cut-blocks of different sizes in the interior cedar-hemlock forests of northwestern British Columbia: sporocarps and ectomycorrhizae*. Can. J. For. Res. 29:1322-1332.

Abstract: We investigated the species richness of ectomycorrhizal fungi based on epigeous sporocarps in an Interior Cedar-Hemlock forest in northwestern British Columbia in gap sizes of 49 to 4526 m² three to four years following harvest. We also determined ectomycorrhizal diversity on *Pinus contorta* var. *latifolia* Engelm. and *Tsuga heterophylla* Raf. seedlings two years after out-planting. Ectomycorrhizal fungal richness, based on epigeous sporocarps, decreased exponentially as gap size increased. There were sporocarps of 15 species along 475 m of transect in gaps larger than 900 m², which was approximately 13% of the number of species present in neighboring forests (115 species along 300 m of transect). These data have implications for foresters who would be interested in managing forests for both timber and edible mushroom harvesting. Ectomycorrhizal richness on seedlings decreased slightly at increasing distances from the edge of the intact forest. The maximum richness was found at 7 m or less from the forest edge for both tree species. The decrease in richness with distance from the forest was associated with an increase in the proportion of *Thelephora* mycorrhizae in the samples. The number of types of ectomycorrhizae on root systems and the number of species producing epigeous sporocarps were not correlated. These results confirm the importance of sampling both sporocarps and root tips to achieve an accurate estimate of the ectomycorrhizal fungal community in forest ecosystems.

Kranabetter, J.M. 1999. *The effect of refuge trees on seedling ectomycorrhizal communities*. Can. Bot. 77: 1523-1528.

Abstract: Live trees within forest disturbances could support refugia populations of ectomycorrhiza fungi from which to reestablish ectomycorrhiza communities during forest succession. I examined the effectiveness of refuge paper birch trees (*Betula papyrifera* Marsh.) in maintaining a forest ectomycorrhiza community on birch seedlings, both in clearcuts and forests, in northwest British Columbia. Seedlings next to refuge birch trees in clearcuts had equal levels of average morphotype richness and evenness as seedlings next to mature birch trees in forests. Seedlings outside of the rooting zone of refuge trees had significantly less average morphotype richness in both clearcuts and forests, decreasing by 38% and 15%, respectively. The ectomycorrhiza communities were also more unique (lower community similarity) next to refuge trees than for seedlings away from refuge trees, especially in clearcuts. These treatment effects could be explained by differences in the ability to disperse and establish between early-stage, multi-stage, and late-stage ectomycorrhiza fungi. The results suggest refuge trees would be effective in forest management as sources of inocula for multi-stage and late-stage fungi.

Kranabetter, J. M., Hayden, S., Wright, E.F. 1999. *A comparison of ectomycorrhiza communities from three conifer species planted on forest gap edges*. Can. J. Bot. 77: 1193-1198.

Abstract: We examined the ectomycorrhiza communities on lodgepole pine (*Pinus contorta* var. *latifolia* Engelm), white spruce (*Picea glauca* [Moench] Voss), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt) seedlings planted together on mature-forest edges in north-western British Columbia. We examined 32 seedlings of each tree species, grouped by pairs along the north and south edges of 8 gaps. We found 74 morphotypes in total, with an average of 52 morphotypes per tree species. Morphotypes with emanating hyphae or strands made up 60% of the overall ectomycorrhiza community. Multi-host fungi averaged almost 60% of total morphotypes in species comparisons, although some of the multi-host fungi appeared to have tree host preferences. The average community similarity, based on morphotype abundance, was 52% between conifer species, and 37% for morphotypes with emanating hyphae or strands. Within planted groups, between seedlings 1 to 2 m apart, community similarity ranged from 2 to 40% for morphotypes with emanating hyphae or strands. In mature, mixed forests, the infrequent occurrence of many multi-host ectomycorrhizae created a wide range in the probability of hyphal linkages between neighboring seedlings.

Steventon, J. Douglas, Ott, Peter K., MacKenzie, Kenneth L. 1999. *Effect of partial cutting on predation risk to artificial bird nests*. Can. J. For. Res. 29:1911-1915

Abstract: Based on relative abundance data, partial cutting has been suggested as a technique to maintain habitat for birds associated with late-seral forests, but there has been little study of partial cutting effects on nesting success. One of the primary limitations to nesting success is nest predation. We compared predation rates (proportion of nests disturbed in a 14-day period) in partially cut (30 or 60% basal area removal), clearcut, and uncut forests in northwestern British Columbia, in two experiments using ground-placed (1993) and shrub-placed (1998) artificial nests. In the ground-nest experiment there was a very low predation rate (0.06) and no detectable difference among treatments ($p = 0.403$). In the shrub-nest experiment, there was a 0.36 predation rate and little evidence of treatment differences ($p = 0.295$). Based on 90% confidence intervals for differences in observed predation rate, the 30% removal clearly did not increase predation risk relative to uncut forest. With the 60% removal, however, we cannot rule out a possible increase in predation risk compared with either uncut forest or clearcuts.

