Evaluation of mass seed crops in *Picea engelmanni* and *Picea glauca* using vegetation indices derived from Landsat Thematic Mapper data

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ABSTRACT

Evaluation of mass seed crops in *Picea engelmanni* and *Picea glauca* using vegetation indices derived from Landsat Thematic Mapper data

Michael Sean Hesketh

Mass seeding is the intermittent and regionally synchronous production of large seed crops among conspecific populations. With conifers, the large female cones, concentrated preferentially in the upper crowns of trees, may occupy a sizable part of the upper canopy during a mass seed event. In this study, I evaluate the utility of Landsat Thematic Mapper (TM) data for the detection of temporal and spatial trends in white (*Picea glauca*) and Engelmann spruce (*P. engelmannii*) mass cone production. Through analysis of vegetation indices (VIs) calculated from TM data along with estimates of cone crop size and stand basal area per area from sites in Kootenay National Park in British Columbia and the Abitibi region of Quebec, I came to three main conclusions. (1) The presence of a mass cone crop is readily detectable in analysis of the difference between the VIs from the mass seed year and the years previous and subsequent. (2) The incorporation of spruce basal area per area allows for accurate spatial modeling of this difference. (3) The direct correlation of the VIs to field cone production estimates may be possible, but will require further research before it yields satisfactory results.

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CHAPTER ONE – INTRODUCTION

Mass seeding, the periodic and synchronous production of large seed crops, is a behavior exhibited by most mid-latitude tree species. It is particularly striking among conifers, where the large female cones may occupy a considerable portion of the forest canopy. While the presence of mass seeding events has long been noted, and a substantial body of literature devoted to the potential proximate and evolutionary causes for this behavior exists, determination of the spatial extent and distribution of these events has been limited to direct observation.

Satellite remote sensing may provide an opportunity to monitor the extent and distribution of mass seeding events by taking advantage of the differing spectral characteristics of ovulate (female) cones and needles. Specifically, Landsat Thematic Mapper data, due to its moderately fine (28.5m) spatial resolution and three-decade data record, has the potential to be effective in examining both spatial and temporal variation in the seed production across continents. While cone production in a typical year represents too small a contribution to the overall canopy reflectance to be detectable, one might hypothesize that the large proportion of the crown covered by cones during a mass seed year (as in Figure 1-1) might lead to a measurable change in reflectance. Studies on the remote sensing of the browning and defoliation of spruce and pine forests due to spruce budworm infestation, which may be similar to a mass seed year in its reduction in the apparent "greenness" of tree crowns, suggest that not only is the presence of such an event detectable, but some measure of its intensity should be distinguishable as well (Godard *et al.*, 1990).

A technique for the remote detection of mass seed crops could be of particular utility in certain forestry practices which rely on dense natural regeneration, such as understudy scarification and patch cuts directly preceding seed fall in a mass seed year. At present, these cheap alternatives to plantations are seldom attempted because, among other reasons, direct observation gives an incomplete picture of the extent of the current regional cone crop. Additionally, change detection techniques applied to long time series of Landsat data might provide an excellent record of the frequency and special synchrony of mass seeding events. These data, combined with historical climatological data, could provide additional insight into the drivers behind the mass seeding behavior, at least in coniferous species. Further, a tested argument relating crop size to the weather one year in advance of the crop (i.e. at the time of reproductive bud initiation) would be of great interest to the forestry sector.

This study has two objectives. The first is to determine if the crop size of white spruce (and the closely-related Engelmann spruce) is spectrally measurable. This will be accomplished by using Landsat TM data, informed by the analysis of the reflectance of individual spruce cones measured with a bench spectrometer. The second, contingent to the first, is to model the local spatial distribution of the seed crop though correlation analysis of crop estimates made at field sites in British Columbia and Quebec and spectral vegetation indices derived from Landsat data.

CHAPTER TWO - LITERATURE REVIEW

This review will cover the literature germane to the objectives of this study, and will be divided into two sections. The first will encompass the pertinent elements of forest reproduction: seed production, mass seeding, and the constraints to juvenile survivorship, particularly with regard to post dispersal granivory. Following that is a review or the relevant aspects of remote sensing, focusing on the remote monitoring of vegetation, and the methods employed in retrieving biophysical parameters from satellite multispectral data.

Forest Reproduction

Seed Production

While asexual recruitment is common among shrubs within the North American boreal and hardwood trees (aspen: *Populus tremuloides*), balsam poplar: (*Populus balsamifera*), and paper birch: (*Betula papyrifera*)), the conifers (except black spruce, *Picea mariana*) seldom produce layers or basal sprouts, and never suckers (Greene *et al.*, 1999), instead reproducing sexually through seed production and dispersal

The factors affecting seed production are interrelated. Like the dormant asexual buds of hardwoods, sexual bud number has been found to be proportional to the basal area (i.e. the cross-sectional area of the tree at the base) of a pre-senescent tree, suggesting an initial minimum size for reproduction of about 4 cm diameter at the bole base. Depending on intrinsic species-specific differences in growth rates, this translates into a minimum age for sexual function for boreal trees of about 5 to 25 years in full sunlight (and much longer in shade), with subsequent production proportional to available sugars (Greene and Johnson, 1994). Seed production is, further, inversely proportional to the size of the seeds produced, as

$$\overline{Q} = 3067m^{-0.58}B^{0.92}$$

where $\overline{Q}$ is the mean annual seed crop size (with losses due to pre-abscission granivory included), m is the seed mass in grams, and B is basal area in square meters (Greene and Johnson, 1994). The relationship may be expressed as a density (Q_D : seeds/m^2)

$$Q_D = 3067m^{-0.58}M_D\sum B^{0.92}$$

where M_D is the density (number/m^2) of source trees. While these relationships are generally valid across species, there are a few caveats. First, the long-term forestry data upon which the figures are based tend to be collected on productive sites, and don't necessarily reflect typical stand dynamics. Second, functions like those stated above argue that production will increase with increased basal area, but don't allow for eventual senescence, where seed production would tend to level off in the largest specimens. Third, the equations do not include the role of light receipt (Greene *et al.*, 2002); they are for canopy trees only. Fourth, within a stand of conspecifics the equation captures only 10-30% of the actual variation in seed production. Finally, temporally, the coefficient of variation ($CV_Q = \sigma / \overline{Q}$) for seed production for boreal species at the scale of a stand are typically enormous (in the range of 1-2), and this marked variation, termed mass seeding, is not dealt with (Greene and Johnson, 2004). Mass seeding, which is treated in depth in the next section, appears to be controlled by the weather one year before flowering in higher latitudes; that is, at the time of bud initiation. All boreal tree species exhibit mass seeding except the aerial seedbank species (jack and lodgepole pine, and black spruce) (Greene and Johnson, 2004).

Aspen and balsam poplar mature their tiny seeds rapidly in the spring and abscise them by mid-June. Others (white and Engelmann spruce, the larches, the true firs, Douglas fir, and paper birch) mature their seeds during the summer, achieve final maturation by mid-August, and begin dispersal by late August. Both of these groups necessarily must seed into a burn from the edge or from patches of survivors (residual stands) embedded within the fire. A third group, those with serotinous seeds (jack and lodgepole pines as well as black spruce) maintain their matured seeds in the cones for several years. Thus, when a fire occurs, the scales flex open, and the dead trees can act as in situ seed sources. This aerial seed bank of course provides a tremendous competitive advantage when a very large fire occurs as these species have then no dispersal constraint (Greene *et al.*, 1999) and almost no competition for the first few years.

Mass Seeding

Mass seeding, or masting, is defined as "synchronously highly variable seed production among years by a population of plants" (Kelly, 1994). The term derives from the Old English "mæst", referring to dense accumulations of large nuts (mainly beech and oak) on the forest floor, used as fodder for livestock; presently, a mass seed crop means a bumper forest crop by any species (Koenig and Knops, 2005). These patterns of fruiting and seeding have implications not just for the recruitment of the plant populations themselves, but also on granivore populations dependent on seeds as a primary food source, and on species at subsequent trophic levels. As an example, a big acorn crop in new England sets off a chain events (described as a "trophic cascade") whereby an increase in mouse and deer populations driven by an oak mass seed crop trigger a decline in gypsy moth populations and an increase in ticks, which, as carriers of Lyme disease, result in an increased incidence of the disease in human populations (Herrera *et al.*, 1998, Koenig and Knops, 2005, Jones *et al.*, 1998).

In exploring the mechanisms driving mass seeding, it seems pertinent to separate the requisite elements, variability and synchrony, and address them in turn. Relative variability, typically expressed in terms of the coefficient of variation of a population (CV_P), is the most visible and easily observed aspect of mass seeding. It is described as the standard deviation of temporal variation in production divided by mean production. Three theories have been put forth to explain the ultimate cause of mass seeding behavior: these are resource tracking, predator satiation, and pollination efficiency. These, as well as more proximate mechanisms underlying synchrony within and between populations, are addressed in the following section.

Of the three theories to explain temporal variation in seed production, resource tracking is the oldest but has perhaps the least evidence to support it. The theory states that “in the absence of selection for (or against) mass seeding, seed crops will vary in response to environmental variation” and the idea that plants will respond to “good” years by flowering more vigorously is undeniably the most mechanistic of the explanations described here (Kelly and Sork, 2002). To a certain extent, there is evidence to support the claim as well. Numerous studies show a relationship between annual variation in climate and seed production, and it is only reasonable to suspect that climate plays some role in determining reproductive dynamics (Kon *et al.*, 2005, Sork *et al.*, 1993). Certainly conditions of extreme weather which can suppress photosynthesis, such as prolonged drought or unseasonable cold, may serve to depress reproduction. Evidence refuting the resource tracking theory derives from two sources. The first is the spatial correlation of the CVs of seed production and climate. If climate were the driving force behind mass seeding, it is to be expected that the variation would be similar. In reality, while a relationship is evident, the variation in seed production is as much as an order of magnitude greater than that of climate (Kelly and Sork, 2002, Koenig and Knops, 2000). Of course, one might counter this criticism by arguing that the relationship between resource availability and sexual bud initiation is highly non-linear. The second is the evidence for a tradeoff between growth and reproduction in mass seed years. It stands to reason that a good year for reproduction should also be a good year for growth, yet studies typically show a negative autocorrelation between the two, termed "switching" (Kelly and Sork, 2002, Koenig and Knops, 1998, Silvertown, 1980). Indeed, the argument for this pattern is that the current mass seed crop represents an alternative use of photosynthate, and so vegetative growth is curtailed. If strict resource tracking fails to explain the variation evident in mass seeding behavior, it follows that it must be an evolved trait, conferring some benefit to the species that exhibit it.

The first adaptive argument, predator satiation, may be as dependent on the low production period between mass seed years as it is on the benefit conferred during mass seeding events. The principle is that low seed production will limit granivore populations. This reduction then increases the benefit derived during a mass seed year, where high seed production coupled with low predator density increases the proportion of seeds that survive pre-dispersal predation due to satiation of the predator population. Some studies have demonstrated proportionately lower losses due to pre-dispersal predation in mass seed years. Silvertown (1980) found a strong relationship between predation pressure and seed production for pre-abscission oak crops (but not for pre-abscission conifer crops). Interestingly, and in contradiction of more recent literature, Silvertown (1980) hypothesizes that predator satiation may be an evolved mechanism to enforce synchrony of reproduction, which responds to more general environmental variation. Another study found a negative relationship between insect predator densities in n versus year n-1 (n-2 for oaks), strongly suggesting that predator populations were controlled by seed production, and timed to the reproductive cycle of the trees (Shibata *et al.*, 2002). (Note: some oak species have a three-year reproductive schedule.)

The second evolutionary hypothesis is that pollination efficiency may be maximized by concentrating reproductive expenditures into large concentrated bursts, thereby taking advantage of the economies of scale that result. This mechanism assumes that the pollination vector will not become saturated, and is therefore most plausible for wind pollination. Smith *et al.* (1990) state that there are two conditions that must be met if mass seeding is to confer an advantage in pollination: 1) the cost of sexual reproduction through female function must be the same regardless of fertilization success, and 2) fluctuations in male and female reproductive efforts must be synchronous (Smith *et al.*, 1990). In testing this through a study of 16 species of Japanese deciduous trees, Shibata *et al.* found that only 5 met both criteria, while an additional 7 met only the second (Shibata *et al.*, 2002). In contradiction, a 14-year study of mass seeding in ash found that while male/female synchrony was strong during mass seed years, male CV was much lower than female, indicating that pollen limitation was not a driver to mass seeding behavior for that species (Tapper, 1996). While it is possible that the pollination efficiency theory could apply additionally to animal pollinated species, the likelihood of saturation by large crops indicates that this is unlikely (Kelly and Sork, 2002). Related to the pollination efficiency argument is the contention that species with *seeds* dispersed by animal vectors stand to gain little from mass seeding behavior, due again to the potential for satiation/saturation producing diseconomies of scale. Herrera *et al.* (1998) found that while this was indeed the case for frugivore distributed species, there was no significant difference in the CVs of wind dispersed and scatterhorder (eg. squirells) dispersed trees such as oaks, hickories, and beeches.

While the previous theories attempt to account for the variability inherent in mass seeding, Koenig and Knops (2000) propose mechanisms governing the synchrony that is characteristic of mass seeding species. The first, chemical signaling through airborne means or plants' root systems, is easily discounted on the basis that it cannot explain the wide scale synchrony observed in mass seeding behavior (detectable within genera across areas as much as 196,000 km^2 and within families across areas of up to 785,000 km^2 (Koenig and Knops, 1998)). More likely is that environmental conditions provide cues triggering reproductive bud initiation. In support of this, Tapper (1996) found that the date of leaf flush the year previous was the most significant predictor of fruiting in ash in a given year, though he determined that this was not a consequence of increased resources, as no relationship was evident between leafing date and growth that year. Similarly, Kon *et al.* (2005) found a significant negative correlation between minimum spring temperature the year before and a given year's seed production in a time series analysis of Japanese beech. Further, they suggest that the cue might be deviation from a local mean rather than an absolute temperature threshold, explaining the synchronous population-level response to changes in latitude. Koenig and Knops (2000) found that variation in seed production with response to latitude correlated strongly with variation in temperature, with the mid-latitudes exhibiting greater variation than the tropics, and the southern hemisphere tending to be more variable than the north. Another study positively related mass seeding to a period of water stress the year previous, suggesting that this may be an adaptation to take advantage of the sparser canopy (and therefore increased light availability at the forest floor) thereby created (Piovesan and Adams, 2005). A further potential synchronizing influence is resource depletion as described by Tapper (1996) and Kelly and Sork (2002) with the presence of significant 1-year lagged negative autocorrelations suggesting a depressive effect of a mass seed year on the following year's production, though Tapper's results speak to the contrary. Koenig and Knops (2000) report a similar depressive effect.

Abscission

Mechanisms for abscission vary by species, though boreal species tend to be wind abscised as well as dispersed (Greene *et al.*, 1999). The process here is governed by decreased moisture in the abscission zone coupled with the gusting of wind. In conifers, the scales on the cones protecting the seeds present an additional barrier. Here, decreasing humidity acts differentially on the bands of fibers composing the inner and outer layer of the dry scales, causing them to flex open in response to decreasing humidity. This prevents conifer seeds from being available for dispersal by wind during events such as rainstorms, which would limit dispersal distances. Provided conditions of relative humidity and wind speed are met, cones still require a motive force to initiate abscission. This may take the form of vibrations along a branch cause by wind or animal (squirrels, birds) or mild suction caused by winding passing beneath the opened cone.

