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Prediction and assessment of bark beetle-induced mortality of lodgepole pine using estimates of stand vigor derived from remotely sensed data

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ABSTRACT

The current outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in British Columbia (BC), Canada, has led forest managers to consider thinning as a means of decreasing residual tree susceptibility to attack and subsequent mortality. Previous research indicates that susceptibility to mountain pine beetle is a function of a tree's physiological vigor and the intensity of attack. Trees able to produce ≥80 g (g) of wood per m^2 of projected leaf area annually are highly resistant, because they are able to shift resource allocation locally from wood to resin production to isolate blue-stain fungi introduced by attacking beetles. Typically, the leaf area of susceptible stands must be reduced by two-thirds to permit most residual trees to increase their vigor to a safe level. We evaluate whether Landsat Thematic Mapper (TM) imagery (30×30 m) provides a means to assess the maximum leaf area index (LAI) of unthinned stands and the extent that thinning reduces LAI. The extent that residual trees in thinned stands may have increased their resistance to attack from mountain pine beetle is predicted from a non-linear relationship between % maximum LAI and mean tree vigor.

We investigated the merits of this approach in the vicinity of Parson, British Columbia using four stands of lodgepole pine (*Pinus contorta* Dougl.), two of which were heavily thinned (stands were spaced to 4 and 5 m, approximately 70% reduction in stand density). An analysis of archived Landsat TM imagery indicated that prior to thinning in 1993, all four stands had full canopy, which, for mature stands, would translate to mean tree vigor between 40 and 70 g of annual wood production per m^2 of foliage. By 1995, based on estimated changes in LAI derived from a second data of Landsat TM imagery, stand vigor in the unthinned stands had not changed; however, in the thinned stands, a nearly two third reduction in LAI resulted in a predicted increase in vigor to between 100 and 160 g wood m^{-2} of leaf area. A subsequent assessment in 2001 indicated that stand vigor remained higher in the thinned stands relative to the control stands. Following an infestation of mountain pine beetle in the study area in 2002, mortality data indicated that the thinned stands experienced no mortality relative to the unthinned stands which experienced 5.5% mortality in the initial years of the attack. In the larger area surrounding the study site, a general relationship was found between predicted stand vigor and mountain pine beetle-induced mortality as estimated from aerial overview survey data ($r^2=0.43$, $p<0.01$).

1. Introduction

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) infestations have impacted large areas of lodgepole pine (*Pinus contorta* Dougl.) forests in British Columbia, Canada, increasing from 164,000 ha in 1999 to more than 11 million ha in 2007 (Westfall & Ebata, 2008). Scientists and forest managers have documented the range expansion of mountain pine beetle into areas at higher elevations (Logan & Powell, 2001), and to north-eastern British Columbia and Alberta (Carroll et al., 2004; Taylor et al., 2006). Tracking the location, spatial extent, and severity of mountain pine beetle outbreaks is typically accomplished using a hierarchy of data sources, ranging from coarse-scale aerial overview surveys to detailed ground surveys (Wulder et al., 2006a). Forest managers also use decision-support tools, such as susceptibility or risk-rating systems to estimate the likelihood of attack, evaluate mitigation options, and to implement policies to reduce the risk of future infestations. A variety of susceptibility and risk-rating systems have been developed to predict future insect activity (Hicks et al., 1987). Several of these classification schemes are specifically designed to describe the relationship between mountain pine beetle populations and forest stand conditions in a quantitative or qualitative manner (Bentz et al., 1993). Some rating systems are based on regional descriptions and current climatic characteristics, whilst others are

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based on stand and host tree characteristics within a defined climatic zone, and take into account differences in tree age, diameter, and stocking level (Safranyik et al., 1974; Amman et al., 1977).

Generally, outbreaks of mountain pine beetle are more likely to occur in lodgepole pine stands with trees older than 60 years and larger than 25 cm in diameter (Cole & Amman, 1969; Amman, 1978; Wellner, 1978). Larger diameter trees have thicker bark, which facilitates the construction of egg galleries, provides better protection from natural predators, and insulates against external temperature extremes and desiccation (Safranyik & Carroll, 2006). In addition, there is a positive relationship between tree diameter and phloem thickness (Amman, 1969; Shrimpton & Thomson, 1985), with the phloem being the primary nutrient source for the beetles and their larvae (Amman, 1972; Amman & Pace, 1976; Berryman, 1976; Klein et al., 1978). Thicker phloem results in larger broods, larger beetles, and enhanced survival rates (Safranyik & Carroll, 2006); however, phloem thickness is not directly related to a tree's ability to resist beetle attack (Shepherd, 1966). Large diameter trees appear more susceptible when their growth becomes reduced — either temporarily, through an event such as severe drought, or permanently, as a result of disease or mechanical damage. Experiments in Norway by Christiansen (1985) indicated that recent growth in basal area of Norway spruce (*Picea abies*) was a good indicator of tree resistance to *Ips typographus* because with greater growth, more resources are available to reallocate to resin production providing a defence against both beetles and blue-stain fungi.