Ashton, P. Mark S., Olander, Lydia P., Berlyn, Graeme P., Thadani, Rajesh, Cameron, Ian R. 1998. *Changes in leaf structure in relation to crown position and tree size of Betula papyrifera within fire origin stands of interior cedar-hemlock*. Can. J. Bot. 76:1180-1187.

Abstract: Dimensions of anatomical and morphological attributes of leaves can influence physiological response to changes in environment over time. Linking structural attributes of leaves to crown position and tree size within naturally developing cohorts of trees can provide a clearer understanding of changes in crown morphology for a species. This study examined leaf anatomy and morphology of *Betula papyrifera* Marsh growing in two stages of stand development of interior cedar-hemlock forest, northern British Columbia. Anatomical and morphological measurements of leaves located at six different positions within the crown were made on trees selected from stands that originated 15 y (small tree size) and 145 y (large tree size) after catastrophic fire. Leaf area and mass were measured in the field. Microscopic measures were made in the laboratory of thicknesses of leaves, cuticle, upper and lower epidermis, palisade and spongy mesophyll. Stomatal density and stomatal aperture lengths were also determined. Leaf anatomy and morphology varied significantly with position in the crown and among size classes of trees. Changes in leaf anatomy observed among positions within the crown reflect the changing availability of light and moisture experienced during crown development. For both size classes of tree the largest anatomical dimensions of leaves were at the outer and uppermost parts of the crown, whilst the smallest were at the lower and innermost parts. Foliage of large trees (145 y) exhibit leaf attributes characteristic of the sun-shade dichotomy reported in the literature, but this was not shown for foliage of young saplings (15 y). For the small trees (15 y) the largest leaves were located at the top of the crown while the smallest were located at the bottom. This has been reported for many tropical pioneers but is in contrast to the usual sun shade dichotomy of temperate pioneers. The large trees (145 y) followed the typical pattern with the smallest leaves at the top of the crown. Information from this study contributes to our understanding of foliar

development of tree crowns by demonstrating how leaf structure changes with crown position and tree size under stand competition.

Kranabetter, J.M. & Wylie, T. 1998. *Ectomycorrhizal community structure across forest openings on naturally regenerated western hemlock seedlings*. Can. J. Bot. 76:189-196.

Abstract: We examined the diversity and distribution of ectomycorrhizal morphotypes on naturally-regenerated western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) seedlings across small forest openings (50-75 m diameter) in northwest British Columbia. The total and average morphotype richness decreased across the 4-year-old forest openings despite the rapid establishment of western hemlock and lack of soil disturbance. Average fungal richness decreased from 13.1 morphotypes under the forest canopy to 9.6 at the forest edge (27% reduction) and to 7.8 in the forest opening (40% reduction). *Cenococcum geophilum*, *Mycelium radialis atrovirens* and *Lactarius* I were the most abundant ectomycorrhizae at each gap position; none of the ectomycorrhizal fungi found in openings were eliminated by 'late-stage' fungi in mature stands. This fungal distribution supports the 'multi-stage' concept of ectomycorrhizal succession. Seedlings under the forest canopy had a total of 38 fungal morphotypes in a relatively even distribution pattern that corresponded well to the 'random niche boundary' hypothesis. Fungal distributions were progressively less even for seedlings at the forest edge and opening than for seedlings beneath the canopy, perhaps because reduced fungal diversity and hyphal inoculum had affected the competitive balance of the ectomycorrhizal community.

Steventon, J.D., MacKenzie, K., Mahon, T. 1998. *Response of small mammals and birds to partial cutting vs clearcutting in northwest British Columbia*. For. Chronicle 74:703-713.