Juvenile survivorship

Two factors, about equally important, affect the mortality of the deposited seeds and subsequent germinants: granivory (seed consumption) and abiotic (seedbed-induced mortality during the first year following the breaking of dormancy. The former factor is of interest here because we would like to know the relationship between estimated pre-abscission crop size and subsequent seed and germinant availability. Other mortality agents, for example fungal infection of seeds and germinants, or herbivory by slugs, hares, etc, appear to be far less important than granivory, at least in the higher latitudes.

The main pre-abscission granivores in the boreal/montane forests are insects, rodents (squirrels, chipmunks, mice, et al), and birds (especially members of the blackbird and finch families). Pre-abscission losses fluctuate enormously in time and space but average perhaps 50% of all initially viable seeds (Greene and Johnson, 1998, Leak and Graber, 1993).

In intact forests, the main post-abscission granivores are rodents and birds. These two taxa remove on average about 60% of all conifer seeds with that percentage varying from essentially 0 to 100% depending primarily on local granivore density.

Deep within a fresh burn, it appears that granivore densities are initially very low due to asphyxiation (Charon and Greene, 2002). It is not clear, but we may presume that colonization by rodents begins at the edge of a burn and proceeds inward. Perhaps by the fifth year, seed losses to rodents are as high as before the fire (Greene *et al.*, 2005).

I can find no quantitative studies on losses to birds following fire for either grasslands or forests. Primarily, we simply have anecdotes reminding us that they are probably not inconsequential.

A Note on Color

While I can find nothing in the literature with respect to the color shift in cones (or other seed packaging apparatuses), it bears discussion because of its direct pertinence to the study at hand. As demonstrated by the photographs in Figure 1, the color of white spruce cones shifts from bright green to a dull brown through the month of August, as the chlorophyll that is initially present is degraded as the cones mature and dry during this period. The visible color shift is augmented by the decrease in moisture content as cones ready their seeds for abscission, and is registered spectrally by decreased near infrared reflectance.

Because most boreal tree species exhibit masting behavior, there may be potential to remotely sense mass seed crops in species other than conifers. Greene and Johnson (1996) suggest that, while individual seed mass varies widely among boreal species, when the seed packaging is included in the account, the differences are much less pronounced. If this is the case, and if the remote sensing of these mass seed crops is dependent primarily on the proportion of the planimetric view or the forest canopy dominated by brown seeding bodies as opposed to green photosynthetic structures, there may be some reason to suppose that the results from the study proposed here may be adapted for use with other species. While seed packaging such as birch catkins should certainly be discernable spectrally, the limiting factor seems to be their orientation within the canopy, and their color shift in relation to the surrounding leaves. That is, for the processes proposed here to transfer to deciduous species, it would be necessary for the seed packages to be oriented towards the top of the canopy (as are spruce and pine: Greene and Johnson, 1996, Raven and Johnson, 1999) and for the seed packages to shift in color sufficiently towards brown before the chlorophyll in the surrounding leaves begins to deteriorate in autumn. For such a study to be considered, research would be necessary to better understand the annual spectral phenologies of the seeding bodies respective to the trees' leaves.

Remote Sensing

The promise of satellite remote sensing to ecology is the availability of data providing a systematic, synoptic view of the earth at potentially large spatial scales and at regular intervals (Nagendra, 2001, Roughgarden *et al.*, 1991, Cohen and Goward, 2004). These data have found application in the mapping and monitoring of the distribution of change and distribution of plant species and land cover types, deforestation, fire and insect damage, and human impact on the environment, as well as the extraction of biophysical characteristics (total above-ground biomass, leaf area index (LAI), canopy cover) which are key components in a variety of ecological models, as well as carbon balance and primary production calculations and climatologically studies (Castro-Esau *et al.*, 2004, Foody, 2003, Kerr and Ostrovsky, 2003, Nagendra, 2001, Lambin, 1999). This section focuses on the elements of remote sensing pertinent to the study goals of evaluating the spatial and temporal distribution of ovulate spruce cones in response to mass seeding behavior of Engelmann and white spruce. Topics addressed are the spectral properties of vegetation, the caveats and potential problems associated with using satellite remote sensed data for this type of study, and the methodologies employed in the extraction of biophysical data.

Spectral Properties of Vegetation

Selecting appropriate image analysis techniques and the interpretation of multispectral forest data requires a prior understanding of the optical and spectral properties of plants, both at the leaf and stand scale. Reflectance at the leaf level are influenced by three characteristics: 1) the internal cellular structure of the leaf, 2) leaf pigment content, and 3) orientation relative to solar radiation (Turner *et al.*, 1999). While leaf morphology is highly variable by species and phenological stage, it tends to be characterized by a relatively open structure, with palisade and spongy mesophyll cells sandwiched between an upper and lower epidermis. The upper layer of the epidermis, called the cuticle, is a thin waxy coating regulating transmittance of radiation into the leaf's internal structure. Chloroplasts are found throughout the palisade and mesophyll cells, but tend to be concentrated towards the upper side of the leaf, provided a horizontal leaf orientation (vertically-oriented or erectophile leaves tend to have chloroplasts distributed along both edges (Jensen, 2000).

Solar radiation interacts with the leaf though absorption and scattering. The cell structures within the leaf are large with respect to the wavelengths of light, though the hair-like strands called grana within the chloroplast are small enough (~0.5x0.05 μm) to induce some scatter. Plants absorb the ultraviolet and visible wavelengths efficiently, though absorption decreases dramatically through the near and mid infrared parts of the spectrum. The structural components influencing these decreases are the large intercellular spaces in the spongy mesophyll (the site of 0_2 and CO_2 exchange), which result in high internal scattering of near infrared radiation, diminishing absorption and increasing reflectance of these wavelengths. This lowered absorption in the higher-energy part of the spectrum is a mechanism to control the thermal properties of the leaf, preventing overheating. Water vapor saturating these intercellular spaces interacts with middle infrared radiation, resulting in absorption peaks at 0.97, 1.19, 1.45, 1.94, and 2.7 µm, and increased reflectance between them (Gates *et al.*, 1965).

Leaf pigment content most directly affects the spectral response in the visible range of the spectrum. Chlorophyll *a* and *b* absorb strongly in the blue and green wavelengths, and much less so in the green. The presence of other pigments within the leaf (carotenes and xanthophylls) with similar absorption characteristics broadens the absorption peaks. The ratio between this high red absorption and near infrared reflectance is exploited in the majority of the index-based approaches to vegetation monitoring. As the leaf matures from initial flush to senescence pigment levels shift, causing an alteration to the measured reflectance and the apparent color of the leaf as chlorophyll levels increase and decrease throughout the growing season, replaced by carotenes and anthrocyanin (Gates *et al.*, 1965). While I can find no studies pertaining directly to conifer cones, if follows that many of the same characteristics should be observed. The decrease in chlorophyll content as the cone matures during August and early September will produce a measurable increase in red reflectance, and decreasing water content should similarly increase near and mid infrared reflectance.

Caveats to Remote Sensing of Vegetation

Aside from the issues of appropriate spatial, spectral and temporal resolutions associated with all satellite remote sensed analyses (Nagendra, 2001), there are certain caveats applicable to mapping and monitoring vegetation that bear review. Specifically the effects of the atmosphere, canopy architecture, and the influence of soil on reflectance should be mentioned.

The effect of the atmosphere on reflectance is described as the difference between the actual top of canopy (TOC) reflectance and measured top of atmosphere (TOA) reflectance. For remote sensed projects where data are compared over either time or space, the effects of scatter in the atmosphere must be accounted for (Myneni *et al.*, 1995). Song *et al.* (2001) suggest four means of correction, which are summarized as follows. The first is dark object subtraction (DOS), by which the effects of atmospheric scatter are registered as the brightening of the darkest objects in a scene. Simply put, the DOS method uses this difference to reduce the brightness of the overall image relative to the difference between the measured and assumed actual reflectance of these dark objects. The dense dark vegetation method (DDV) assumes the presence of such vegetation in the scene and that the atmosphere has a negligible effect on the far infrared (2.2 μm or Landsat TM7). Based on these assumptions and the equations $\rho 1 = \rho 7/4$ and $\rho 3 = \rho 7/2$ (numbers correspond to Landsat channels), the difference between the expected and apparent reflectance may be accounted for. The path radiance (PARA approach uses a similar set of relationships between the blue, red, and middle infrared bands to approximate and correct for the effects of atmospheric aerosols. Finally, relative atmospheric correction takes advantage of the presence of pseudo invariant features over a time series of images to account for atmospheric effects. This method does not require any estimation of any atmospheric optical properties, and can correct for systematic variance as well as atmospheric, but is unsuitable in cases where extreme phenological or environmental changes have take place between the images, or where images are spatially distributed.

Similarly, topographic and forest structural characteristics can influence the measured reflectance. Distortions due to bi-directional reflectance from the canopy, caused by the position of the sun relative to the sensor, may cause "hot spots" in imagery when sensor is positioned between the sun and the target. Changes in canopy closure, gap spacing, and leaf clumping with the canopy can also induce variation in reflectance. While the effects of topography on reflectance are well appreciated, the impact of the application of existing topographic correction techniques to forest reflectance studies is unclear, as the vegetation cover may largely mask the effect of the underlying topography (Myneni *et al.*, 1995).

Because the radiance measured above a vegetated surface is a composite of both the vegetation itself and the background surface (usually soil), it is important to appreciate the contribution of both. Soil effects are most felt in areas of low canopy closure and low LAI, and spectral indexing methods may attempt to reduce sensitivity to its effects for studies where soil registers as background noise, obscuring the object of interest (McDonald *et al.*, 1998). Conversely, when surface parameters such as the albedo are under study, it is important to accurately include the soil's contribution to total reflectance.

Methods for Retrieval of Biophysical Characteristics

Parameterization of land surfaces is required in the data collection procedure for calculation of models of ecosystem process, biosphere-atmosphere transfer, and carbon exchange (Hall *et al.*, 1995). The goal of studies in this area has been to develop methodology by which to accurately extract characteristics that are not commonly included in forest inventories, such as LAI, accurately from remotely sensed data over large areas without further fieldwork. Though techniques involving neural networks have shown promise (Carpenter, 1997, Kalácska *et al.*, 2005, Running *et al.*, 1986), research here has focused primarily on two methods. Spectral vegetation indices, based on empirical relationships between the ground sampled measurements and their spectral properties, exploit differences in characteristic spectral regions of the reflected electromagnetic radiation (Kalácska *et al.*, 2004, Running *et al.*, 1986, Turner *et al.*, 1999). Due to the relative simplicity of application, these methods are by far the most popular (McDonald *et al.*, 1998). Conversely, modeling approaches employing the inversion of physically based spectral models have been investigated with some success (Jacquemoud *et al.*, 1996, Kuusk and Nilson, 2000, le Maire *et al.*, 2004). Because the spectral properties of mature (dry) spruce cones show separability from the surrounding green leaf area (as demonstrated by Figure 1), it follows that the dramatic increase in cone production during a mass seed year will have a measurable depressive effect on the LAI. As such, these latter two methodologies are explored here under the premise that this inverse relationship may be exploited with regard to adapting techniques for LAI measurement to evaluate the presence and distribution of these mass seed crops.

Numerous ratio-based vegetation indices have been statistically related to LAI, typically exploiting the variation in the red and near infrared reflectance of green plants, caused by strong absorption of red radiation by chlorophyll and intense reflection of near infrared caused by scatter in the air-water interfaces in the mesophyll. The goal in the development of these indices is to maximize the sensitivity to changes in the characteristic under study (like chlorophyll content) while minimizing sensitivity to background effects (such as soil or atmospheric effects).

Among ratio-based vegetation indices, the normalized differential vegetation index (NDVI), (ρNIR-ρR)/(ρNIR+ρR), and simple ratio (SR), (ρNIR/ρR) are most commonly used in vegetation analysis and LAI estimation, and show high sensitivity to changes in leaf area at low to moderate values, reaching an asymptote at index values of 3-5 (Chen and Cihlar, 1996, Turner *et al.*, 1999, White *et al.*, 1997). These indices, however, are also sensitive to atmospheric perturbations and soil brightness, prompting the development of more complex indices aimed at minimizing the impacts of these confounding variables while maintaining sensitivity to vegetation change. McDonald *et al.* (1998) investigated a set of these indices and evaluated their relative merits in estimation of biophysical parameters of conifer forests. In addition to the NDVI and SR indices, they considered three soil adjusted indices, the perpendicular, soil adjusted, and transformed soil adjusted vegetation indices (PVI, SAVI, and TSAVI), as well as the global environmental monitoring index (GEMI) which was designed to reduce soil and atmospheric effects (description of indices in Appendix 1). They compared the effectiveness of each index in estimating canopy cover (as opposed to LAI) through evaluation using canopy reflectance models rather than empirical data. The authors found a high degree of variation in the strength of the relationships between the indices and canopy cover with the weakest found at low cover. All the soil-adjusted indices were found to reduce perturbations due to soil brightness, though theses did not necessarily translate into increased sensitivity to crown cover. They found overall that SAVI and TSAVI were the most sensitive to leaf are index overall, with sensitivity over a relatively wide range, though GEMI was most appropriate in instances of low canopy cover. Conversely, in a similar study using a physical model to test the relationship between vegetation indices and LAI, Eklundh *et al.* (2001) found poor relationships between LAI and both the NDVI and SR indices, likely related to their finding that the near infrared region was of little importance in LAI estimation, which has pronounced effects in ratio-based indices where NIR is the numerator.

Empirical studies have had mixed results, and while there seem to be strong relationships between LAI and vegetation indices, the best index for a given land cover type seems to be highly variable. Huete *et al.* (1997), in a study on predictive potential of NDVI and SARVI2 (soil and atmospherically resistant vegetation index)[*], found SARVI2 to be more effective for estimating LAI over coniferous forests, owing to an increased sensitivity to the near infrared. In a similar study over the Costa Rican tropical moist forest, Kalácska *et al.* (2005) found the highest correlation with a modified simple ratio (MSR)[**], noting that indices emphasizing change in the red region respond more accurately to LAI changes than do those emphasizing the NIR, such as NDVI. Turner *et al.* (1999) summarize that the relationships between vegetation indices from satellite multispectral data may be useful for retrieving LAI, and note some issues that must me managed if these estimations are to be accurate. They remark on the impact of image processing procedures and the importance of corrections for

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[*] $SARVI2=2.5(\rho NIR-\rho R)/(1+NIR+6\rho R-7.5Pb)$

[**] $MSR = \frac{\rho NIR/(\rho R-1)}{\sqrt{\rho NIR/(\rho R+1)}}$

atmospheric effects, particularly when carrying out analyses between multiple sites or dates, though they found that, while topographic corrections had a marked effect on the raw vegetation index values, they had little to no effect on the strength of the index-LAI relationships. Additionally, they recognize the tendency for vegetation index values to reach an asymptote at LAIs greater than 5 (which is more or less consistent among all the studies cited here), and note the importance of selecting vegetation indices that are appropriate for the cover type under evaluation, which is also indicated by the varying results of the above studies.