There is debate over whether thinning is an effective treatment for managing mountain pine beetle infestations because it increases tree vigor (Mitchell et al., 1983; Waring & Pitman, 1985) or because thinning alters the microclimate (e.g., temperature and wind patterns), producing unfavourable conditions for beetles (Bartos & Amman, 1989; Amman & Logan, 1998). Regardless, increases to tree vigor and alterations to stand microclimate are both known outcomes of thinning treatments (Waring & O'Hara, 2005), and likely play some role in reducing stand susceptibility and subsequent mortality due to mountain pine beetle attack, although perhaps over different time horizons (Amman et al., 1977). In this paper, we use vigor as an indicator of stand susceptibility, although we acknowledge the role of microclimate and stand dynamics in determining susceptibility.

Stress, caused by factors such as competition or drought, will increase susceptibility of host trees to mountain pine beetle attack (Safranyik & Carroll, 2006). Under stress, growth is generally reduced more rapidly than leaf area, thereby reducing vigor (Waring & Pitman, 1985). Changes in leaf area is not captured in most forest inventories (which are the data commonly used to assign susceptibility ratings), nor are these attributes included in any of the existing susceptibility models for mountain pine beetle. Our ability to quantify changes in leaf area and to project growth over large areas would facilitate the development of management strategies in the face of new challenges such as climate change, which contribute to the range expansion of the mountain pine beetle (Carroll, 2007).

In this paper, we capitalize upon the linkage between maximum stand leaf area and stress and utilize relationships that relate reduction in stand leaf area to improvement in stand vigor. We apply our approach to four stands in British Columbia, where two were thinned prior to infestation. We first demonstrate the ability to predict stand leaf area index (LAI) with Landsat imagery, and then go on to model the extent that observed reductions in that variable might improve stand vigor. Ground-based observations, combined with aerial overview surveys of killed trees, serve to confirm whether an increase in stand vigor is matched by a decrease in tree mortality.

2. Methods

2.1. Site descriptions and field data sources

The study area is situated near the town of Parson located in south-eastern British Columbia, Canada (51° 05' N Latitude, 116° 39' W Longitude). Fig. 1 is an aerial photograph acquired by the BC Ministry

Fig. 1. True color aerial photograph of the Parson study site. In 1993, prior to the beetle infestation, thinning treatments and untreated controls were established in four mature lodgepole pine stands (Table 1). A and B are the control sites and C and D are thinned stands. The larger areas showing bare soil were clear felled. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of Forests and Range in 2000 depicting the study area. Whitehead and Russo (2005) report on the establishment of two thinning treatments and two untreated controls in four mature lodgepole pine stands (age 90–110 years) in 1994 (Table 1). Two 9-ha blocks were thinned to uniform 4 m and 5 m spacing (C and D in Fig. 1), while two adjacent stands were left untreated (A and B in Fig. 1). In 2002, a mountain pine beetle outbreak was underway in the area, with the ratio of currently attacked (green) to previously attacked (red) trees being 20 to 1 (known as the green to red attack ratio). In 2004, Whitehead and Russo conducted ground surveys over a sample of these four stands (Table 1 — area assessed) to determine the proportion of attack in each of the stands, the total number of attacks, the green-to-red ratio, and the amount of beetle-caused mortality. The unthinned control stands were 7.3% and 1.4% attacked, while the thinned stands were 0% and 0.4% (1 attacked tree). In terms of the proportion of trees in the stand that were killed, the unthinned stands experienced 5.5% and 0.9% mortality, while the mortality in the thinned stands was 0% (Whitehead & Russo, 2005).

2.2. Estimating vigor

Originally, Waring and Pitman (1980) defined tree vigor as the percentage of sapwood basal area accumulated in a year. Using this index, they found that no lodgepole pine attacked by mountain pine beetle was killed if annual growth exceeded 5% of sapwood basal area. At index values below 5%, proportionally fewer beetle attacks appeared required to kill a tree.