Abstract: A challenge facing forest managers is providing habitat for wildlife that are associated with mature or old-growth forests while minimizing reductions in timber supply. One approach is to use partial cutting which maintains forest cover while still allowing for timber harvest. We compared small mammal (mice, voles and shrews) and bird abundance after 2 intensities of partial cutting (30% and 60% volume removal) in previously unmanaged stands, to clearcuts and uncut natural stands in coast-interior transitional forests in north-western British Columbia. The 30% removal showed no significant difference in the bird community compared to the unmanaged stands, while the southern red-backed vole (*Clethrionomys gapperi*) increased in abundance. The 60% removal treatment was still closer to the unmanaged forest in bird and small mammal community structure than to the clearcuts, but began to include species typical of clearcuts such as the meadow vole (*Microtus pennsylvanicus*) and Lincoln's Sparrow (*Melospiza lincolnii*). At least one bird species, the Yellow-rumped Warbler (*Dendroica coronata*) preferred the 60% removal treatment. Several species were most abundant in clearcuts, and scattered aspen and birch trees left in 2 clearcuts were used as nesting sites by cavity nesting birds such as the Red-breasted Sapsucker (*Sphyrapicus ruber*) and Tree Swallow (*Tachycineta bicolor*). We conclude that both partial cutting treatments maintained a significant component of the mature forest small mammal and bird communities, although the heavy removal was beginning to show a shift towards early seral species. Since no single treatment is optimal for all species, we recommend that partial cutting be considered as part of a landscape strategy to provide a range of forest habitats similar to those occurring under natural disturbance regimes.

Wright, E.F., Coates, K.D., Bartemucci, P. 1998. *Regeneration from seed of 6 tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position*. Can. J. For. Res. 28:1352-1364.

Abstract: Canopy gap size can play a major role in determining composition of tree regeneration after disturbance. The effect of different positions within gaps and within the intact forest has received less study. We seeded 6 tree species onto 2 substrates (organic and undisturbed moss) in 3 positions along a north-south gradient within 8 replicate 600 m² canopy gaps and in the intact forest off the south end of each gap (the gap positions), in 1995 and 1996. Germination of all species was strongly affected by gap position, seedbed substrate and year, but there was little evidence of partitioning by gap position among the species. Average germination was higher in north-facing positions of gaps and within the intact forest, and significantly higher on organic than undisturbed moss substrates (with the exception of *Abies lasiocarpa* (Hook.) Nutt which showed no preference for seedbed). Seedling survival was greatest for all species in the south end of the gap (north facing position) where soil moisture remained highest and light levels

around 20% full sun were adequate for survival. Survival rapidly decreased with time in the intact forest, especially for the more shade-intolerant species, suggesting a possible species trade-off in the understory. In order to predict regeneration success in these forests, for either silvicultural purposes or to permit a better understanding of community dynamics and succession, it is important to consider the influence of position inside and outside of gaps and the nature of the seedbed substrate.

Wright, E.F., Coates K.D., Canham, C.D., Bartemucci, P. 1998. *Species variability in growth response to light across a climatic gradient in northwestern British Columbia*. Can. J. For. Res. 28:871-886.

Abstract: We characterize variation in radial and height growth of saplings of 11 tree species across a range of light levels in boreal, sub-boreal, subalpine and temperate forests of northwestern British Columbia. Shade tolerant species had the greatest response to an increase in light at low light levels, but had low asymptotic growth at high light. Shade intolerant species had weaker responses to increases at low light, but had the highest growth rates at high light. The effects of climate on intraspecific variation in sapling response to light were also related to shade tolerance: across different climatic regions, the most shade tolerant species varied in their response to low light but not high light, while shade intolerant species varied only in their high-light growth. Species with intermediate shade tolerance varied both the amplitude of growth at high light and the slope of the growth response at low light. Despite the interspecific trade-offs between high and low-light growth, there was a striking degree of overlap in the light response curves for the component species in virtually all of the climatic regions. Successional dynamics in these forests appear to be more strongly governed by interspecific variation in sapling survival than growth.

Coates, K.D. 1997. *Windthrow damage two years after partial cutting of the Date Creek silvicultural systems study in the Interior Cedar-Hemlock forests of northwestern British Columbia*. Can. J. For. Res. 27:1695-1701.

Abstract: Partial cutting that removed either 30 or 60 percent of the volume as single trees or small groups up to 0.5 ha had little effect on wind damage to merchantable trees (≥ 17.5 cm diameter). On average, 6.7 stems per hectare of windthrow occurred across unlogged and logged units, representing approximately 1.9% of the standing trees. Over two years, $0.63 \text{ m}^2 \text{ ha}^{-1}$ of merchantable basal area was damaged or 1.5% of the original standing basal area. In the partial cuts, 2.2% of the trees were damaged compared to 1.1% in unlogged areas. The 1.1% increase in damage in partial cut units was well below the 10% effect size considered large enough to warrant either management intervention or to deem the partial cutting a failure. The greatest wind damage occurred in the old-growth stands. For 8 of the 9 tree species examined, no individual tree characteristics seemed to predispose them to wind damage. *Abies amabilis* (Dougl. ex Forbes), *Populus tremuloides* (Michx.) and *Abies lasiocarpa* ((Hook.) Nutt.) were the most susceptible species to windthrow.