Somewhat less common than vegetation index approaches are those relying on the inversion of canopy reflectance models, such as those by Li and Strahler (Li and Strahler, 1992, Li and Strahler, 1986), using reflectance as input to derive biophysical variables such as LAI. Such models calculate canopy reflectance by incorporating nested models of the spectral properties of the individual contributing factors. An example is the model by Kuusk and Nilson (2000), which incorporates the PROSPECT2 leaf optical model (Jacquemoud *et al.*, 1996), the 6S atmospheric transfer model (Vermote *et al.*, 1997), and the MCRM canopy reflectance model (Kuusk, 1995), accounting also forest inventory and structural characteristics, as well as the effects of soil and ground BDRF. Raitianen (2005) found that, while this process only slightly overpredicted LAI values, such an approach is suspect to error from a multitude of sources, most importantly the input parameter relating to stand characteristics, which must be taken from forest inventories (if available) or generalized. The ground truth LAI data is also subject to error, as they are generally modeled as well, taken form allometric equations. Even optical methods used for measuring LAI *in situ* operate on the often-incorrect assumption of randomly dispersed clumping in the canopy. Privette *et al.* (1996) similarly note that while inverted physical models have the virtue of accounting for bidirectional effects, and requiring potentially less prior calibration than vegetation indices, they are computationally more demanding, and require *a priori* knowledge of the vegetation characteristic of the study site, which may not be readily available.

Hyperspectral Data

While the above treats methods for the utilization of multispectral data, the incorporation of hyperspectral data from a number of sources is increasingly common in vegetation analyses. Hyperspectral remote sensing (also: imaging spectrometry) is "the simultaneous acquisition of images in many relatively narrow, contiguous and/or non-contiguous bands throughout the ultraviolet, visible, and infrared portions of the spectrum" (Jensen, 2000). Hyperspectral data for environmental studies comes from three sources: lab spectroradiometers, aircraft-mounted instruments such as AVIRIS and CASI, and, most recently, space borne sensors such as MODIS and Hyperion.

The theoretical advantage to hyperspectral data is that the increased number of narrower spectral bands provides for better differentiation of subject matter. With regard to vegetation studies, this heightened spectral resolution has been used to isolate the absorption features of plant components and pigments such as chlorophyll a and b, found respectively at 0.64 and 0.66 µm, a difference that would be impossible to discern using multispectral data (Wulder, 1998). Lab-based studies on tree foliage have included investigation of leaf water absorption features (Sims and Gamon, 2002) and pigment content (Gamon and Surfus, 1999). Species discrimination has also been addressed through comparison of hyperspectral signatures of leaves from sympatric species by Castro-Esau *et al.* (2004), who used principle component analysis and pattern recognition techniques to distinguish between liana and tree species at a tropical dry forest site.

When applied to forest studies, this translates into an improvement in the relationships between remote spectral measurements and biophysical characteristics. In a study comparing the relative strengths of AVIRIS and Landsat ETM+ data for the estimation of LAI, Lee *et al.* (2004) cite the increased number of spectral bands as the primary advantage of AVIRIS over ETM+, noting that other technological improvements such as increased radiometric resolution seemed to have little effect on the strength of the relationships observed. Similarly, Ustin and Xiao (2001) noted an improvement of between 43 and 74% over SPOT in the accuracy of forest classification in central Alaska. Teillet *et al.* (1997) addressed the effect of more, spectral ranges on NDVI, noting that the both the bandwidth and position of the red band used in the index calculation had a profound impact on the resulting values.

MODIS data has been widely used in land cover classification (eg. Huete *et al,* 1997) but the coarse resolution of the sensor (250-500m) precludes finer-scale analysis. There are comparatively fewer studies conducted using data from high resolution space borne hyperspectral sensors, as imagery is limited to archived data from the Hyperion sensor aboard EO-1, which has been operational only since 2000, and is collects data only upon request, as opposed to Landsat, which continuously archives new imagery (USGS, 2006). Hyperion maintains the 30m spatial resolution of Landsat, but divides the visible, near infrared, and shortwave infrared spectral regions into 242 bands (400-2500µm) with 10µm bandwidths (Pearlman *et al.*, 2003). In a study comparing the effectivness of Hyperion with IKONOS, Advanced Land Imager (ALI), and Landsat ETM+ sensors in modeling and classifying rainforest vegetation, Thenkabail *et al.* (2004) found that Hyperion narrowband data consistently outperformed the broadband sensor, explaining 36-83% more of the biomass variablility, and accounting for 45-52% greater accuracy in landuse-landcover classification. Gong *et al.* (2003) explored the fine-tuning of vegetation indices using narrowband Hyperion data for stronger correlation with LAI, suggesting that Hyperion's increased resolution in the near and shortwave infrared regions of the electromagnetic spectrum. It is clear that these data hold much promise for the future evaluation of forest characteristics, though this is presently undermined by the lack of available archived data.

CHAPTER THREE - METHODOLOGY

Study Sites

Data collection for this project was carried out in two areas. Primary data was collected in Kootenay National Park, in British Columbia during the summers of 2005 and 2006. The park is situated along approximately 84km of highway 93 between Radium Hot Springs, British Columbia and the Trans-Canada highway (centered at ≈ 50°59.5' N, 115°57.5' W). The average temperature ranges from -11°C in January to 14.2°C in July with an annual mean of 2.3°C, and the mean annual precipitation is 511.2mm (Environment Canada, 2004). Situated along the Vermillion and Kootenay rivers within the Boreal montane forest, the forest is dominated by *Pinus contorta* (lodgepole pine) and *Picea engelmannii* (Engelmann spruce), with lesser amounts of *Pseudotsuga menziesii* (Douglas fir). Engelmann spruce and the closely-related white spruce (*Picea glauca*) in the western provinces experienced an extremely large mass seed year in 2003. For these two spruce species in the west, the crops in 2004 and 2006 were very poor, while 2005 yielded a modest crop. Log scale estimates from central Alberta put the relative strengths of the 2002, 2003, and 2004 crops at approximately 30, 10 200, and 1 cones per tree, respectively (V. Peters, personal correspondence). The study sites are located along the valley bottom, where the topographic characteristics are more moderate, with an elevation differential of 240m over the study area and an average slope of 13 degrees.

A secondary study area was established in the Abitibi region of Quebec in October 2006 during a mass seed crop for white spruce; particularly the area between Lac Duparquet and Lac Abitibi (centered at ≈ 48°32.5' N, 79°43.5' W). Average temperatures in the region range from -17.2°C in January to 17.2°C in July, with an annual mean of 1.2°C. Annual precipitation averages 913mm (Environment Canada, 2004). Located within the Boreal Shield ecozone, the forest composition is more diverse than the montane region surveyed in Kootenay Park. The species mix is dominated by *Picea glauca, Abies balsamea* (balsam fir), *Betula papyrifera* (paper birch), and *Populus tremuloides* (trembling aspen) on the more mesic sites, *Picea mariana* (black spruce) on the poorly-drained sites, and *Pinus banksiana* (jack pine) on sandy sites. The area is somewhat flatter than the valley bottom at Kootenay, with an average slope of 7.8 degrees, and an elevation difference of 288m.

Field Data Collection

Due to the timing of the mass seeding events under study, the cone crop estimates were collected differently in B.C. and Quebec. Because the Engelmann spruce mass seed crop in Kootenay occurred in 2003, two years previous to the first year's data collection, and no subsequent mass seed year occurred, ground surveys conducted in $25m^2$ plots were used to estimate the

2003 crop strength at different locations. Plots were situated in roadside stands for ease of access, and located at intervals of approximately 8km. At each site, I recorded the total cones/m^2, as well as the species and total basal area of all standing trees with a diameter at breast height (DBH) of 10cm or greater. Cones dating from before the 2003 crop were easily recognizable on the forest floor by their more advanced decomposition and were not included in the counts. A modest spruce cone crop occurred in 2005. As the cones were still on the tree at the time of the 2005 ground surveys, this crop had no impact on the data collected that year. To adjust for the small effect of the conefall from the 2005 crop on data collected in 2006, the ground counts for that year were reduced according to 2005 crop conefall estimates made in the area by K. Richardson (unpublished data).

A subsequent set of field data from Kootenay (referred to here as Kootenay 2007) was collected in June 2007, and consisted of basal area per area (m^2/ha) measurements. At 20 sites throughout the study area, basal area was measured with a sighting prism, separated by species. GPS coordinates for the center of each plot were recorded three times for later comparison with the Landsat data.

In Quebec, because the crop under study was still on the trees at the time of data collection (October 2006), photography was used to estimate crop size. Again, roadside stands were selected, and 20m sections were photographed with a telephoto digital camera. There was sufficient detail that the individual cones, at least on the outside of cone clusters, were clearly visible. Because the subject of interest is the measurement of the impact of white spruce mass seeding events using Landsat TM data, sites were chosen where white spruce represented at least 20 percent of the species mix, and were not overtopped by the deciduous canopy. As in Kootenay, total basal area was recorded as well as the depth of the photographed stand (from the forest edge to the extent of the canopy of the rearmost spruce tree visible in the photograph).

The photos were organized by site and the number of cones estimated. I transformed these one-side counts into full-tree estimates using an equation developed for white spruce by LaMontagne *et al.* (2005). This equation, found to account for 94 percent of the variation between the one-sided photographs they used and the actual crop size, is:

$$\text{Total cones} = 10^{\{0.073 + 1.189 \times \log(\text{cone count from photo})\}}$$

Note with this equation that when cone numbers are small, the adjustment increases the cone count very little. By contrast, during a mass seeding year, an apparent crop of, say, 1000 cones is actually about 5 times larger than it appears. The reasons for this are the (1) the big crops occur as clusters of cones and one can only count the cones on the outside each cluster; and (2) large clusters on the near side of the crown prevent an observer from seeing clusters on the far side. The transformed counts for each tree were the summed for each site, and divided by the plot area to yield the measure cones/m^2.

Preliminary Cone Phenologies

The spectral phenologies were derived from measurements made using cones collected from planted white spruce in Queen's Park Cemetery in Calgary, Alberta over August and September of 2005. These cone samples, collected weekly in Calgary throughout August and September (during which the cones undergo their final maturation, changing from bright green to brown), were analyzed at the Earth Observation Systems Laboratory in Edmonton. At times when the cones needed to be stored for more than 24 hours, they were kept frozen at -32°C to prevent pigment deterioration. Spectral measurements were carried out with an ASD FieldSpec Pro FR spectroradiometer, which measures a spectrum from 350 – 2500 nm, interpolated to a 1 nm sampling resolution for a total of 2151 contiguous bands (Analytical Spectral Devices, Boulder, CO). Five to ten cones per week were measured, and the reflectances averaged by date. The phenology of cone reflectance generated by these data was used to aid in the interpretation of the results of the Landsat analysis.

Image Preprocessing

The satellite data for the Kootenay analysis were a set of Landsat 5 TM scenes (28.5m spatial resolution, Path 44 (43 in 2003), Row 24), acquired for mid-August of three consecutive years: 2002-4. Two further Landsat TM scenes covering the Quebec field sites (Path 19, Row 26) were obtained for late summer of 2006 and 2004 (no suitably clear imagery was available for 2005, the year preceding the mass seeding event). This imagery was preprocessed by the United States Geological Survey (USGS) to correct for systematic and atmospheric distortions and georeference it to the Universal Transverse Mercator (UTM) projection.

Because of the need for accurate temporal comparison between imagery from successive years, additional corrections were required. All image data were orthorectified in Geomatica X (PCI Geomatics, Richmond, ON) using control points from Landsat 7 ETM+ orthoimages of the same scenes obtained from Geobase (Canadian Council on Geomatics, 2007) and 1 arc second digital elevation models (DEM) obtained from the USGS (USGS, 2007) to a UTM projection. Root mean square processing error in the geometric correction was less than 0.5 pixels (15m) in both *x* and *y* directions. Radiometric corrections of all images were carried out using ATCOR2 in Geomatica. ATCOR2 corrects for haze and atmospheric inconsistencies assuming a relatively constant elevation, which is the case in Quebec and is acceptable for the Kootenay valley bottom stands where the differences in elevation were minimal. The processed results were subsequently rescaled to ground reflectance.

Values at the study sites were extracted as the average reflectance of a 2x2 pixel grid, centered on the coordinate of each plot. For evaluation of the response of canopy reflectance to cone crops, eight spectral vegetation indices (Table 3-1) were calculated for each site for each year of image data at both the Kootenay and Quebec study sites.

Image Analysis

Detection of the effect of mass seeding on canopy reflectance was carried out through image differencing and an analysis of the ratios of vegetation indices calculated from the TM 3 and 4 bands for mass seed years and the year previous (two years before the mass seed crop at the Quebec site due to a lack of cloud free 2005 data for the study site). In addition to a comparison of values at the study plots, pseudo-invariant features (PIFs) were also measured at each location. PIFs included deep oligotrophic lakes as well as rock and manmade features, such as paved and urban areas. Additionally, lodgepole pine dominated stands within the Kootenay study site were used to account for effects of temperature and water stress that may influence the vegetation indices. Because this species maintains an aerial seedbank and the production of new (green) cones does not vary greatly from one year to the next, it should not exhibit marked changes in reflectance due to crop size. Stands of black spruce, another species which maintains aerial seedbanks and has little annual fluctuation in fecundity, were used for this purpose at the Quebec site. To incorporate the basal area per area data collected in 2007, the difference and ratio of the pre-mass year and mass seed year vegetation indices (2002-2003, and 2002/2003, respectively) were calculated for the 2007 study plots. These data were then compared with the measured basal area using a simple linear regression to evaluate the role of stand composition on changes in vegetation indices in the study years.

To monitor the spatial variation in production during a mass seed year, correlation analysis was performed between the cone crop estimations made in the field and the vegetation indices. This is similar to methods used to measure leaf area index (Kalácska *et al.*, 2004, Turner *et al.*, 1999, Chen and Cihlar, 1996), though the observed relationship in this case was expected to be negative, with increasing (non-photosynthetic) cone numbers in August resulting in a decreased response from the indices.

CHAPTER FOUR - RESULTS

This project focuses on the detection of mass seeding events both temporally and spatially. Data were collected at field sites in British Columbia and Quebec, and then compared with Landsat Thematic Mapper data to evaluate the potential for the detection of these events and their intensity (cones per m^2).

Preliminary Data

Hyperspectral measurements of individual cones were carried out from August through October of 2005. Figure 4-1 summarizes the change in reflectance undergone by spruce cones during the month of August. This was the period when the cones' reflectance became increasingly dissimilar to the surrounding needles as the chlorophyll was broken down and the cones became drier and turned from green to brown. Where Figure 4-1 shows the changes in measured cone reflectance relative to white spruce foliage during August, Figure 4-2 depicts the change in reflectance at intervals over the August – October study period, with the hyperspectral data averaged to simulate Landsat TM bands. Though the magnitude of the change was greatest in the short-wave infrared (TM 5) region, which is a result of decreased water absorption as the cones dry, the areas of greatest interest are the red and near infrared areas of the spectrum (TM 3 and 4), which are the wavelengths used in the calculation of the vegetation indices. Those indices are shown in Figure 4-3, plotted at intervals between August 11 and October 12. The indices, derived from simulated TM red and near-infrared bands calculated from the hyperspectral data (Table 3-1), show a general downward trend with a spike in mid September which is more exaggerated in some indices than others.

Of especial interest was the rather sudden decline in the indices from August 18 to August 25. This marks the period when, qualitatively, it appeared that the cones rapidly dried and turned brown.

Field Data

Table 4-1 summarizes the measurements on the sizes of cone crops and trees at the sites. The magnitude of the recorded values was quite different at the two sites: Kootenay and Abitibi had median cones per m^2 values of 5.13 and 26.71 respectively. The coefficient of variation (CV), however, was quite similar for the two areas; 1.27 and 1.23, respectively. Note that the values in Table 4.1 are based on pairs of years but in each case one of the years produced essentially no cones, so really we are looking at the mass seeding year in each region.