To make the index more physiological, Waring and Pitman (1985) established a linear relationship between sapwood basal area at breast height and leaf surface area, with each cm^2 of sapwood representing 0.15 m^2 of crown leaf area. They went on to convert growth in basal area to increment in stem volume and mass using locally-established allometric relationships.

In a regional thinning study, where the projected leaf area index (LAI) of unthinned stands varied from 2.6 to 7.5 m^2/m^2, Mitchell et al. (1983) noted that stands averaging >80 g of stemwood growth per square meter of leaf area suffered little mortality (Fig. 2a). We recognize that the maximum basal area of lodgepole pine stands varies with site index and approaches an asymptote by age 80 (Dahms, 1964; Cole & Edminster, 1985). Because sapwood in lodgepole pine makes up the majority of the stem cross-sectional area, we reanalyzed data presented by Mitchell et al. (1983) to express variation in mean stand vigor as a function of maximum LAI (Fig. 2b). The relationship is highly significant ($r^2=0.90$, $p<0.001$), and indicates that regardless of the site potential, fully stocked mature stands of lodgepole pine can be expected to exhibit low vigor ratings, averaging ~40 g wood produced annually per square meter of leaf area. The relationship between maximum basal area and mean stand vigor was identical in form to that shown with maximum LAI.

It is recognized that the ratio of sapwood to leaf area, as well as the allometric relations between stem diameter and wood mass may change with geography (Kolb et al., 2007), but we assume, without the availability of locally-derived information, that the general relationship between maximum basal area and maximum leaf area that was found at the sites sampled by Mitchell et al. (1983) still hold in British Columbia.

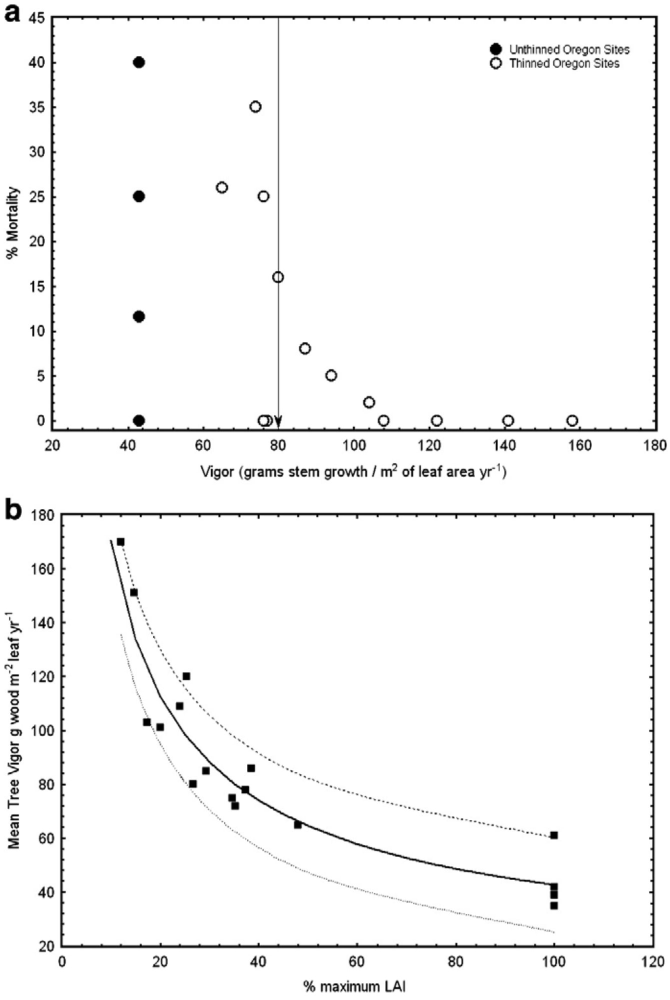

Fig. 2. (a). Although tree mortality varied in lodgepole pine stands attacked by mountain pine beetle in Oregon, those with a mean vigor index >80 generally lost <10% of total stocking during an epidemic (after Mitchell et al., 1983). Fig. 2(b).There is a non-linear correlation between mean tree vigor and the percentage of leaf area (LAI) present in reference to the maximum ($617(\%\text{max LAI})^{-0.5764}$) that is highly significant ($r^2=0.90$, $p<0.001$) (after Mitchell et al. (1983). This relationship (with 95% confidence bounds) provides the foundation for the use of remote sensing techniques to estimate mean stand vigor.

Table 1

Properties of the lodgepole pine stands at the Parson site in 1994, from Whitehead and Russo (2005).