Coates, K.D. & Burton, P. J. 1997. *A gap-based approach for development of silvicultural systems to address ecosystem management objectives*. For. Ecol. Manage. 99:337-354.

Abstract: Foresters have traditionally managed forests with silvicultural systems that prescribe stand homogeneity for optimized tree growth. The primacy of timber as the dominant objective is giving way to broader objectives such as sustaining the function and dynamics of ecosystems, maintaining ecosystem diversity and resilience or protecting sensitive species, while providing for a variety of ecosystem services of value to humanity. Protection and production of more diverse forest values demands consideration of the fine-scale variability found within forest stands and an understanding of the spatial and temporal response of forest ecosystems to manipulation. Studies of gap dynamics have contributed significantly to our understanding of the role of small-scale disturbance in forest ecosystems, but have been little used by foresters for predicting ecosystem response to partial cutting. We review the gap dynamics literature paying special attention to papers that use gap size or position as predictive variables for responses indicative of silvicultural success or maintenance of ecosystem function. Like canopy gaps created by natural tree death or windthrow, gaps are also generated by silvicultural systems which remove dominant trees. Results from the Date Creek silvicultural systems study in northwestern British Columbia are presented that demonstrate the utility of a gap-based approach for understanding ecosystem responses to tree cutting. We propose a gap-based approach for study of stand response to silvicultural manipulation that: 1) aids development of cutting prescriptions that maintain functional mature

or old-growth conditions; 2) refines and extends our understanding of how biological structures, organisms and ecosystem processes are affected by fine-scale variation within stands; and 3) leads to development of novel silvicultural systems that meet timber production objectives without compromising ecosystem management principles.

Coates, K.D., Banner, A., Steventon, D., LePage, P., Bartemucci, P. 1997. *The Date Creek Silvicultural systems study in the Interior Cedar-Hemlock forests of northwestern British Columbia: overview and treatment summaries*. Land Manage. Handb. 38, B.C. Min. For., Res. Branch, Victoria, B.C.

Abstract: The Date Creek silvicultural systems study was one of several research projects established throughout British Columbia in the early 1990s to examine alternatives to traditional clearcut harvesting. Large-scale clearcutting had been the silvicultural system of choice in the province (90% of the crown land harvested between 1984–1994; British Columbia Ministry of Forests 1994). However, public demand and changing professional perspectives resulted in new forest policy that calls for a broader range of forest management options. British Columbia's new Forest Practices Code requires forest managers to consider a range of silvicultural systems to promote forest regeneration and maintain biodiversity. To meet new silvicultural, ecological, and social management objectives, silvicultural systems must evolve beyond their traditional emphasis on timber production to include the broader objectives of protecting sensitive species, sustaining ecosystem function (diversity, productivity, nutrient cycling and resilience), and identifying sustainable levels of use for a broad range of renewable resources. An understanding of forest dynamics and succession is critical to effectively manage forests for both conservation and timber production. The Date Creek silvicultural systems study comprises a multidisciplinary set of experiments that examines ecosystem processes and timber production in undisturbed, partially cut, and clearcut stands within the transitional coastal-interior forests of northwestern British Columbia. This report provides background information on the Date Creek silvicultural systems study. This information is presented in three major sections. The first section gives an overview of the Date Creek study area; its climate, soils, vegetation; and the experimental design and treatments used in the research. The second section supplies detailed background information on the Date Creek research area (ecosystem mapping and soils) and the individual treatment units that comprise the Date Creek silvicultural systems study (ecosystems, soils, pre- and post-treatment stand structure). Finally, we briefly describe the various experiments that are under way and the names of the individual researchers involved.

Kobe, R.K. & Coates, K.D. 1997. *Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia*. Can. J. For. Res. 27:227-236.

Abstract: We have developed models of sapling mortality for the eight dominant tree species of northwestern British Columbia in order to better understand forest community dynamics and succession in this important forest region. The species-specific models characterize an individual's probability of mortality as a function of recent growth (a surrogate for whole-plant carbon balance). Interspecific comparisons of survival under low growth rates (i.e. suppression) provide a quantitative measure of the effective shade tolerance of these tree species. In particular, more shade tolerant species exhibited more rapid decays in mortality probability with increased radial growth. The broad and continuous range in shade tolerance ranking was: [*Thuja plicata* (Dougl. ex D. Don)] > [*Tsuga heterophylla* (Raf.) Sarg.] = [*Abies lasiocarpa* (Hook.) Nutt.] > [*Picea glauca* (Moench) Voss x *sitchensis* (Bong.) Carr.] > [*Pinus contorta* var. *latifolia* Engelm.] > [*Populus tremuloides* Michx.] > [*Populus balsamifera* ssp. *trichocarpa* Torr. & Gray] = [*Betula papyrifera* Marsh]. At low growth rates, mortality varied between *T. plicata* and *B. papyrifera* by more than an order of magnitude. For some species, the three replicate sites exhibited significant variation, suggesting that shade tolerance may vary with site conditions (presumably soil moisture in our study sites). The mortality models are consistent with previous qualitative categorizations into shade tolerance classes and parallel the dominance of different species in post-disturbance succession. Our results suggest that species differences in non-catastrophic mortality are critical to understanding and predicting forest dynamics.