Basal area per area (m^2/ha) was also collected at each site with the exception of three sites in Abitibi which I was physically unable to reach (this did not effect the crop estimates as I measured the cone crop photographically). Table 4-2 summarizes the total basal area/area (m^2/ha) for each site, as well as the separated spruce basal area for Kootenay (basal area was not collected by species in Abitibi). The zero values at the Quebec study area refer to control plots recorded in the field but not included in the analysis. Comparing the summed values, Abitibi showed a higher overall coefficient of variation in basal area per area than did Kootenay (0.74 vs. 0.56).

Figure 4-4 shows the percent composition, by number of stems, of white spruce, other conifers, and broadleaf species at each of the Abitibi study sites. The CV for the percent spruce composition of the stands studied was 0.61, much closer to the spruce-only separated basal area per area value for Kootenay than the summed Quebec basal area results reflect.

In summary, the stands I chose at the two sites were similar in their spruce composition and in the relative variability of the cone crops. However, the absolute magnitude of the cone crops was quite different.

Red and Near Infrared Reflectance

Because the results of this study depended heavily on vegetation indices, addressing the red and near infrared reflectance (NIR) with respect to cone production is instructive in interpreting the sensitivity of the resulting indices to the cone values. The relationships between the red and NIR TM channels with the cones/m^2 data from Kootenay and Abitibi (log transformed to normalize the data) are shown in Figures 4-5 and 4-6. In Kootenay, the red and NIR relationships were negative and positive, respectively, with R^2 values of 0.4106 and 0.1628. The relationships were weaker in Abitibi, with respective R^2 values of 0.0441 and 0.122.

Temporal and Spatial Changes

As a first step in the detection of the effect of a mass seed crop with the spectral data, I employed image differencing, subtracting the vegetation index results for the mass seed year from the year with essentially no crop. If a large mature cone crop has a depressive effect on the vegetation index value at a given location, this difference should be consistently positive. That an observed positive trend was indeed the result of increased cone production and not due to inconsistencies in image processing or some other non-reproductive temporal effect such as poorer growing conditions or water stress, was evaluated through examination of pseudo invariant features (PIFs). Large rock outcrops, man-made features, and deep, oligotrophic lakes were selected as PIFs to check for consistency in the imagery from one year to the next. Also, stands featuring high proportions of aerial seedbank species known to show little inter-year variation in cone production (i.e. lodgepole pine, jack pine, and black spruce) were used to evaluate the impact of increased cone production, as these should demonstrate a much lower difference than the spruce-dominated test sites.

Figure 4-7 shows the results of the image differencing (2002-2003) for the sites in Kootenay National Park, as well as the PIFs for that area. Only the SR and MSR indices are included, as they proved most sensitive in this analysis, but the remaining 6 indices tested showed a similar trend (Table 4-3). Of the eight test sites, all but the site "cross pp" showed the expected strongly positive difference between the two years.

Demonstrating the consistency of this trend outside of the Kootenay study plots, Figures 4-8 and 4-9 show the SR and MSR indices for 2002-4 assigned to, respectively, the red, green, and blue channels of a composite image. The variation in the index values from year to year are represented graphically, with dominance of red indicating that the highest VI values are from 2002, green from 2003, and blue from 2004. In both instances, the lack of green in the image (dominated by purplish shades due to higher VI values in both pre- and post-mass seed years) suggests the lower response of the vegetation indices in 2003, the mass seed year. (A fire in the area that occurred in late summer 2003 is visible as bright pink and yellow because of its alteration to the values from 2004.) The "mc pine" site, used to contrast the effect of spruce cone production to the relatively invariant production by lodgepole pine, is an average of three pine-dominated sites. While the image difference was positive, the values were lower than all other study sites (save the anomalous cross pp).

Can one predict the cones/m^2 in a mast year knowing only the VI for stands differing markedly in basal area per area? The results of the correlation of cones/m^2 and the eight SVIs for Kootenay National Park are pictured in Figure 4-10. Contrary to the predicted negative relationship (recall that increased non-photosynthetic vegetation was expected to depress the index results), significant positive relationships were observed between cone crop intensity for all eight indices tested (the significant correlation coefficients ranging as R = 0.67 (NLI) to 0.75 (SR)). These results are also shown in Table 4-4, alongside the similar regression results from the sites in Quebec, which were not similarly significant.

I also used the Kootenay 2007 dataset (basal area/ha data collected in 2007 in a different set of sites) because of the well-known correlation between cone production and spruce basal area (e.g. Greene *et al*, 2002); i.e., basal area should be a good proxy for cone production estimates. I evaluated the relationship between basal area per area and both the difference between the index results from the two study years (2002-2003) as well as the ratio of the 2002 and 2003 results (2002/2003). Both showed strong significant positive relationships (Figures 4-11 and 4-12) with the SR and MSR indices, again, the best correlates among the tested indices. Using the difference, as above, the R^2 values for SR and MSR were 0.5756 and 0.5775 Substituting the 2002/2003 ratio for the difference produced a stronger R^2 (0.6060) for SR but a slightly weaker correlation (R^2 =.5167) for the MSR index. The 2002/2004 vegetation index ratio showed no relationship. 2004/2003 showed a positive trend, but it was not significant using either the SR or MSR indices ($R^2<0.1$ in both cases). Mann-Whitney tests revealed significant differences ($p<0.05$) between the 2002 and 2003, and 2003 and 2004 index values (u= 28 for both years, both indices), and no difference between 2002 and 2004 (u= 94.5).

Due to the difficulty in finding pure pine stands to attempt to isolate the impact of spruce cone production on the change in canopy reflectance during a mass seed year, the percent spruce composition in the Kootenay 2007 data was compared with the vegetation index differences, with the results shown in Figure 4-13. While significant, the results (R^2 values of 0.3582 and 0.3517 for SR and MSR, respectively) were not quite as strong as with the comparisons using spruce basal area.

Carrying out the image differencing for the sites located in Abitibi was complicated by the difficulty encountered in locating cloud-free Landsat data for 2004. (Other possible years had even worse August imagery available.) Indeed, only two of the seventeen sites with data from both years showed useful results. Figure 4-14 shows the differencing in the two remaining sites as well as with the PIFs established within the image. As with the study sites in Kootenay, both sites with cloud-free data from both years showed a difference far greater than seen for the invariant features. Two black spruce sites (75% or greater black spruce composition) serve as contrast to the spruce sites in Abitibi. The image difference at both sites was comparable to the non-vegetative PIFs.

The results from the sites in Abitibi were much weaker than for Kootenay. Though there was little cloud cover in the 2006 image, the cloudiness of the 2004 image precluded difference or ratio analyses. The correlation analysis for the stands using only the 2006 image uncovered no strong relationships for any of the indices tested. Figure 4-15 shows the results of the eight regressions. In all cases, the relationships were insignificant, with the greatest correlation coefficient of 0.2663 produced using RDVI. In summary then, the Quebec data seem to be quite different from the Kootenay sites, both in the strength of the relationships and in the relative sensitivity of the indices to variation in cones/m^2.

CHAPTER FIVE - DISCUSSION AND CONCLUSIONS

The primary objective was to use remotely sensed vegetation indices as predictors of mass cone crops. In this chapter I will discuss the results and also outline what the next steps should be as subsequent researchers refine the approach.

Because of major differences in the field methods, and thus in the analyses, the Kootenay National Park and Abitibi study sites will be discussed separately. The discussion in both cases will focus around three themes: (1) the temporal effect of mass cone production on spectral vegetation indices, calculated as the difference between the pre-mass year and mass year values; (2) the relationship between the degree of change in vegetation index response between the pre-mast and mast year and the basal area per area of the stands under study; and (3) the relationship between measured cone production and the vegetation indices.

Preliminary Lab Spectra

The cone data measured on in the lab in 2005 was intended to determine the potential for spectral separabilty of white spruce cones from the surrounding foliage, as well as to explore the spectral phenology of the cones during their maturation. In the context of this study, these data were incorporated in this thesis primarily to help explain the results of the multispectral study, particularly with regard to speculation concerning the degree of maturation (chlorophyll degradation and drying) the cones may have undergone by the date of Landsat image capture. The sharp decline in vegetation index values during the period of August 18 through September 1 is of particular interest, as this period encompassed the capture date of the image data used in this study. Unfortunately, this record from a different year, with a sample set taken from a different location, cannot convince us that the 2003 Kootenay cone crop had indeed become markedly brown by the date of the Landsat image.

This data collection is ongoing, however, with a sample set from 2006 in frozen storage awaiting analysis, and plans in place for future collection (2007 is a very good year in Alberta and British Columbia for both white and Engelmann spruce). In a follow-up study, these phenologies will be compared against regional climatic records to better understand the rate and timing of cone maturation. This will be of particular value as we attempt to evaluate the effects of cone production on canopy reflectance in cases where historic data is used without the benefit of direct observation of the stands under consideration at the time of satellite image capture.

Kootenay

The first issue with a study relating the cone density measured on the ground years after the crop to remotely sensed data from the year of the crop is the veracity of the field measurements. Specifically, in 2005 and 2006 I sampled the fallen 2003 cones. According to D.F. Greene (personal communication), the 2002 crop was quite minimal; therefore the problem is the estimation of the 2003 crop size. Two factors might influence the reliability of the recorded data.

While there was essentially no cone crop in the park in either of the years preceding or following the 2003 mass seed crop, there was a modest cone crop in 2005. As I was counting already fallen cones, this had no impact on the 2005 data collection, but had some potential to result in overestimation of the counts I made in 2006. To control for this, I reduced the cones/m^2 results of the data collection for that year using the average cones/m^2 taken from a set of permanent plots in the park that had been established in 2004. The rate at which emptied cones fall is not understood. According to unpublished data of D. Greene (Colorado and Ontario) and A. Rive (Quebec) for the 2006 crop, little falls until the leaves flush from the buds in the late spring; about 80% of the crop is still retained on the branches by this date. Subsequently, during the next month, the bulk of the empty cones fall. My own qualitative estimate of the 2003 crop in Alberta was that about 25% remained by mid-summer of 2004. If these generalizations are correct, then two things follow. First, a mass year may still have a big effect on the reflectance in August of the subsequent year. Second, this could explain the low estimates of fallen cones from the 2005 crop taken from the Kootenay permanent plots in 2006 (0.22 cones/m^2 on average). As a result my estimates of the magnitude of the 2003 cone density on the ground in 2006 should not be greatly affected by the 2005 crop.

The second potential problem with the Kootenay data collection is the basal area/area measurement. This was measured as the circumference at breast height (CBH) of all trees in each 25 m^2 plot and later converted to basal area per area (m^2/ha). A consequence of the small size of the plots, however, relative to the 4-pixel area drawn from the imagery, is that there is great potential for error. Further, I made the mistake of placing the tape outside of boles that were intersected by the plot edges. This means my field estimates of basal area/area will all be overestimates. Certainly, the average total basal area per area (78 m^2/ha) was more than 2 times greater than what was obtained with a prism in 2007 (35m^2/ha) for these old spruce stands.

In response to these problems with the original basal area/area data, I remeasured this quantity in 2007 (although in different stands than previously). Given that the bias in the 2005-06 measurements was constant, however, one might expect any trends observed (e.g. correlations with vegetation indices) to be valid (although with an unnecessarily small correlation coefficient).

Spectral Results

The first of the research objectives, detecting the dramatic increase in cone production during a mass seed event using Landsat TM data, was addressed using the difference in response of the indices from 2002 and 2003. A positive result was expected due to the depressive effect of the increased cone production on the indices. As we saw, the difference was strongly positive for all stands except the site labeled "cross pp".

In order to appreciate the degree to which the positive trend observed in the image differencing was attributable to mass cone production of Engelmann spruce and not the result of environmental stress or a general change in growing conditions, it was necessary to establish a vegetative control in addition to the non-vegetative PIFs. Because lodgepole pine does not exhibit mass seeding behavior, I located pine-dominated stands for use as control sites (pure pine stands could not be found). The three sites (averaged as "avg mc pine" in Figure 4-7), produce somewhat ambiguous results: the difference was positive although not nearly as strongly positive as with the other study sites (save the anomalous "cross pp").

I used the field data collected in 2007 in three ways: relating the 2002-2003 VI difference to both the spruce basal area (in m^2/ha) and the percent contribution of spruce to the stands, and substituting the ratio of 2002/2003 for the difference. In all cases the results of the regression were significantly positive ($p=0.05$). This implies that the extent to which the indices exhibited some depressive effect, ostensibly a result of increased cone volume due to mass seeding, is a direct function of the contribution of spruce to the canopy. The corollary is an implied negative relationship between the degree of change and the contribution of lodgepole pine, which is the typical co-dominant in these montane sites. This makes it more certain that the positive results of the image differencing analysis were indeed the result of the 2003 mass seeding event, and not another non-reproductive factor. That this trend prevails throughout the Park was reinforced by Figures 4-9 and 4-10, which contrasted the weakness of the response of the 2003 indices with the dominance of the other two years.

The results of the second objective, to evaluate the spatial variation of the intensity of the mass seeding event using TM data for the 2003 image only, were surprising. Overall, eight regressions were performed, with the log of each index related to the measured cone production values (also log transformed to normalize the data). In each case the relationship observed was significantly positive ($p<0.05$), rather than, as expected, negative. There are several potential explanations for this, though at this stage it is impossible to determine with confidence why this relationship should be so far removed from the expected results.

Problems with field methods in 2005 and 2006 would not explain the consistently positive relationships. One possible explanation is that because of the early capture date of the TM imagery (August 20, 2003), the cones on the trees were, perhaps, midway through their maturation, and hadn't turned fully from green to brown. Examination of the indices derived from the bench spectrometer cone measurements from 2005 (Figure 4-3) indicates that the bulk of this color change occurred rapidly over the period of August 18 through September 1 of that year. Because the timing of cone production and maturation is somewhat variable and related to a number of environmental factors, the possibility exists that cones were still green at the date of capture, and that this is the cause of the unexpected positive relationship. But a counter-argument would be that the clusters of cones conceal green needles, and so there need not be any increase in the 2-dimensional cover of green tissue in a spruce crown during a mass seeding event. Further, if this conjecture were true, why would the ratio of 2002/2003 show such a strong positive relationship with spruce basal area per area?

A very different (but still speculative) explanation is that increases in spruce basal area are associated with factors that are increasing the amount of green tissue per area. For example, the crowns of spruce are more dense than those of pine, especially in the older stands (>200 years of age) as the earlier-senescing pines begin to lose leaf area. The strength of the relationship observed here between cone production and SR is within the range found by Chen and Cilar (1996) between LAI and SR (R^2=0.42 and 0.66 for mid summer and late spring, respectively), raising the notion that perhaps what is being detected is not the cones themselves but rather a related forest structural characteristic. Note that using the ratio of 2002/2003 (the 2007 field data set) would in effect hold such correlative factors constant within each stand. Given that the 2007 data set did indeed show the expected negative relationship, this speculative explanation is unlikely.

Finally, there exists the possibility that the coarse pixel size of Landsat TM data provides insufficient detail to effectively detect the spatial variation in cone production. The success of studies observing the relationship between TM vegetation indices and leaf area index (e.g. Chen and Cilar, 1996; Kalácska *et al*, 2004), was used as a precedent for this study, but it may be that cone production is insufficiently consistent at the pixel scale to track well with the spectral data, especially when compounded by variation in species composition among the study sites.