Site ID	Treatment	Mean density	DBH	Basal area	Age	Evidence of attack	G:R ratio	Mortality
		(stems ha^{-1})	(cm)	$\text{m}^2\ \text{ha}^{-1}$	(years)	(%)		(%)
A	Unthinned 1	770	28.2	48.1	90	7.3	2.9	5.5
B	Unthinned 2	1089	24.1	49.7	90	1.4	0.3	0.9
C	Spaced to 4 m	386	22.3	15.1	110	7.3	0	0.0
D	Spaced to 5 m	258	25.3	13.0	90	1.4	0	0.0

During an epidemic outbreak of mountain pine beetle, we would expect tree mortality to be much higher in unthinned stands than in heavily thinned stands described in Table 1. The challenge to applying this basic understanding of tree health to large areas is dependent on the accuracy by which changes in LAI can be monitored with remotely sensed imagery.

2.3. Remotely sensed data

LAI is a very commonly measured vegetation biophysical characteristic and has become a central and basic descriptor of vegetation condition in a large range of studies (Asner et al., 2003). Optical remote sensing does not directly measure LAI, rather observations of reflected radiation from the vegetation canopy are converted to LAI estimates from field studies or modelling (Myneni et al., 1997). These developed relationships have been found to differ depending on the vegetation biome, and can become less accurate depending on atmospheric and geolocation errors with the remotely sensed data. In addition scaling field studies to larger satellite pixels (such as pixels up to 1–5 km) is an ongoing area of research (Cohen et al., 2006). In this paper we utilised a similar approach to Cohen et al. (2003) to model LAI from 30 m spatial resolution Landsat-5 Thematic Mapper (TM) imagery using regression analysis which a popular empirical method for modelling the relationship between spectral values and LAI (Chen & Cihlar, 1996, Turner et al., 1999, Cohen et al., 2003).

Four Landsat scenes (with a nominal 30 m spatial resolution) were acquired over the Parson site pre- (1993) and post-thinning (1995), and pre- (2001) and post-infestation (2007) of mountain pine beetle (Table 2). Both Landsat-5 TM and Landsat-7 Enhanced Thematic Mapper Plus (ETM+) images are utilized in this study. These images were all captured within the summer/fall seasonal window to maximise the amount of red attack damage and associated changes in spectral reflectance (see Wulder et al., 2006b). Data pre-processing involved two critical steps. First image-to-image geometric registration was undertaken using a nearest-neighbour 2nd order polynomial transformation to minimise any geometric offsets or distortions within the image stack. Then the 1995 orthorectified image was used as the base image to which all other images were referenced to with a root mean square error <0.5 pixels (<15 m).

As variations attributed to different atmospheric conditions, solar angle, and sensor characteristics are likely to limit the ability to characterise spectral change associated with mountain pine beetle attack (Chen et al., 2005), the second critical step involved the radiometric normalisation of images to ensure that changes in spectral reflectance between years correspond to meaningful physiological events. To do this, we first atmospherically corrected the 1995 base image to derive surface reflectance using the COST model (that corrects for cosine of the solar zenith angle) (Chavez, 1996). Next, we utilised the Multivariate Alteration Detection (MAD) algorithm to normalize the multi-date imagery (Canty et al., 2004; Schroeder et al., 2006) which utilises canonical correlation analysis to locate invariant pixels for use in matching the remaining images to our atmospherically corrected base image. The invariant pixels located within each of the image subsets were used to develop band-wide regression equations for relative normalization. MAD has the advantage of being an automated approach that has been demonstrated to work well in forested landscapes. We applied this approach to correct all images for atmospheric effects while simultaneously converting to units of surface reflectance (Schroeder et al., 2006). Our implementation of the MAD algorithm followed that of Schroeder et al. (2006), differing only through our use of four 1000×1000 pixel image subsets (instead of one) to locate invariant pixels. Using additional image subsets will ensure that the full range of spectral variation is sampled, as a single subset may not cover a sufficient range of cover types.

To predict LAI from the processed Landsat imagery, we utilised the regression parameters developed for LAI of lodgepole pine and other coniferous species under similar ecological conditions by White et al. (1997) in Glacier National Park, approximately 200 km from the Parson site. To derive LAI, the broad-band simple ratio (SR) vegetation index was used, as recommended by White et al. (1997). We also had available standard forestry inventory maps of the region derived from aerial photography where forest stands were optically delineated by trained interpreters. Stands were assigned damage categories and digitized according to Vegetation Resources Inventory (VRI) standards (BC MSRM, 2002) with each forest stand delineated as a separate polygon and labelled with a unique identification number and a series of attributes that included species composition. From this layer we created an analysis mask to restrict the analysis to those stands that the inventory indicated contained lodgepole pine. We then interrogated those stands, over the entire scene to extract the stand with the maximum LAI observed in 1993 (pre thinning and infestation) which was then used as the maximum LAI value required for the sites in Fig. 2b.