Perdue, M. 1996. *Comparison of bat activity in four forest management regimes*. BSc. thesis. Univ. B.C., Fac. For., Vancouver, B.C.

Abstract: The purpose of this study was to examine bat use of partially cut forests. Two intensities (percentage timber removal) of partial cuts were compared to uncut and clear-cut forests. Use was compared in terms of number and

duration of echolocation signals. The duration of activity was categorised as search flight (flypast) of feeding (prey attack). The influence of individual stand opening characteristics and weather variables on the probability of detecting a bat, and the lengths of time bats were heard, were also considered. Echolocation signals were detected using an integrated system of automated ultrasonic receivers and recorders. Sampling occurred from 25 min before to 25 min past official sunset-twilight. Detections were determined by listening to tape recordings. Species of bats were not distinguished. Field data were collected at the Date Creek silvicultural systems research site in the coast-interior transitional forests of northwestern British Columbia. Sixty-four samples were completed between May and September of 1995. Four species of bat, including *Lasionycteris noctivagans*, *Myotis evotis*, *Myotis lucifugus*, and *Myotis volans*, were considered to inhabit the Date Creek study area. There were 22 detections for an overall detection rate of 34.4% or 0.0069 detections/sample minute. Detection times totalled 27.4 minutes from the 3200 sample minutes. These results were tested with three statistical analyses. The occurrence of bat use was examined using Freidman's non-parametric test for randomized blocks. Logistic regression and logistic analysis were used to model stand characteristics and weather factors to duration of bat activity. Treatment type did not significantly ($p=0.48$) affect the number of detections. However, when bat activity was ranked according to the length of detections, management regime tended to have a significant effect ($p=0.09$). This increased activity appears to be a result of increased feeding, specifically prey attack, although this conclusion is speculative. There was no apparent relationship of bat activity to temperature-humidity, temperature, humidity, area, perimeter, or area/perimeter in this study. The preliminary conclusion is that partial cutting silvicultural systems maintain bat foraging habitat. However, the impact of partial cutting on roosting habitat is unknown. Further research may provide evidence that partial cutting systems will maintain bat habitat while allowing extraction of timber.

Perdue, M., & Steventon, J.D. 1996. *Partial cutting and bats: a pilot study*. In Bats and Forest Symposium, October 19-21, 1995, Victoria, British Columbia, Canada. R.M.R. Barclay and R.M. Bingham (editors). B.C. Min. For. Res. Branch, Victoria, B.C. Work. Pap. 23/1996, pp. 273-276.

Abstract: We conducted a preliminary study of bat presence and activity, using ultrasonic detectors, in 2 intensities of partial cutting compared to clearcuts and uncut forest. The study was conducted in coast-interior transitional forests at the Date Creek silvicultural systems research site in north-western British Columbia. The presence of bats in the study area was confirmed, and bat use (indexed by number and length of detections) of partial cut treatments was at least as great as for the uncut forest. Bats were also detected in clearcuts, but at a lower rate. We tentatively conclude that the creation of canopy openings in dense forest favours bat travel and foraging. Roost site requirements is the greatest need for further study in relation to partial cutting.

Thibodeau, E.D., R.D. Krag, I.B. Hedin. 1996. *Date Creek silvicultural systems trial: performance and productivity of ground-based harvesting systems in the Interior Cedar-Hemlock ecosystems of the Prince Rupert Forest Region*. FERIC report SR-114.