Abitibi

The analysis of the data for the sites in northern Quebec did not uncover results of the same strength as those from Kootenay. Because the crop was on the trees in Abitibi at the time of data collection (early October 2006, approximately one month after the Landsat image capture date), I was able to evaluate the actual cone crop as it would be detected, although I had a much smaller area for the field sampling than the 4-pixel square I would subsequently use for the analysis. The limitation in the photographic method employed in crop measurement was that only edge stands could be surveyed, as the photographs required a clear view of the canopy from sufficiently far away so as to observe the top of the crown without it being obscured by lower branches. The bias should be in the direction of exaggerating the cone counts that would be observed in the TM pixels, centered a bit further into the forest, because the extra light accruing to edge trees increases their seed production (Greene *et al*, 2002). Nonetheless, the field data should be well-correlated with the unknown stand averages of cones/area for the spruce trees further in.

Another field issue was the location of sites where the conifer component of the stands was not overtopped by the deciduous canopy, and where this state was maintained for a large enough area to relate well to the spatial resolution of the Landsat pixel. These criteria compounded the difficulty in obtaining good quality, cloud free imagery from the summers preceding the mass seed year, and in the resulting dataset, only two of the sites surveyed were useable in both the 2004 and 2006 images. These two sites did, however, exhibit the same strongly positive results in the image differencing analysis that were found in Kootenay. Vegetative control sites in relatively pure black spruce stands show little to no variation in index response between the two study years. Additionally, both the lack of sites with clear imagery in both years and the fact that basal area was not separated by species precluded the index difference versus spruce basal area analysis conducted with the Kootenay data.

While the cones/m^2 data were collected in a more ideal manner than in Kootenay, and the 2006 TM image was of good quality and cloud-free over the study area, still no relationship was detectable between the stand cone data and any of the vegetation indices used. An explanation for this may be that the presence of deciduous hardwoods complicated the relationship, causing any effect of the variation in cone production among sites to be lost. That is, the increased heterogeneity within each pixel relative to the Kootenay sites may have made it difficult to separate spectral changes due to cone production from those due to variation in stand composition. The quality of the satellite data used here was the same as the data used in Kootenay and can quite safely be eliminated as the source of the poor correlations found with the measured cone data from Abitibi. Indeed, the study site is superior to the site in B.C. in terms of topography as well (ie. the average slope and altitude differential are lower), leaving the more complex stand composition as the most likely source of the low r^2 values observed in the correlation analysis.

This problem could have been mitigated if I had a 2004 image with less cloud coverage (or, more obviously, had chosen the sites *after* I obtained the image.) Then, I could have regressed the ratio of the index for the poor cone crop year to the index for 2006 against the cones per area; i.e. the same approach as at Kootenay. Of course it may be that the edge trees will not be typical of a 60 x 60 m area. Conversely, the problem of mixed pixels may be addressed by substituting for Landsat a satellite product with either increased spatial (eg, Quickbird or IKONOS) or spectral (eg, Hyperion) resolution. The complication with these alternative data, and thus the attraction of Landsat as a platform, is the lack of available imagery, and the shorter history of archived data.

Continuing this line of inquiry: recommendations

Because spruce make up at least 50% of each stand in the data on which the relationship at Kootenay was based, it seems pertinent to evaluate in the future whether the cone signal can be detected when (a) mass seeding spruce make up a low percentage of a stand or (b) the cone crop is small. That is, we need to determine the threshold detection value for cones per area. The easiest way to do this would be, as here, during a mass seeding event, examining stands with a wide range of spruce basal area per area. The one thing we cannot do however is separate the effects of cones/area and spruce basal area/area for a single image. That is because crop size per basal area is relatively constant across a much greater spatial extant than is a Landsat image.

As we saw, using the ratio of the vegetation index for a poor crop year and a mass seeding crop enabled us to see differences related to basal area per area within a landscape. That is, we could detect the presence of a major cone crop. More generally, this approach could be extended to any number of years: one uses a year known to be virtually devoid of cones as a reference year, and so its index value becomes the numerator in the ratio. Stand differences that have nothing to do with cones are then rendered unimportant. For this analysis, we would need field data on the magnitude of the cones/basal area averaged across the landscape for each year.

One problem with using a reference year approach (or any attempt at multi-year analysis) is finding suitable imagery. We seem to be limited to a very narrow window for brown cones. As pointed out, it was difficult to obtain images from two years (let alone, say, 10 successive years) that fell within this window and were also cloud-free. In coniferous forests, the latest date could be extended to the beginning of the snow season (longer of course at more southern latitudes). But in mixed forests, the loss of hardwood leaves starting in early to mid-autumn will impose a fixed limit. Conversely, one could argue that using a reference year (as above) would ease this problem: each stand would have the same amount of hardwood cover from year to year. Again, however, this would require obtaining cloud-free imagery from approximately the same time for each year (we cannot compare a time with 50% leaf loss with another time where there is 90% leaf loss).

A second issue to be dealt with in a multi-year study is the effect of residual cones; i.e. the cones that are still persisting on the tree from one year to the next. I made an informal evaluation of a few trees at a site near Kootenay in the early summer of 2004, and concluded that about 25% of the cones were still on the branches. By contrast, Greene (personal communication) found that about 75% of the 2006 crop was still on the branches of Engelmann spruce trees near alpine treeline in Colorado just after snow melt in the early summer of 2007. Explaining this discrepancy perhaps, A. Rive (personal communication) has informed me that the bulk of the 2006 cones collected in her seed traps in the Abitibi region fell in the month after the new spruce leaves flushed (i.e. in late May and early June). Roughly, then, one might guess that by August of the year after a major crop, about a quarter of the old cones still remain. This is a substantial number of cones and would certainly influence any remotely sensed appraisal of the size of the cone crop in the next year.

For both of the preceding issues—hardwood leaf-fall and residual cones—there is the difficult problem of phenology. In a multi-year study one wants to hold all the factors constant. But the timing of major phenological events like mean time of leaf-fall can easily vary by a week or more (Lechowicz, 2001). There are no existing year-to-year studies of the phenology of cone maturation for any species.

The opening of the scales in response to low relative humidity, a response that begins, roughly, in late August after the cones turn brown, may be a further issue for multi-year comparisons. There are two problems. The first is that the scale opening will increase the apparent size of the cone; indeed, as seen from above for a perfectly vertical cone, full flexing of the scales (very low relative humidity) approximately doubles the apparent area of a single cone. The second problem is that we might imagine comparing two images, both cloud-free, with one from a mid-afternoon at low relative humidity and the other the next day in the early morning when the relative humidity was much higher (because the temperature was far lower). Even though the images came from the same time of year, they might have different reflectance values, However, it may be that scale-opening is not a serious problem during a mass seeding crop as the cones are appended in dense clusters and so the scale opening increases the diameter of an entire cluster quite marginally. At the other extreme, when crops are minimal and so flexed cones might appear to have double the crop size of unflexed cones, we probably could not detect the crop at all.

A final potential problem involves squirrel predation. In all conifer-dominated forests, squirrels are the major seed predators while the cones are still on the trees, clipping the pedicels so that cones fall to the ground for later retrieval. Cone removal begins in late July while cones are still green (Peters *et al.*, 2003). Pre-dispersal harvesting by squirrels in other forest types has been observed to range from 54% of sugar pine (Tevis Jr, 1953) to 80% of limber pine and southwestern white pine (Benkman *et al.*, 1984), and Peters *et al.* (2003) measured harvesting of 47.3 – 58.3% over three years of white spruce cone production. There is some evidence that mass crops are so large that squirrels can take only a small fraction, much smaller than that observed in the above studies. However, this predator satiation argument of Silvertown (1980) seems valid only for weevil infestation of the acorns of various oak species. The data on predation rates for conifer crops does not tend to show any inverse relationship between predation rate and crop size. We can imagine however that squirrel populations in a stand can fluctuate tremendously due to, for example, disease. If so, a multi-year study might reveal a very a noisy relationship between observed cone crop and reflectance values if the binocular estimations are done before August.

White and Engelmann spruce seldom form monocultures and I have offered above a number of speculations regarding the effect of other species within a stand. Many of the potential problems associated with non-cone components of stands could be dealt with via a linear spectral unmixing analysis. This assumes that pixel values are linear combinations of the reflectances of their constituents, called endmembers. Provided the number of endmembers doesn't exceed the number of spectral channels, this analysis is capable of resulting in images representing the fraction of each endmember on a pixel by pixel basis, essentially mapping the spatial variation of each element (Brown, 2001). While typically performed with hyperspectral data, due to the greater number of narrow spectral bands, Adams *et al,* (1995) demonstrated the effectiveness of multispectral unmixing in mapping land cover change in the Amazon basin, and Brown (2001) employed the results of a unmixing analysis to adjust vegetation indices to improve correlation with LAI.

There is an unresolved issue: when and where should one collect the stand data on cone production? One can, as in Abitibi, estimate cone production from an edge during the year the crop is produced. But this value then has to be extrapolated into the forest a few tens of meters away from that edge. The approach carries a further problem: one may find out later that the already-selected stands are not available in a cloud-free Landsat image for the relevant time interval. It seems more useful to estimate the size of the fallen crop using traps that are emptied periodically (and over several years if this is to be a multi-year study). Of course, this would have to be done in many well-separated stands to increase the likelihood that a reasonable number will be found in cloud-free patches of subsequent imagery.

This study demonstrates the utility of Landsat TM imagery in evaluating the spectral effect of mass seed production of white spruce using vegetation indices compared across successive years. The incorporation of basal area per area data to control for stand composition further allows for the evaluation of the spatial variation of the magnitude of this effect. While the relationship between field estimates of cone production and the tested vegetation indices did not yield the expected results, the significant relationships found at the Kootenay study site indicate the potential for future research to better refine the method. One might conclude this thesis by talking about the many issues in forestry (e.g. predicting recruitment into small clearcuts) or applied ecology (e.g. the temporal fluctuations in the resources available to seed-eating animals; the weather cues that govern crop production) that could be better understood via this approach. But clearly we are very far from proving that the approach has the required versatility or accuracy to be of real use to forest managers or add even incrementally to those on-going discussions in the published literature.

FIGURES

Figure 1-1. Mass cone crop in Abitibi (2006)

Figure 4-1. Photographic and spectral comparison of *P. glauca* cones and needles at the beginning and end of August, 2005

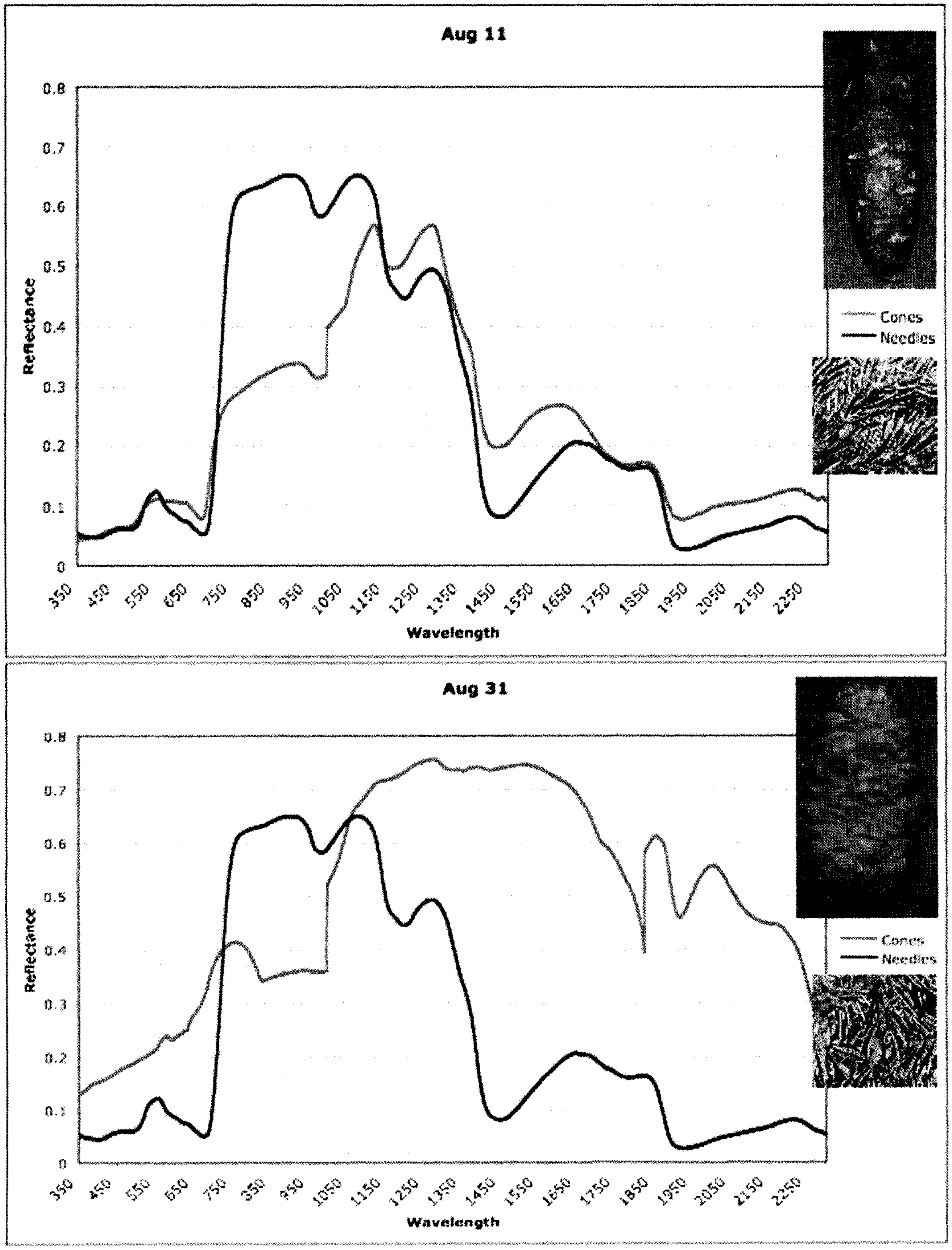


Figure 4-2. Spectral signatures of *P. glauca* cones at intervals throughout the 2005 growing season

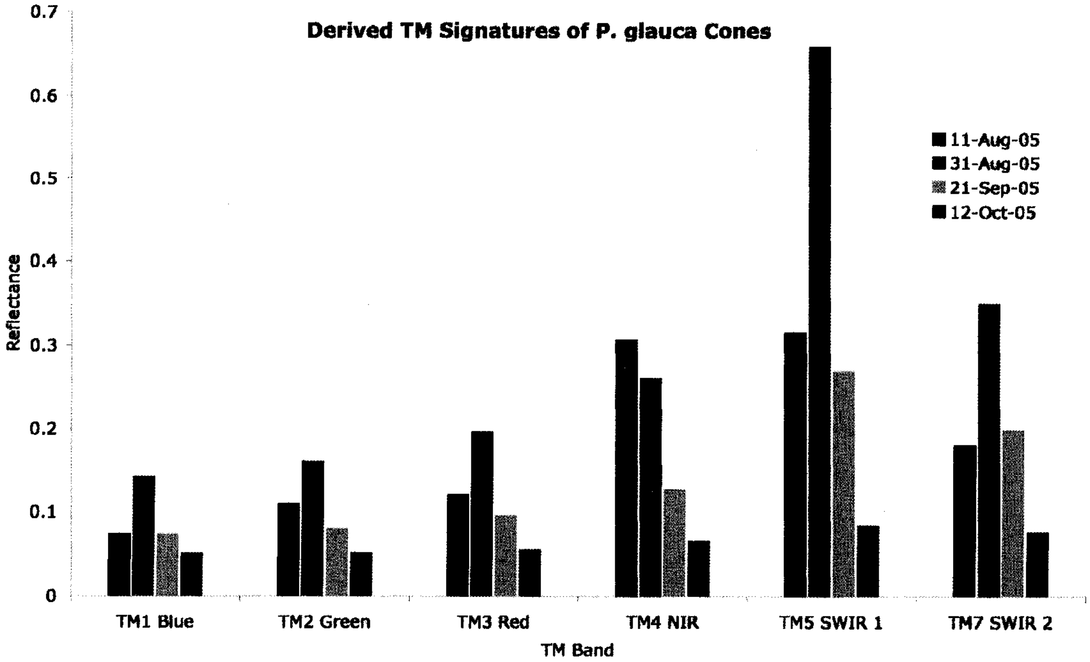


Figure 4-3. The eight vegetation indices, plotted by date. Indices were derived from bench hyperspectral data, averaged to simulate Landsat TM bands