Table 2
Landsat imagery and dates when stand conditions were sampled.

Imagery	Date image acquired	Stand condition
Landsat-5 TM	9th Sept. 1993	Pre-thinning
Landsat-5 TM	13th July 1995	Post-thinning
Landsat-7 ETM+	23rd Sept. 2001	Pre-major beetle infestation
Landsat-5 TM	15th August 2007	Post-major beetle infestation

2.4. Aerial surveys of beetle mortality

Detailed aerial surveys of mountain pine beetle damage are conducted over forest management units using a helicopter with a GPS receiver and a trained observer who records the centroid of individual infestation clusters (hereafter noted as heli-GPS). For each point, the number of infested trees are recorded. Heli-GPS surveys are considered by the British Columbia Ministry of Forests to be the “operational benchmark for accuracy, delivery time, and cost for detailed aerial surveys” and “the most commonly used detailed aerial survey method at this time”. Whilst aerial survey data does provide important information on tree infestation it has the same limitations as other targeted forest heath surveys in that there is a greater likelihood of omission error, resulting from the typical non-systematic nature of the survey design, and the collection of damage information exclusive of data for healthy trees. As a result mortality figures, as a percent of total number of trees is not possible to estimate. Heli-GPS locations are estimated to be spatially accurate to within ±20 m however the size of the clusters of trees can vary and the cluster area, shape, and compactness are not recorded. Nelson et al. (2006) assessed the accuracy of heli-GPS survey points with concurrently collected field data, and found that 92.6% of the heli-GPS survey points had errors of ±10 trees. Heli-GPS surveys from 2004 to 2005 were used in this study.

In addition to the detailed aerial survey data available from provincial agencies, we recognized that Landsat imagery can also be used to detect mountain pine beetle red attack damage (Franklin et al., 2003; Skakun et al., 2003; Wulder et al., 2006b,c). When the spectral Landsat channels are re-projected along the principal directions of brightness, greenness, and wetness (known as the Tasseled Cap Transformation (TCT) (Kauth & Thomas, 1976; Crist & Cicone, 1984; Crist et al., 1986)), information can be acquired on tree mortality, as well as natural and anthropogenic disturbances (Healey et al., 2005). Following examples in the literature illustrating the strength of approaches based upon the TCT for capturing change, the Enhanced Wetness Difference Index (EWDI) was developed (Franklin et al., 2000, 2001). Skakun et al. (2003) developed an approach for identifying trees killed by mountain pine beetle (red attack) based upon the application of a user defined threshold to the differences found between the TCT wetness components for two dates of imagery (EWDI). The results of this type of threshold based approach are products that are binary in nature, with pixels identified as either having dead trees (red crowns), or not having red-attack damage. The EWDI is calculated by subtracting the wetness values from the most recent image date (T2) from the wetness values from the older image date (T1) (Wulder et al., 2006c). Positive values therefore represent a relative decrease in moisture and are correlated with red crowns of trees killed by mountain pine beetle (Franklin et al., 2003; Skakun et al., 2003; Wulder et al., 2006c). To synoptically assess stand infestation levels over the areas surrounding the study site, we utilized a pair of Landsat scenes that corresponded to pre- (2001) and post-infestation (2007) periods. Following the creation of a TCT for each of the calibrated Landsat TM and ETM+ images, an EWDI was derived by subtracting the 2007 wetness value (post-infestation) from that acquired in 2001 (pre-infestation). The heli-GPS data coordinates indicating stands of beetle induced mortality were then overlaid and the EWDI of the individual pixel locations compared.