Abstract: The Forest Engineering Research Institute of Canada (FERIC) monitored productivities and costs of mechanized, conventional, and horse skidding harvesting systems on six study blocks (two clearcuts, three heavy removals, and one light removal). FERIC's objectives were to assess planning and harvesting productivities and costs; assess soil disturbance levels; and identify ways to improve operational planning and implementation of partial cutting silvicultural systems in Interior Cedar-Hemlock ecosystems. Based on the actual workloads by study block and assumed productivities, the heavy removal and light removal prescriptions required 2.3 and 1.9 times the planning effort (on a per-hectare basis), respectively, of the clearcuts. However, the heavy removal prescription recovered a substantially larger proportion of the devoloped timber volume and therefore using planning resources more efficiently than the light removal prescription. Costs of planning and layout were estimated at \$0.65/m³ for clearcut harvests, \$2.66/m³ for heavy removal harvests, and \$4.66/m³ for light removal harvests. Overall planning, falling and skidding costs were estimated at \$5.85/m³ for mechanized clearcut operations, \$9.60/m³ for conventional clearcut operations, \$14.46-\$14.51/m³ for combined conventional/mechanized operations in heavy removals, \$19.00/m³ for conventional operations in heavy removals, and \$28.95/m³ for horse skidding in the light removal. Relative to the mechanized system, the conventional system had higher falling and skidding costs in the clearcut prescription, and higher skidding costs in the heavy removal prescription. The horse skidding operation in the light removal prescription had the highest

costs in all phases as well as overall. The mechanized system is clearly the most cost-effective option for clearcut prescriptions and can work effectively in partial cutting if patch cutting is employed, at least for the site and stand conditions observed in this trial. Finally, although expensive, horse skidding was well-suited for light removal in this trial in terms of ability to work in high-density stands. However, production rates and costs cannot be readily compared to the other mechanical and conventional operations.

Goward, T. 1995. *Nephroma occultum and the maintenance of lichen diversity in British Columbia*.

Mitteilungen der Eidgenössischen Forschungsanstalt für Wald, Schnee und Landschaft 70:93-101.

Abstract: Based on field studies conducted in British Columbia in 145 forested sites of different ages, the distributional ecology of *Nephroma occultum* is described. Three macroclimatic “range classes” are recognized for this species: 1) a primary range, in which it is restricted to the upper and middle canopies of old growth forests; 2) a secondary range, in which it colonizes the middle and lower canopies of old growth and seral forests alike; and 3) a tertiary range in which it is confined to the lower canopy of old growth forests. In British Columbia, *N. occultum* is judged to have its widest ecological amplitude in its secondary range, which may therefore be termed this species’ “effective ecological epicentre”.

Any viable conservation strategy intended to maintain *N. occultum* throughout its current distribution area must effectively treat this species as a separate ecological entity within each of its range classes. It is concluded that the range class model may prove useful for expressing the distributional ecologies - and hence the conservation requirements - of other old growth-dependent lichens.

LePage, P. 1995. *The structure and development pattern of mixed-species forest stands in the Interior Cedar-Hemlock zone: Moist Cold subzone of northwestern British Columbia*. MSc thesis. Oreg. State Univ., Corvallis, Oreg. 91p.

Abstract: A field study was established to explore stand structure and development patterns of mature, mixed-species forests in the Interior Cedar-Hemlock (ICH) zone: moist cold subzone of northwestern British Columbia. The species of interest in the study area were: western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn), lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), hybrid spruce (*Picea glauca* (Moench) Voss x *sitchensis* (Bong.) Carr.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and paper birch (*Betula papyrifera* Marsh.). Eighty stand structure plots, 150 to 600 m² in size, were used to assess the species, size and age variation within the study area. Three representative plots, 1,000 m² in size, were then selected for destructive sampling. Stand reconstruction techniques were used to: 1) characterize the existing species, age and height / diameter structure, 2) describe and quantify the historical height development pattern, 3) describe the development stage and spatial pattern of the stand and its different components and 4) determine the influence of the above characteristics on the current stand composition and structure. The study stand is 135 years old and originated after a stand destroying wild fire. The resulting mixed-species stand had a very long recruitment period and is currently near the end of the stem exclusion stage of development. Because of the variety of growth patterns exhibited by the different species, neither individual tree height nor diameter were good indicators of stand age structure. The age structure and stage of development were much better defined by direct measures of age, stand density, the diameter distribution / mortality relationship or the overall spatial pattern. Although partially influenced by age structure and spatial arrangement, the developmental pattern of the mixed-species stand was most strongly related to individual height growth characteristics and inter-tree competition. While lodgepole pine, hybrid spruce, western redcedar and paper birch developed in height along characteristically predictable lines, western hemlock exhibited a number of different growth patterns. Subalpine fir followed an atypical, aggressive height growth pattern, developing more like a pioneer species. The variety of height growth patterns frequently allowed younger trees to overtop older individuals, both within and between species. This resulted in numerous shifts in height dominance by different species during the first 80 years of stand development. Forest structure is intimately related to disturbance type and intensity, site quality and the availability of seed or propagules for regeneration. This study examined the structure and development pattern of one type of mixture of tree species common to the ICH zone of northwestern British Columbia. Any difference in the factors listed above would likely produce a different species mixture and therefore a different structure and development pattern. Because most silvicultural operations are tied to the different structures at various stages of stand development, a more complete understanding of these patterns will allow managers to better predict the growth impacts of a variety of treatments and work with, rather than against the natural system.