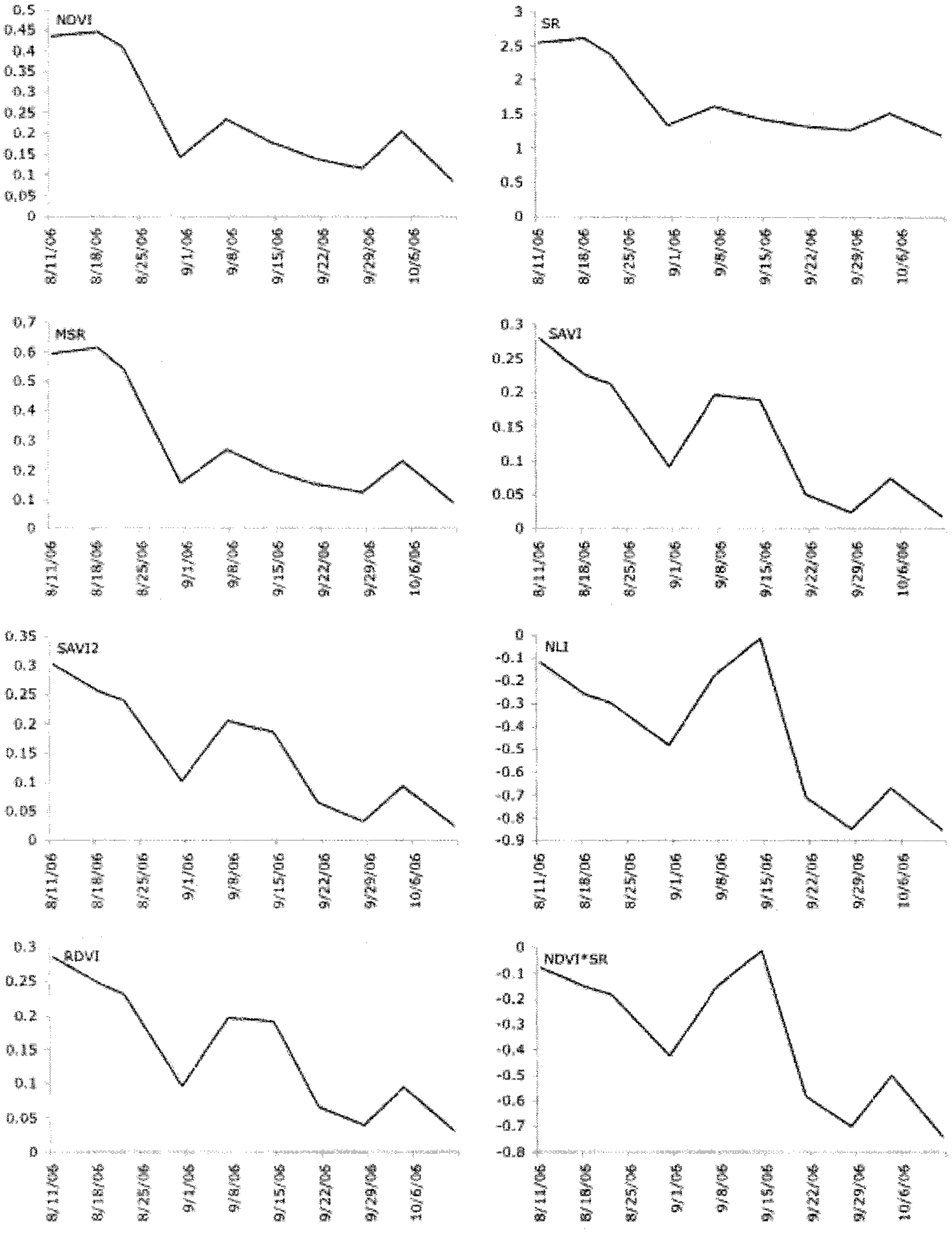


Figure 4-4. Percent composition of the Abitibi sites. WS=white spruce, OC=other conifer, BL=broadleaf

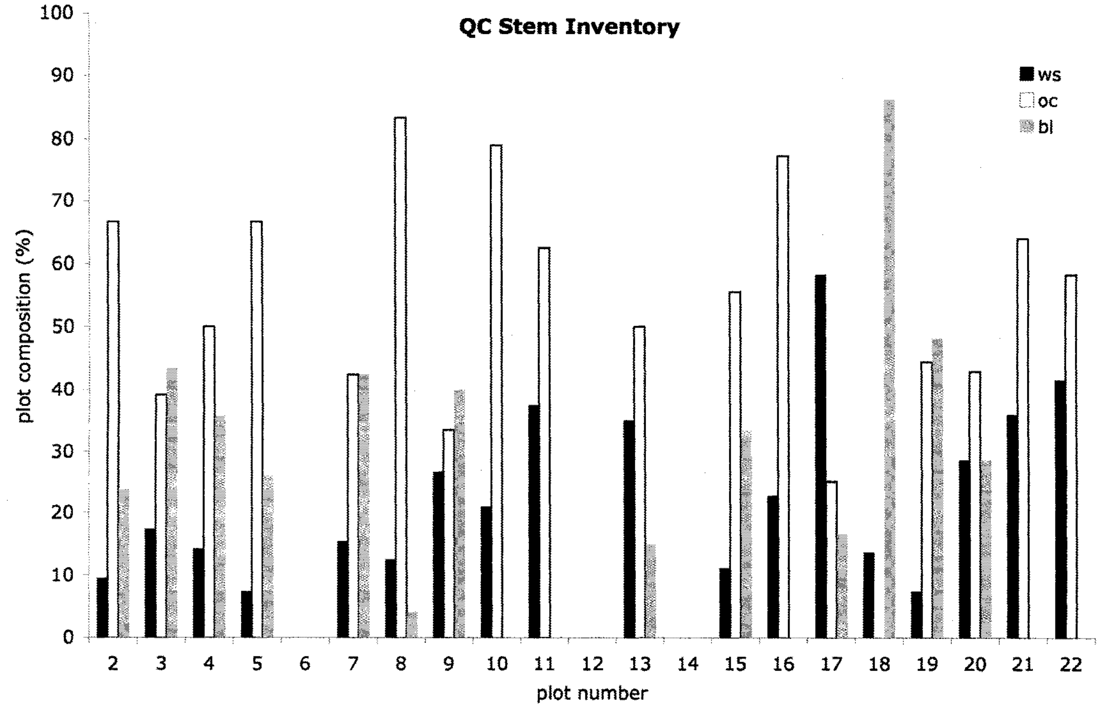


Figure 4-5. Red and near infrared (NIR) reflectance (%) for study sites in Kootenay during the mass seeding year (2003)

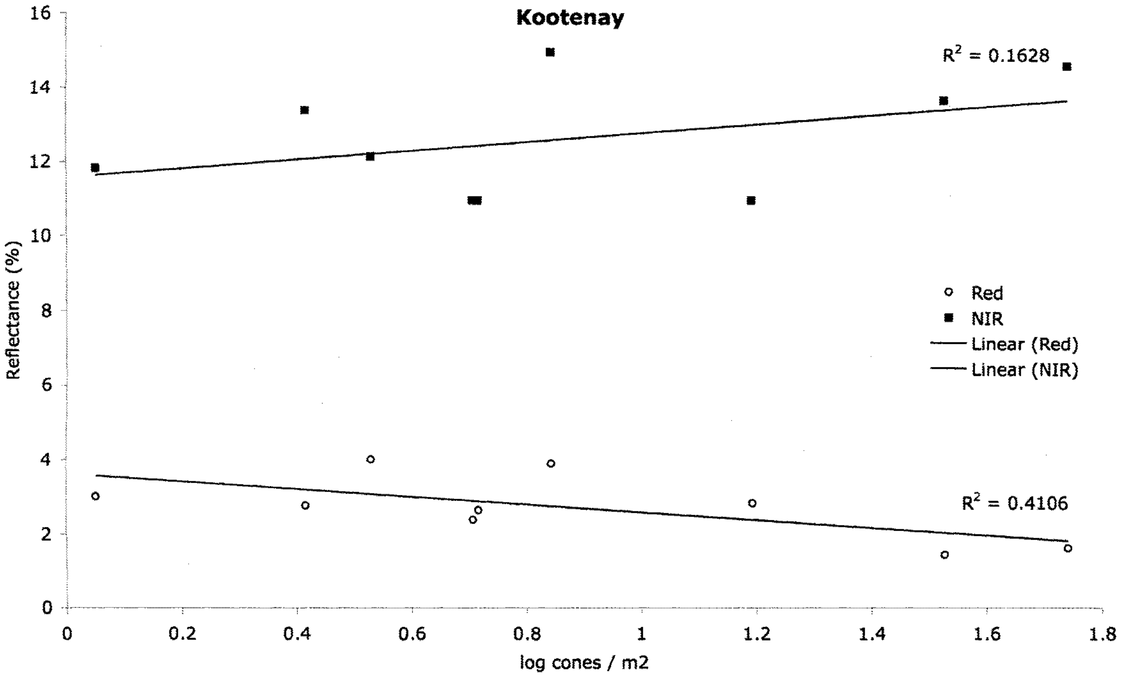


Figure 4-6. Red and near infrared (NIR) reflectance (%) for study sites in Abitibi (2006)

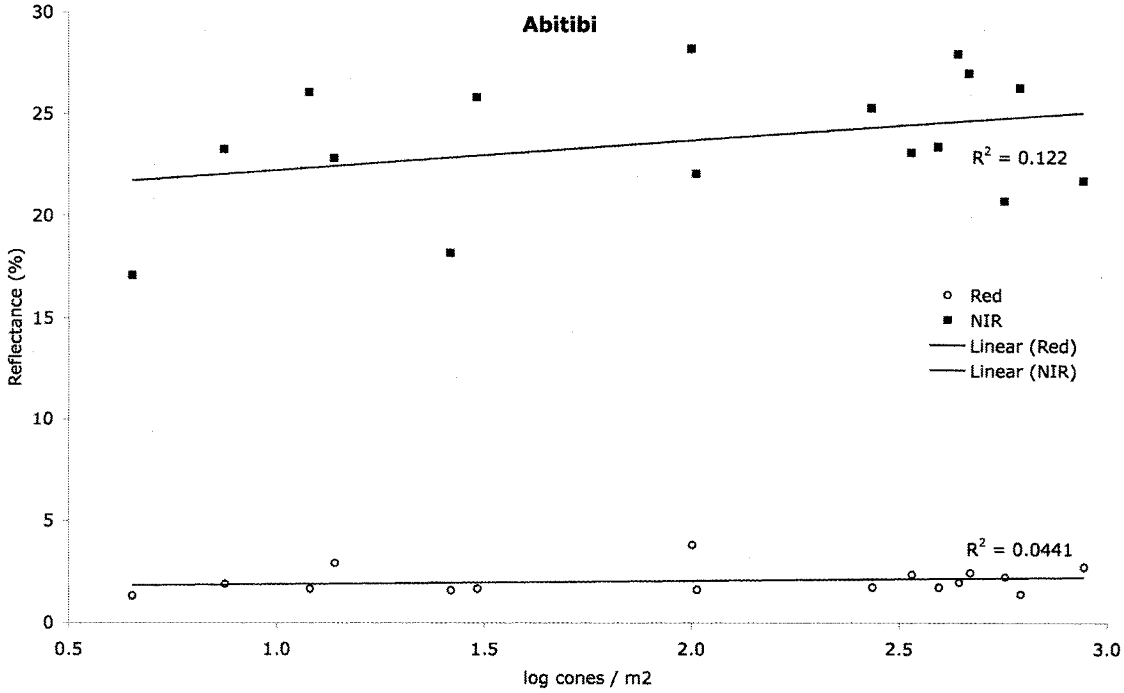


Figure 4-7. Vegetation index differencing for the Kootenay study sites (SR and MSR indices). The four categories at right are results for PIFs and the pine-dominated control sites

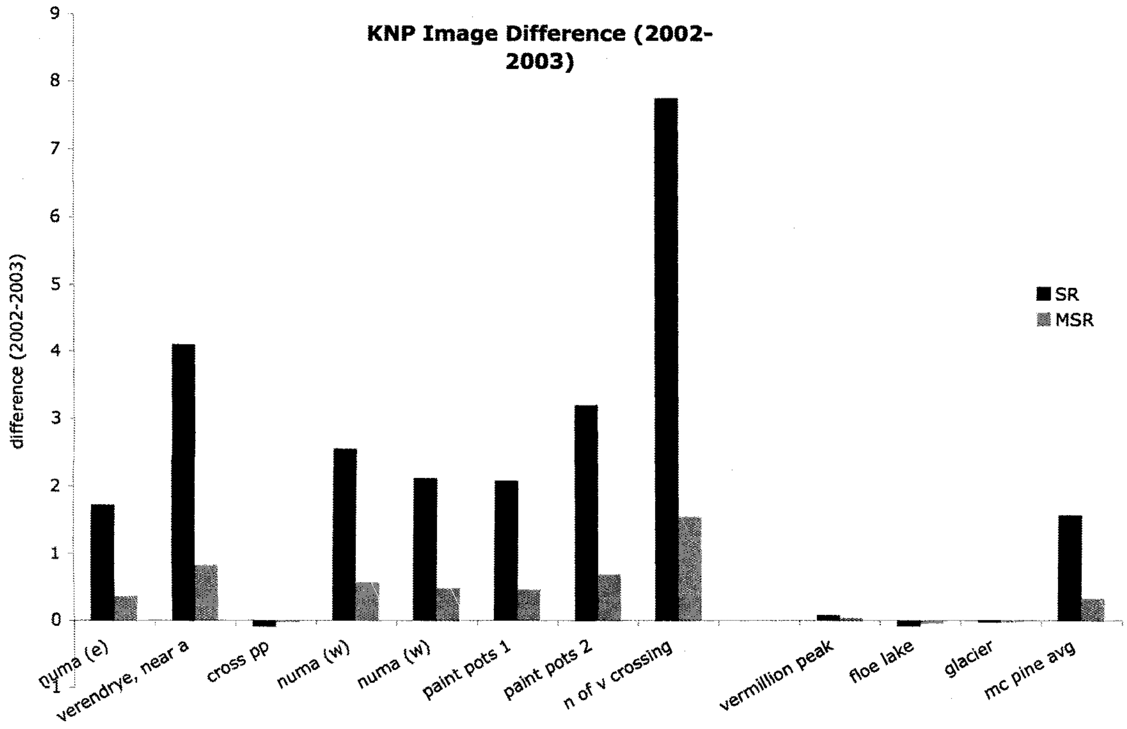


Figure 4-8. RGB Composite of the SR index results from 2002, 3, and 4, from Kootenay. A dominance of red (2002), green (2003), or blue (2004) in a part of the image indicates that the index value for that year was strongest, and is negatively related to cone production