We utilised Landsat imagery to predict stand LAI for our four stands (two control and two thinned stands) at Parsons, British

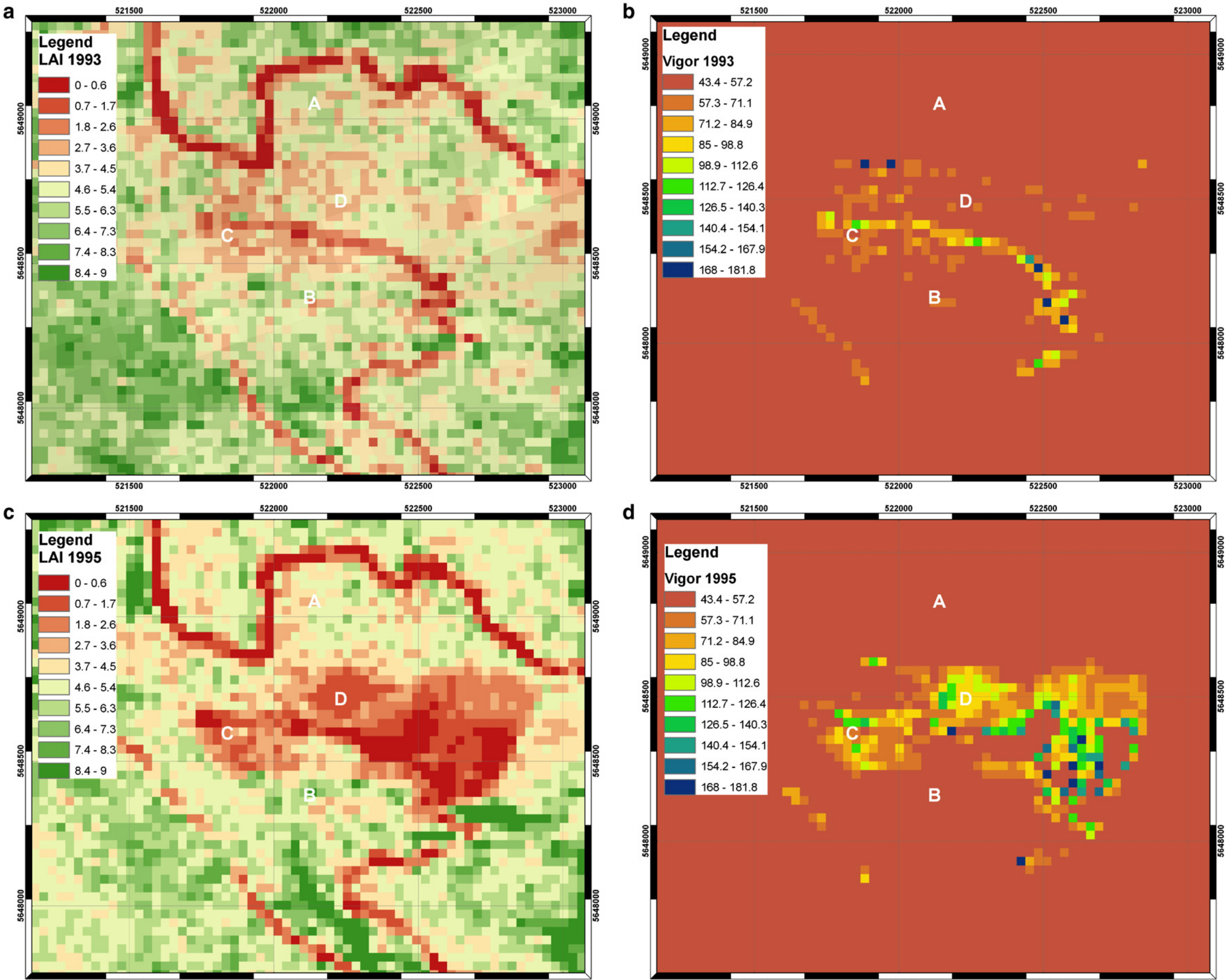

Fig. 3. Landsat Thematic Mapper predictions of LAI in (a) 1993 [pre-thinning] and (c) 1995 [post-thinning], and predicted stand vigor in (b) 1993, and (d) 1995.

Columbia, and the surrounding area. We quantified LAI of the thinned and unthinned stands and surrounding area in 1997 (post-thinning), 2001 (pre-beetle infestation), and 2007 (post-beetle infestation). To identify the impact of mountain pine beetle within our four sites and in the surrounding area, we used ground surveys collected in 2004, detailed aerial surveys collected in 2004 and 2005, and a synoptic map of red attack damage generated from an EWDI approach using Landsat imagery from 2001 and 2007 (Table 2). We then compared these estimates of damage to vigor ratings derived from the relationship between vigor and proportion of maximum LAI shown in Fig. 2b.

3. Results

The Landsat predicted LAI and vigor pre- and post-thinning are shown in Fig. 3(a)–(d). In Fig. 3(a), all four stands have moderate LAI with pixels ranging from 1.9–6.6 prior to thinning (mean = 4.8), as would be expected in 90–110 year-old lodgepole pine stands. In Fig. 3(b), the predicted values for vigor pre-thinning, were estimated using the relationship developed in Fig. 2b, indicating a range in vigor estimates from 41–80 g (mean = 60 g) of wood production per m^2 of foliage. In 1995, the thinned areas are visible in Fig. 3(c) and (d), with mean LAI values reduced by two-thirds (1.2–1.8) resulting in a predicted increase in mean vigor (100–160 g) (Fig. 3d).