Goward, T. 1994. *Notes on old growth-dependent epiphytic macrolichens in inland British Columbia, Canada*. Acta Bot. Fennica 150: 31-38.

Abstract: The occurrence of 24 species of epiphytic macrolichens, many of which have previously been assumed to have strictly coastal distributions in western North America, is documented for five humid forests in inland British Columbia. These lichens were detected only in very old forests, and appear to be essentially absent from younger forest types in this region. Old growth forests possibly favour such species by reason of their equable microclimate and relative environmental stability. The possibility is raised that some species may be relicts from the “Little Ice Age”, when climatic conditions were presumably more favourable to long-distance dispersal by lichens outside their current primary ranges. Not all old growth forests are equally rich in old growth-dependent lichens. Diversity appears to be positively correlated with forest age or, more precisely, with environmental continuity. In support of this, it is observed that successful long-distance dispersal by old growth dependent lichens occurs only rarely; older old growth forests can therefore be expected to support a fuller component of such species than younger oldgrowth forests. The possibility is raised that oldgrowth-dependent lichens may provide a rough index of environmental continuity in the oldest of British Columbia’s inland forests. The term “antique” is applied to such forests. It is concluded that oldgrowth forests (=“antique forests”) are more valuable for the purposes of lichen conservation than young old growth forests.

Goward, T. & Goffinet, B. 1993. *Nephroma silvae-vetris, a new lichen (Ascomyctina) from the Pacific Northwest of North America*. The Bryologist 96 (2): 242-243.

Abstract: *Nephroma silvae-vetris* sp. nov. is described from British Columbia, Canada, where it occurs as an epiphyte in old-growth forests in humid localities. Constrictic, cryptostictic, norstictic, stictic, and usnic acids (and possibly Pcr4) are its primary phenolic constituents. *Nephroma silvae-vetris* is morphologically somewhat similar to, but chemically distinct from, the blue-green phototype of *Nephroma arcticum*.

Extension Notes

available at: http://www.for.gov.bc.ca/rni/Research/Extension_notes/Extension_Notes.htm

Goward, T and Pojar, J. 1998. *Antique forests and epiphytic macrolichens in the Kispiox Valley*. Extension Note #33, B.C. Min. For., For. Sci. Sec., Smithers, B.C.

Kranabetter, M. 1997. *The Effects of Timber Harvesting on Mushrooms and Mycorrhizae of the Date Creek Research Forest*. Extension Note #25, B.C. Min. For., For. Sci. Sec., Smithers, B.C.

LePage, P. 1997. *Stand Structure and Height Growth Patterns of Mature, Mixed-Species Forest Stands in the ICH Zone*. Extension Note #22, B.C. Min. For., For. Sci. Sec., Smithers, B.C.

LePage, P. 1995. *The Size and Age Structure of Mature, Mixed-Species Forest Stands in the ICH Zone*. Extension Note #12, B.C. Min. For., For. Sci. Sec., Smithers, B.C.

Manuscripts in Progress

Coates, K.D., Canham, C.D., and Hall, E.C. Effects of Partial Harvesting and Proximity to Edges on Susceptibility to Windthrow in Interior Cedar-Hemlock Forests of British Columbia.

Draft Abstract: Forestry practices in many regions of North America have shifted from even-aged management to partial harvesting regimes that seek to maintain structural complexity in managed stands. There is concern among some forest managers that partial harvesting increases the risk of windthrow of the residual trees, but there has been surprisingly little rigorous examination of this issue. In this study we use data from both measurement of rates of windthrow following experimental partial harvesting treatments, and comparative field studies from sites that had experienced a wide range of prior

harvest regimes and storm severities, to directly address how partial harvesting affects the rates and pattern of windthrow in managed, complex-structured, mixed-species forests. Our specific objectives were to evaluate how harvest intensity and the proximity of a tree to a logging created edge affects susceptibility to windthrow for a suite of tree species in the interior cedar-hemlock forests of northwestern British Columbia. Both data sets show clear differences in susceptibility to windthrow as a function of tree species and size, but neither dataset revealed any increased susceptibility to windthrow as a function of the level of prior partial harvesting. Our comparative field study suggested that, if anything, partial harvesting has a potential beneficial effect on reducing the susceptibility to windthrow of smaller trees. Proximity of trees to edges of gaps and small patches (< 1 ha in size) created by partial harvesting did not elevate the susceptibility to windthrow of the two dominant tree species, but did increase the risk of windthrow for the less common conifer species and for the deciduous species. This suggests that during partial harvesting operations in these forests, tree-marking guidelines should include removal of the most windthrow prone species from edges around small openings.