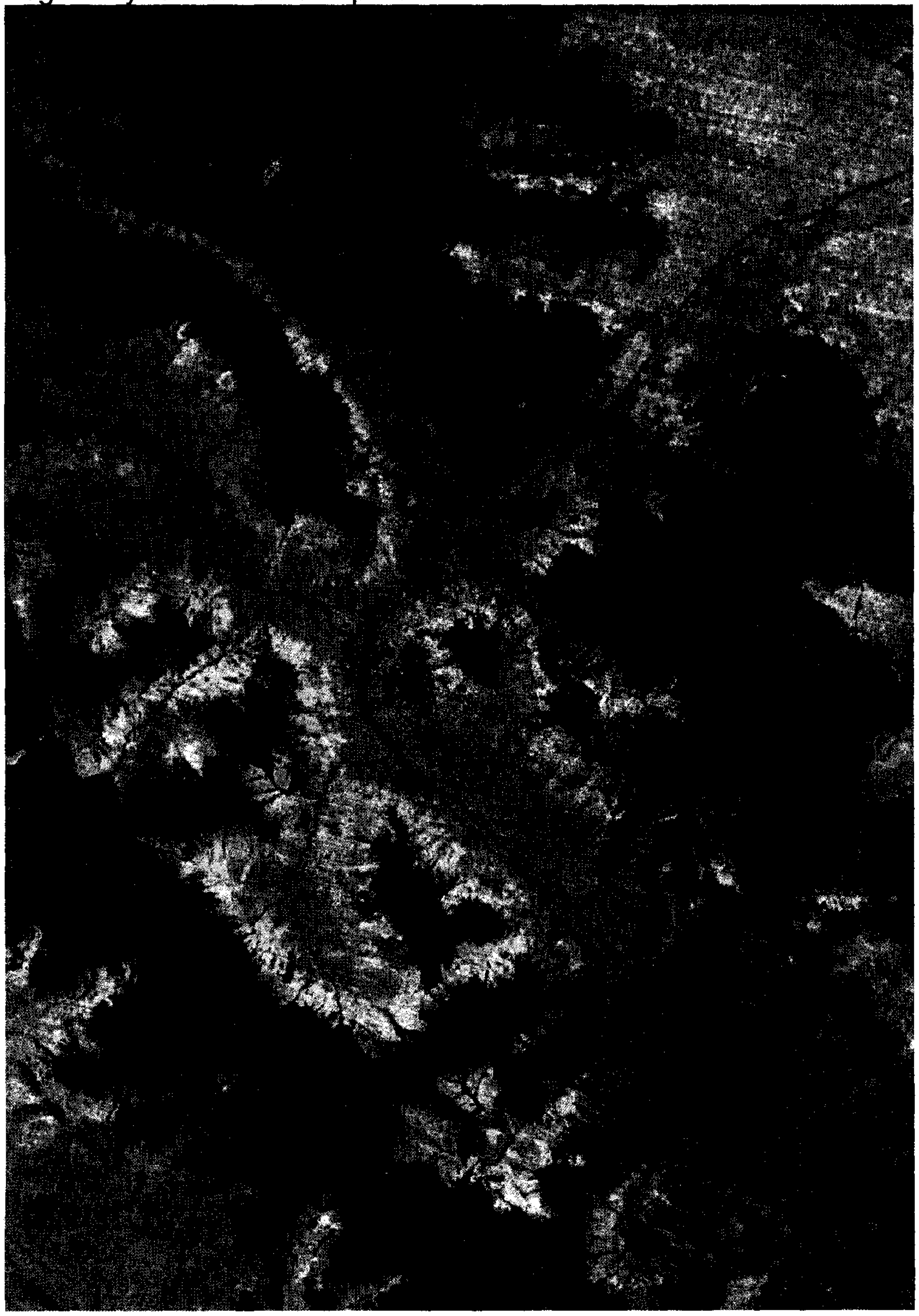


Figure 4-9. RGB Composite of the MSR index results from 2002, 3, and 4, from Kootenay. A dominance of red (2002), green (2003), or blue (2004) in a part of the image indicates that the index value for that year was strongest, and is negatively related to cone production

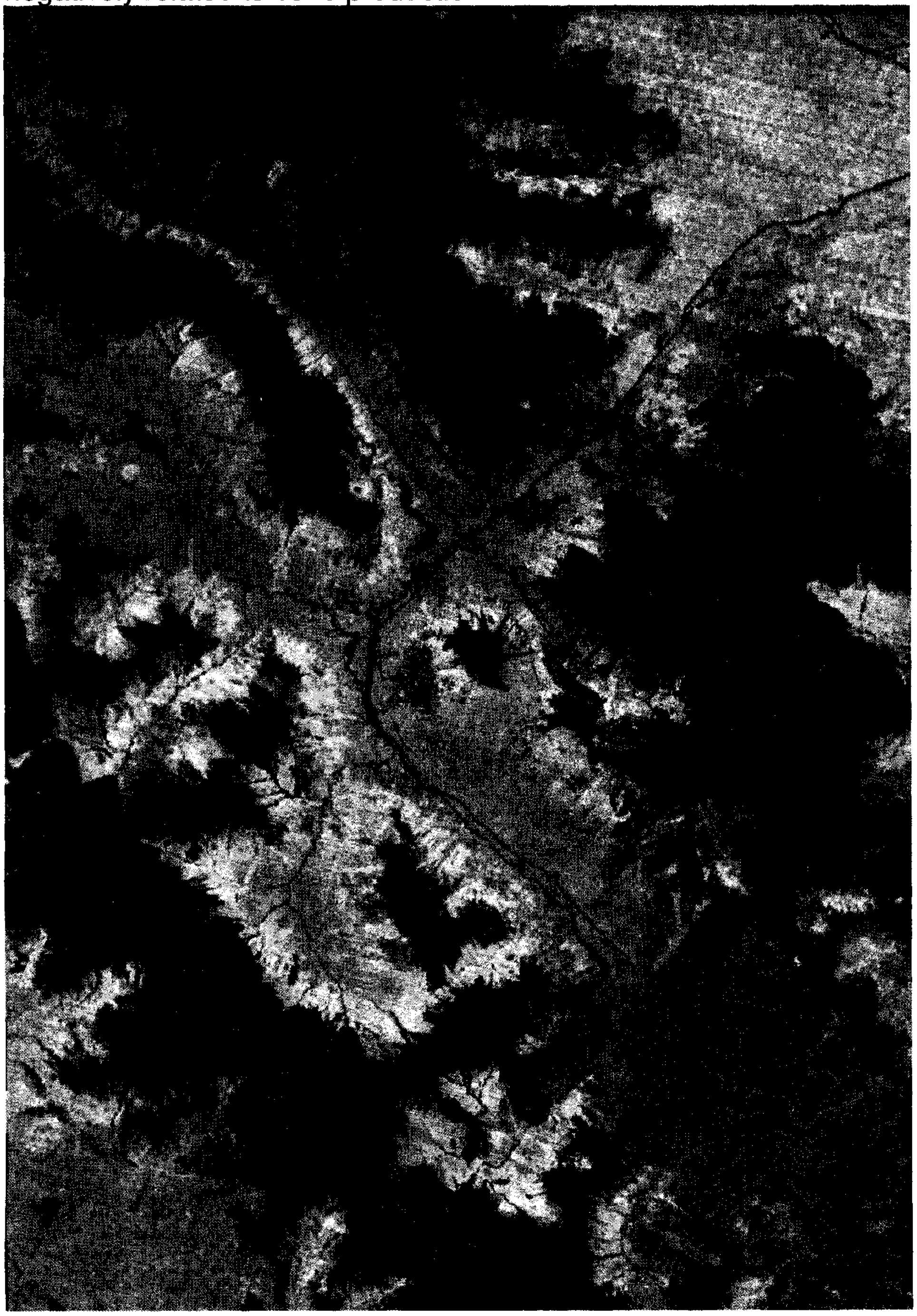


Figure 4-10. Regressions for cones/m^2 vs. the eight vegetation indices for Kootenay (all values are log transformed)

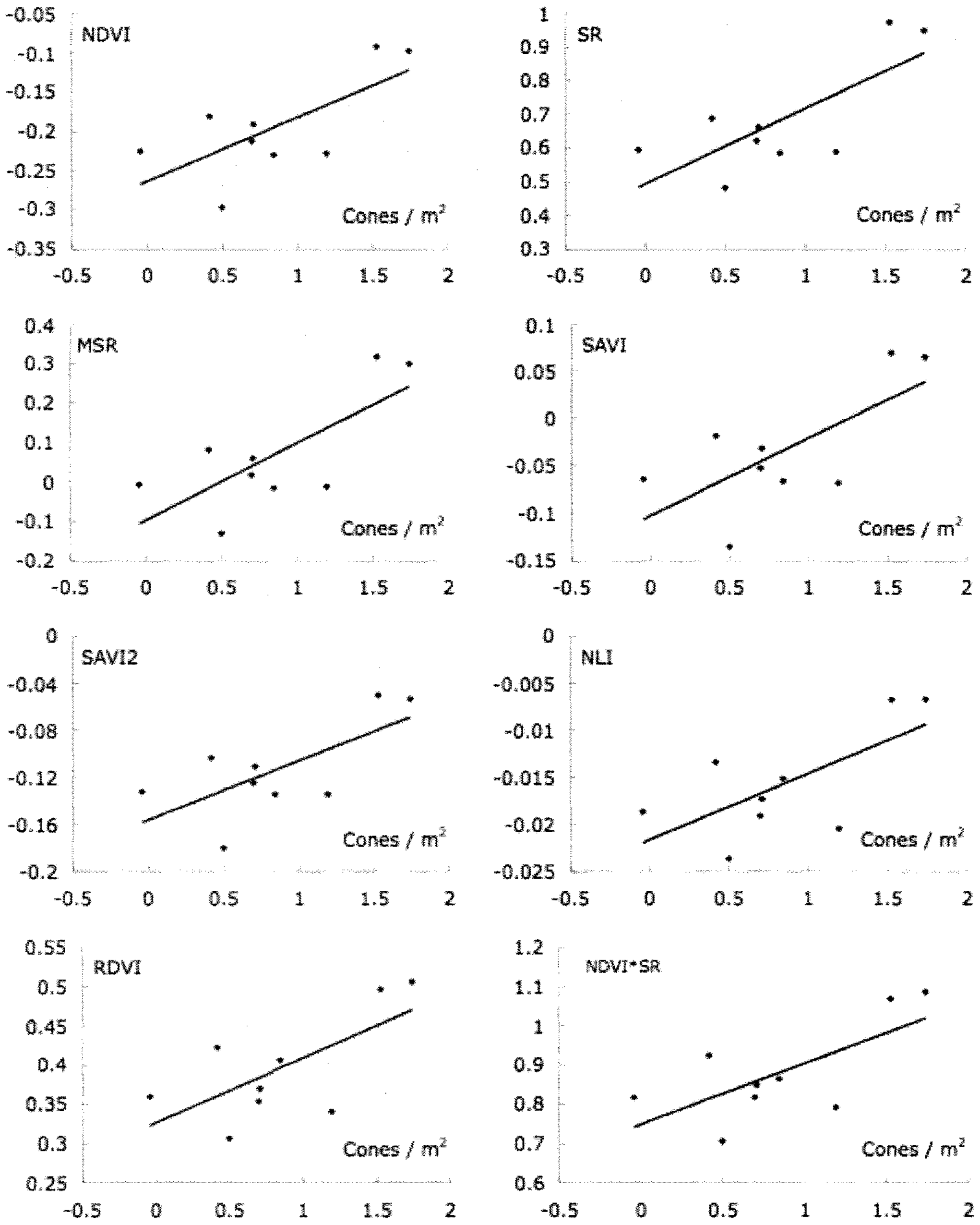


Figure 4-11. Relationship between spruce basal area per area (m^2/ha) and the 2002-2003 SR and vegetation index (VI) differences for Kootenay

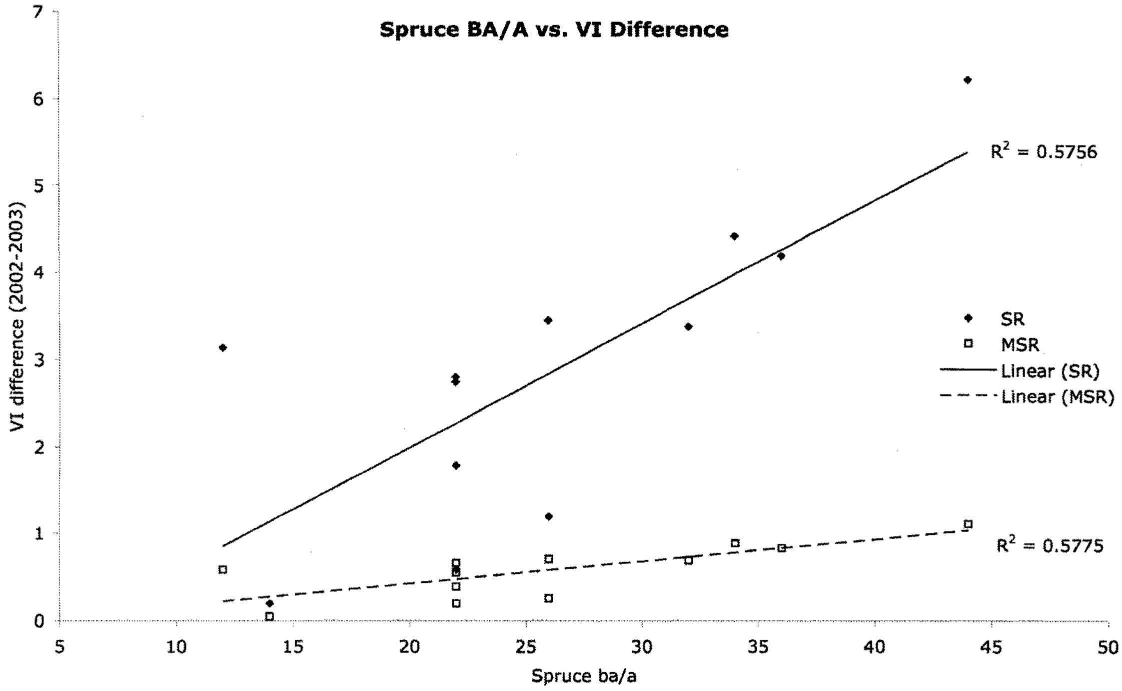


Figure 4-12. Relationship between spruce basal area per area (m^2/ha) and the 2002/2003 SR and MSR vegetation index ratios for Kootenay