The variation in LAI among the four stands from 1993 to 2001 is shown in Fig. 4a. To obtain these values, the stand boundaries of the four thinning experiments (the two thinned stands and two controls) were delineated from the aerial photography and that boundary used to extract both the mean and the standard deviation (shown as box and whiskers) in Landsat derived LAI for each stand. Using the equation derived from Fig. 2b, vigor was estimated for each stand (Fig. 4b). The trend in LAI of the control stands from 1993 to 2001 (pre-outbreak) is what one would expect for mature lodgepole pine, between 4.8 and 5.5 (as summarised in Reed et al., 1999). Following thinning, the estimated LAI in 1995 ranged between 1.5 and 2.0, or about 30–36% of the maximum mean LAI value for all lodgepole pine stands in the scene in 1993. The maximum LAI across all lodgepole pine stands in the scene prior to thinning in 1993 was 8.0. This reduction in LAI would result, according the relationship in Fig. 2b, in an increase in mean tree vigor from 40 g pre-thinning to 100–160 g post-thinning. By 2001, the LAI of the thinned stands remained significantly lower than the unthinned stands at 2.8–3.0 LAI, equivalent to vigor ratings between 82 and 86 g wood production per m^2 of foliage, still above the threshold value where trees should be susceptible to beetle attack.

Prediction of LAI in 2007 shows a general reduction in LAI due to beetle mortality and the locations of stands with red attack mortality identified in detailed aerial surveys in 2004 and 2005 are shown overlaid as red points, scaled in size according to the number of observed trees in the heli-GPS surveys (Fig. 5).

Fig. 6 shows the relationship between number of kill trees due to beetle infestation (from the heli-GPS surveys) and vigor, as derive from the 2001 Landsat image. The relationship as expected, is noisy, given the natural variability in the stands, however, the figure indicates that stands with higher vigor have fewer trees killed by the beetle. An envelope regression line, fitted to the number of trees killed in relation to maximum observed vigor, presents a significant negative power relationship ($r^2 = 0.43$, $p<0.01$).

Finally, at the landscape level we compared the impact of the beetle as estimated by the EWDI with the 2001 vigor estimates. At each heli-GPS site we extracted the EWDI values calculated between 2001 and 2007. As anticipated heli-GPS locations where dead (red) crowns were present are associated with higher EWDI values (indicative of a loss of moisture in the crown), and at sites where the thinning had been undertaken there is a relative increase in the canopy wetness index from 2001 to 2007 (Fig. 7).

4. Discussion

Although it is common knowledge that poor sites support less biomass than good sites, and also proportionally less basal area and leaf area (see review by Waring, 1983), this paper differs from previous bark beetle susceptibility rating systems by defining an appropriate thinning regime in reference to maximum stand LAI rather than some fixed level of basal area or tree spacing. In this study, the maximum LAI for the four stands assessed in this study was typical, around 5.0, but on poorer sites values <3.0 have been reported, and on better sites >7.0 (Mitchell et al., 1983). The maximum LAI inferred through remotely sensed indices has been linearly related to site productivity across a wide range in environments (Waring et al., 2005).