Kranabetter, J.M., Simard, S.S., Guy, R.D., and Coates, K.D. An investigation into factors causing height suppression of understory conifers.

Draft Abstract: A challenge in modelling forest stand development is the interaction between tree size and light availability on sapling growth rates in multicohort stands. These more complex growth patterns are apparent at the Date Creek research forest in northwestern British Columbia, where 13-year old understory hybrid white spruce (*Picea glauca* x *Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) saplings (at 25% light availability) have declined in annual height increment by 60% and 27%, respectively, in the last 5 years. We tested 3 hypotheses of acute moisture stress, reduced foliar nitrogen concentrations, and declining light availability as a cause of this height suppression by comparing these understory saplings with trees of the same age located in large forest gaps. Xylem potential between understory and gap trees were consistent throughout the summer, with no indication of extreme moisture stress, despite the narrower radial increments accrued under shade. Foliar nitrogen concentrations were not significantly different across understory and gap microsites, or between species. The natural abundance of ¹³C in radial wood increments from the 5 year period was significantly different between understory and gap trees, as expected, but too consistent over time to suggest large declines in light availability for the understory saplings. Western hemlock had a higher ratio of foliar to wood biomass in the understory than hybrid spruce, which likely contributed to differences in shade tolerance. We suggest the reduction in growth rates associated with larger, shaded trees was most likely due to the increased respiratory demands of nonphotosynthetic biomass and ontogenetic changes in sapling morphology. The results from this study demonstrate the rapid changes in growth patterns and ongoing species interactions that can occur during development of complex stands.

Topics Currently Under Study

1. Bird population dynamics in northern temperate forests (10th year measurements – see Steventon et al. 1998 for earlier results).
2. Response of planted trees and natural regeneration to opening size and position in opening (Coates).
3. Understory biodiversity responses (Banner).
4. Moss is Boss; the effect of bryophytes on forest floor dynamics and nutrient availability (Kranabetter).
5. Monitoring biodiversity responses to natural and anthropogenic disturbances in BC's forests: the application of DNA barcoding (Jeremy DeWaard, UBC).
6. Transplantation of *Lobaria pulmonaria* thalli in B.C. (Swiss PhD student).
7. Retrospective study of tree regeneration in canopy gaps: effects of gap size and position within gap in 30-40 year old partially logged Interior Cedar-Hemlock forests (Coates).

Unpublished File Reports (available from Min. For., Research, Smithers, B.C.)

- Allen, E. 1992. Isolation and identification of decay fungi from the Date Creek study. Can. For. Ser., Victoria, B.C.
- Goward, T. and Miede, D. 1996. Notes on the distributional ecology of epiphytic macrolichens in the Kispiox and Nass valleys, with special reference to species of old-growth forests. Part 1: The interior cedar-hemlock zone (moist cold subzone). Min. For. Sci. Sec., Smithers, B.C. 30 p.
- Kroeger, P. 1997. Forest mushrooms of Date Creek: some key field characteristics of ectomycorrhizal fruitbodies documented in July and August, 1996. B.C. Min. For., For. Sci. Sec., Smithers, B.C.

- Loedel, M. and P. Beaudry. 1993. A study of forest interception at the Date Creek silvicultural systems study. B.C. Min. For., For. Sci. Sec., Smithers, B.C. 19 p.
- Patchke, S. 1995. Comparison of soil moisture between a forested site and two silviculture treatment sites at the Date Creek research forest. B.C. Min. For., For. Sci. Sec., Smithers, B.C. 19 p.
- Patterson, D.A., and Steventon, J.D. 1993. Amphibians of the Date Creek research area. B.C. Min. For., For. Sci. Sec., Smithers, B.C. 14 p.
- Silvicon Services Ltd. 1992. Tomentosus root disease survey. B.C. Min. For., For. Sci. Sec., Smithers, B.C. Contract report, 22 p.
- Thomson, S., Harris, D.K., and L. Horrocks. 1996. An extension plan for the Date Creek Research Forest. B.C. Min. For., Res. Branch, Victoria, B.C., 46 p.
- Wooldridge, C., Maloney, D. and Wilford, D. 1997. The effect of clear-cutting on air and soil temperature in the ICH. B.C. Min. For., For. Sci. Sec., Smithers, B.C.