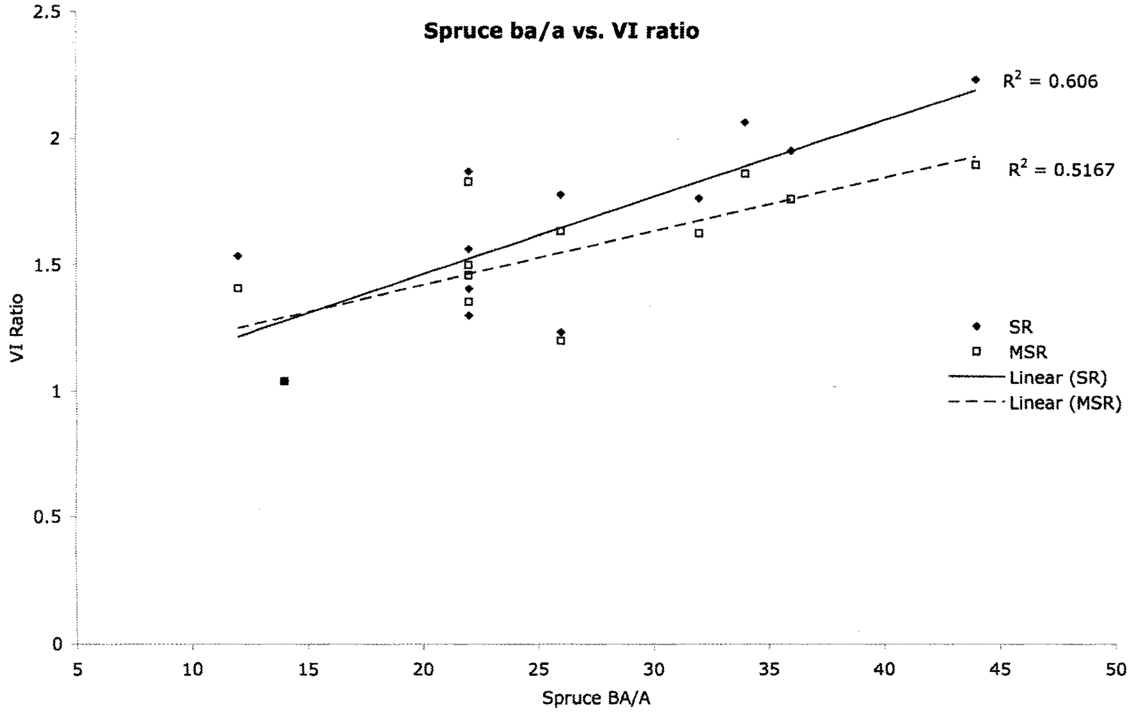


Figure 4-13. Relationship between the spruce contribution to stand composition (%) and the 2002-2003 SR and MSR vegetation index differences for Kootenay

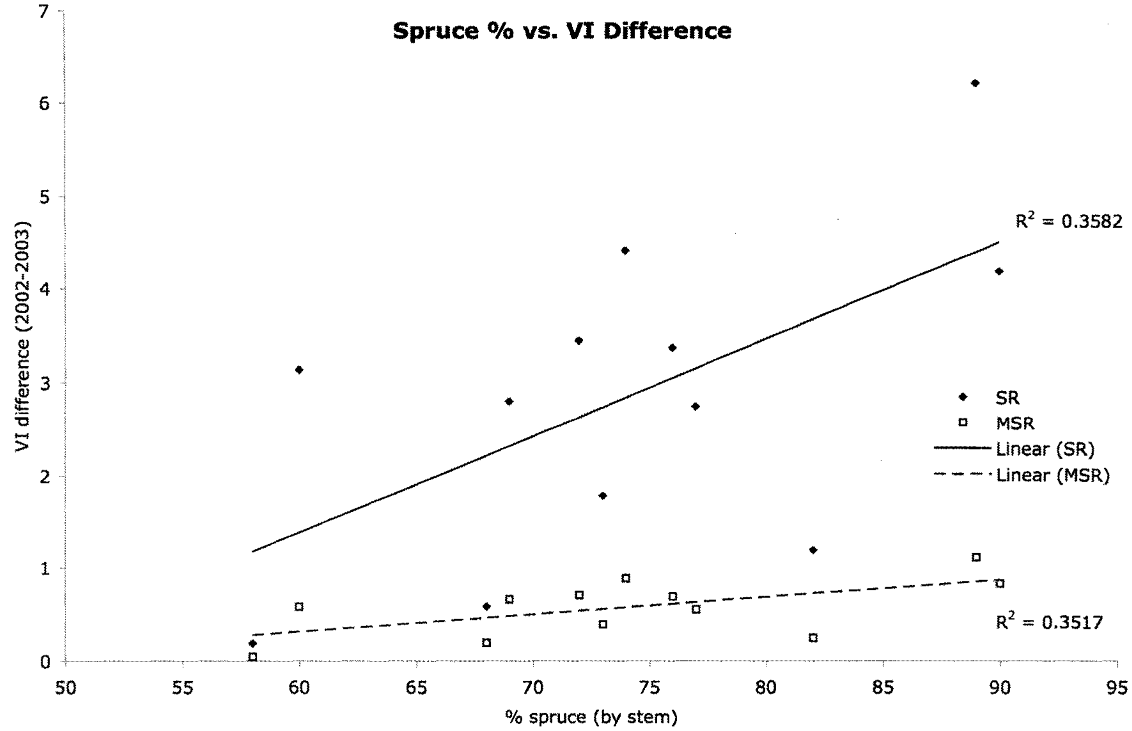


Figure 4-14. Vegetation index differencing for the Abitibi study sites (SR and MSR indices). The five categories at right are results for the PIFs

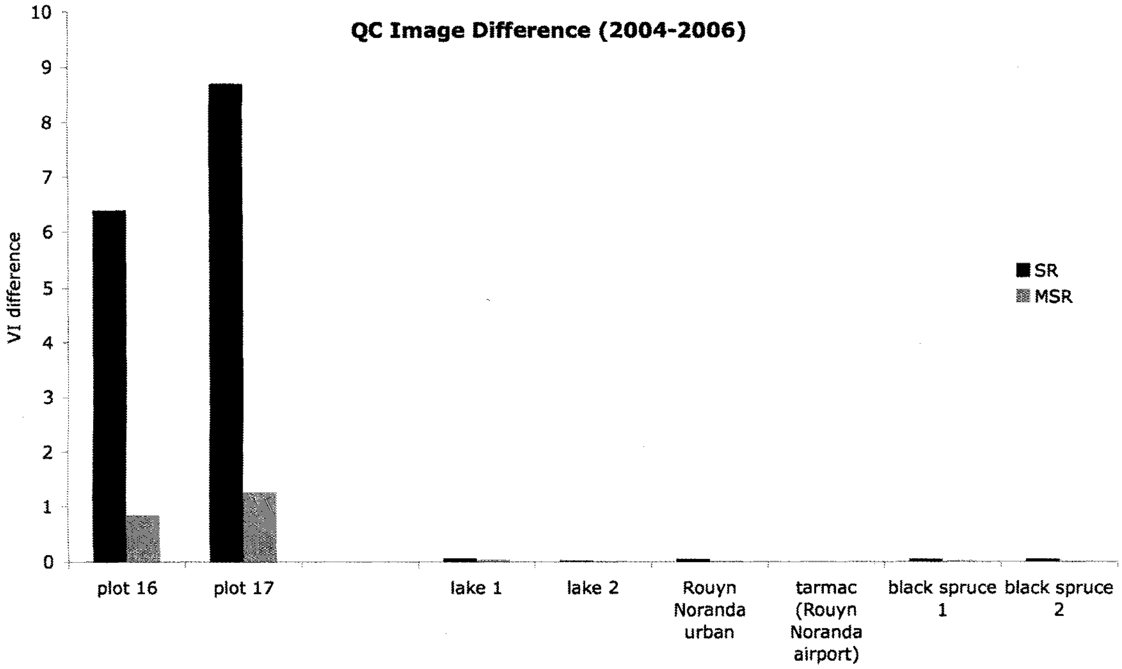
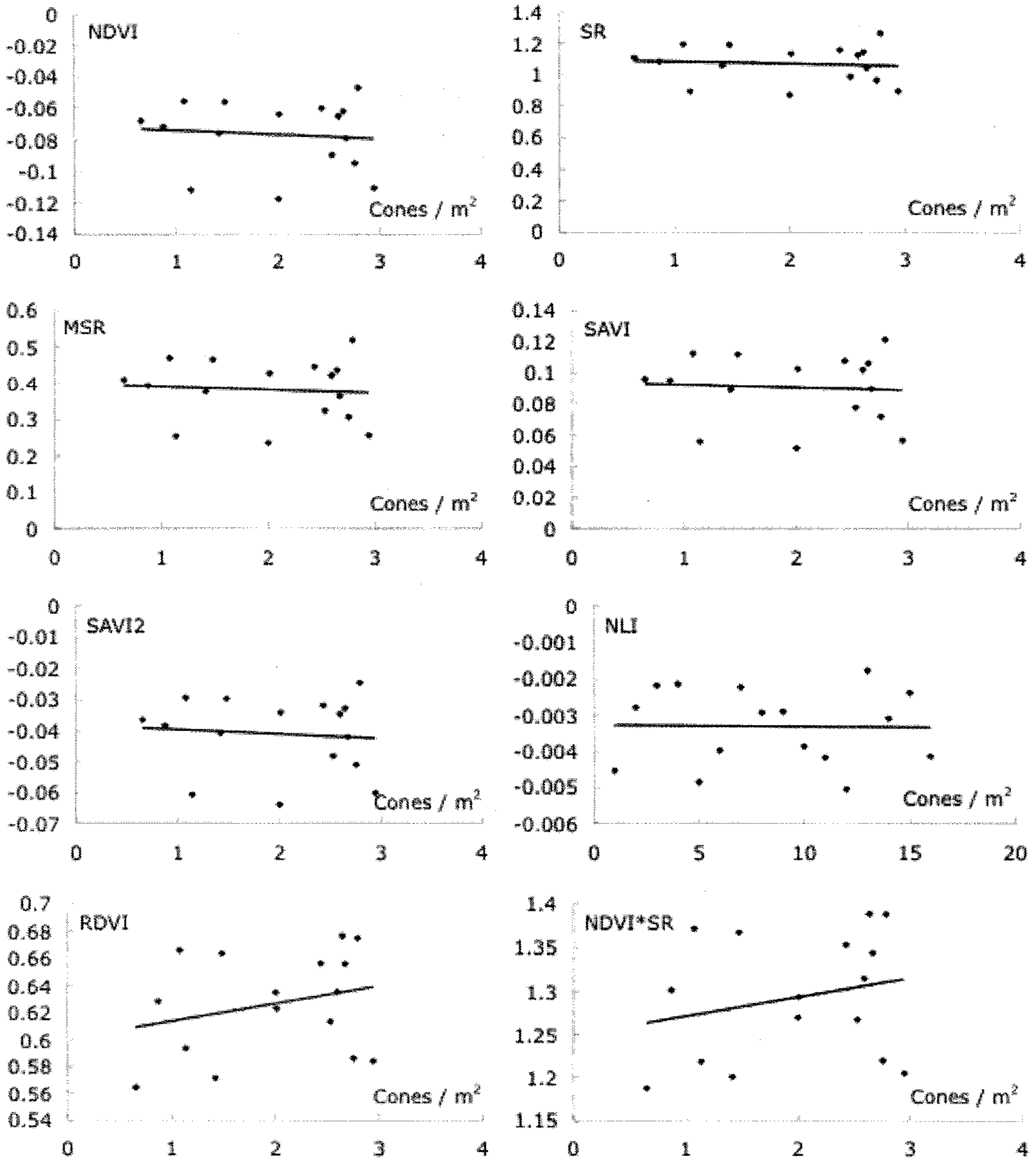


Figure 4-15. Regressions for cones/m^2 vs. the eight vegetation indices for Abitibi (all values are log transformed)



TABLES

Table 3-1. Vegetation Indices used in the study

NDVI – Normalized Differential Vegetation Index	$(\rho NIR - \rho R) / (\rho NIR + \rho R)$
SR – Simple Ratio	$\rho NIR / \rho R$
MSR – Modified Simple Ratio	$\left(\left(\frac{\rho NIR}{\rho R}\right) - 1\right) \Big/ \left(\sqrt{\left(\frac{\rho NIR}{\rho R}\right)} + 1\right)$
SAVI – Soil Adjusted Vegetation Index	$((\rho NIR - \rho R) * 1.5) / (\rho NIR + \rho R + 0.5)$
SAVI2 – Soil Adjusted Vegetation Index (modified)	$(\rho NIR + 0.5) - \sqrt{(\rho NIR + 0.5)^2 - (2 * (\rho NIR - \rho R))}$
NLI – Nonlinear Index	$(\rho NIR^2 - \rho R) / (\rho NIR^2 + \rho R)$
RDVI – Renormalized Differential Vegetation Index	$(\rho NIR - \rho R) / (\rho NIR + \rho R)^{0.5}$
NDVI*SR	$(\rho NIR^2 - \rho R) / (\rho NIR + \rho R^2)$

Table 4-1. Summary statistics for cones/m^2 at the two study areas. Kootenay values represent the combined sites for both years, although 2002 contributed almost nothing to the sums. N=20 and 21 stands for Kootenay and Abitibi

	Kootenay	Abitibi
Min	1.13	0.00
Max	55.08	238.98
Median	5.13	26.71
Mean	10.65	65.33
Std Dev	13.54	72.60
Coef. of Var.	1.27	1.23

Table 4-2. Summary statistics for basal area per area (m^2/ha) at the two study areas

	Kootenay (all species)	Abitibi	Kootenay (Spruce only)
Min	25.20	0.00	13.45
Max	203.42	70.00	183.43
Median	64.92	31.00	64.92
Mean	76.01	28.71	68.34
Std Dev	42.68	21.35	42.90
Coef. of Var.	0.56	0.74	0.63

Table 4-3. Vegetation index difference values for the eight indices tested in Kootenay. The top eight lines are the study sites, the bottom four are PIFs and the pine control sites

	NDVI	SR	MSR	SAVI2	SAVI	NLI	RDVI	NDVI*SR
numa (e)	0.0773	1.7197	0.3604	0.0532	0.0532	0.0532	0.0532	0.0532
verendrye, near a	0.1672	4.1071	0.8293	0.1206	0.1206	0.1206	0.1206	0.1206
cross pp	-0.0055	-0.0853	-0.0200	-0.0088	-0.0088	-0.0088	-0.0088	-0.0088
numa (w)	0.1420	2.5526	0.5679	0.1036	0.1036	0.1036	0.1036	0.1036
numa (w)	0.1234	2.1111	0.4775	0.0914	0.0914	0.0914	0.0914	0.0914
paint pots 1	0.1108	2.0714	0.4564	0.0797	0.0797	0.0797	0.0797	0.0797
paint pots 2	0.1593	3.1989	0.6871	0.1157	0.1157	0.1157	0.1157	0.1157
n of v crossing	0.3264	7.7545	1.5431	0.2418	0.2418	0.2418	0.2418	0.2418
vermillion peak	0.0416	0.0781	0.0403	0.0867	0.0867	0.0867	0.0867	0.0867
floe lake	-0.0396	-0.0812	-0.0401	-0.0500	-0.0500	-0.0500	-0.0500	-0.0500
glacier	-0.0128	-0.0260	-0.0129	-0.0247	-0.0247	-0.0247	-0.0247	-0.0247
mc pine avg	0.0727	1.5768	0.3327	0.0509	0.0509	0.0509	0.0509	0.0509

Table 4-4 Regression models for cones/m^2 vs VIs, both log transformed, for Kootenay and Abitibi. Entries in bold are significant ($p<0.05$)

	Kootenay		Abitibi	
y	model	R^2	model	R^2
NDVI	**0.0813x - 0.2636**	**0.4827**	-0.0027x - 0.0714	0.009
SR	**0.225x + 0.4942**	**0.5562**	-0.012x + 1.0947	0.0061
MSR	**0.1935x - 0.0951**	**0.5332**	-0.009x + 0.4014	0.0068
SAVI	**0.0814x - 0.1018**	**0.4846**	-0.002x + 0.0949	0.0051
SAVI2	**0.0501x - 0.1557**	**0.4691**	-0.0014x - 0.0381	0.0085
NLI	**0.007x - 0.0215**	**0.4487**	9E-05x - 0.0035	0.0046
RDVI	**0.0836x + 0.3256**	**0.4608**	0.0129x + 0.6012	0.0709
NDVI*SR	**0.1566x + 0.7491**	**0.4837**	0.0218x + 1.2494	0.057

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