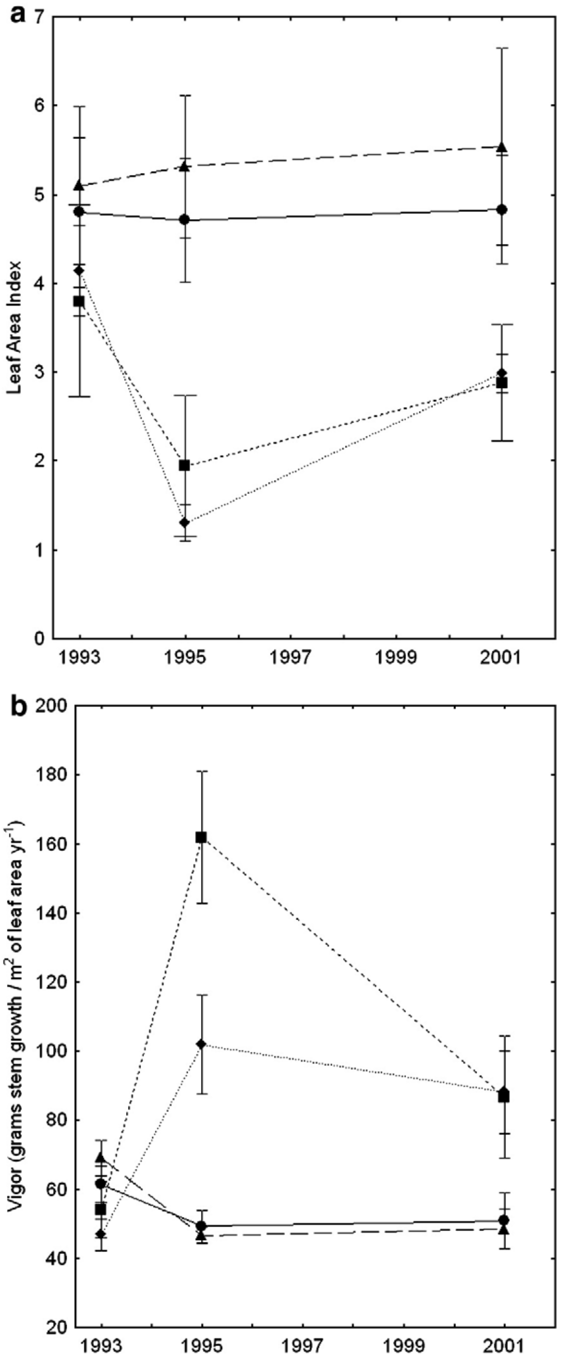

Fig. 4. Predictions of the mean and standard deviation of (a) LAI and (b) vigor for the 2 thinned (■ (C), ♦(D)) and 2 control sites (▲(A),●(B)) (Area assessed 1.9–2.9 ha).

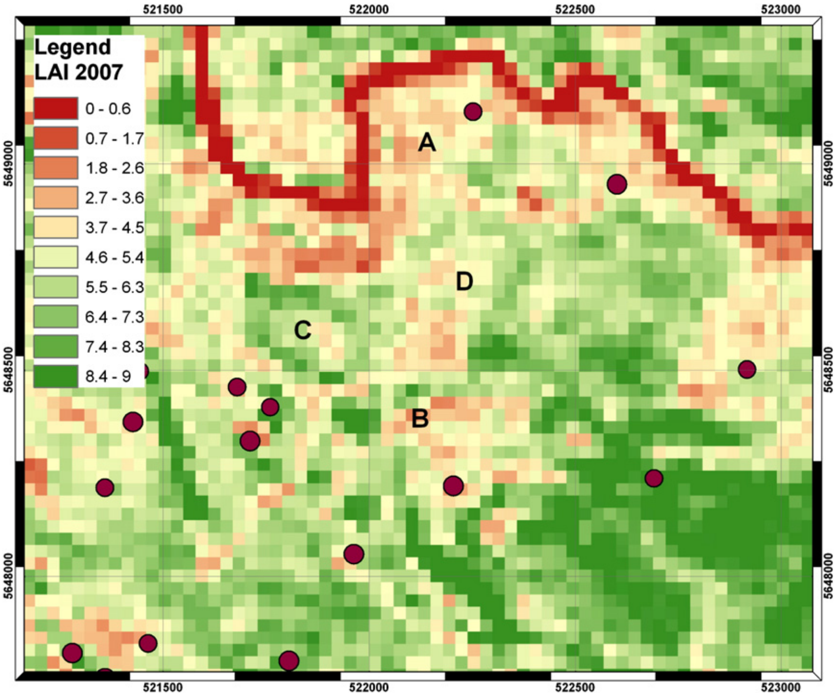

Fig. 5. LAI derived from the Landsat TM image acquired in 2007 shows the compartments where stands were thinned and the surrounding forest. The general low LAI in many compartments reflect the impact of the beetle infestation on the landscape. Locations where red (dead) trees were observed from aerial surveys in 2004 and 2005 are also identified.

The application of the model described in this paper relating vigor to stand maximum LAI is based on a number of assumptions:

1) that stands have not been previously thinned;
2) that stands have reached an age where growth in basal area has reached a plateau;
3) that initial stocking density was not so high as to cause growth stagnation;
4) that thinned trees were not previously injured; and
5) that a sustained drought or chronic air pollution will limit the response to thinning.

Furthermore, we note from long-term thinning experiments designed to maintain a narrow range in basal area that surviving trees develop crowns that provide a higher vigor rating than would be the case if thinning is delayed until stands are mature (Waring, 1983).

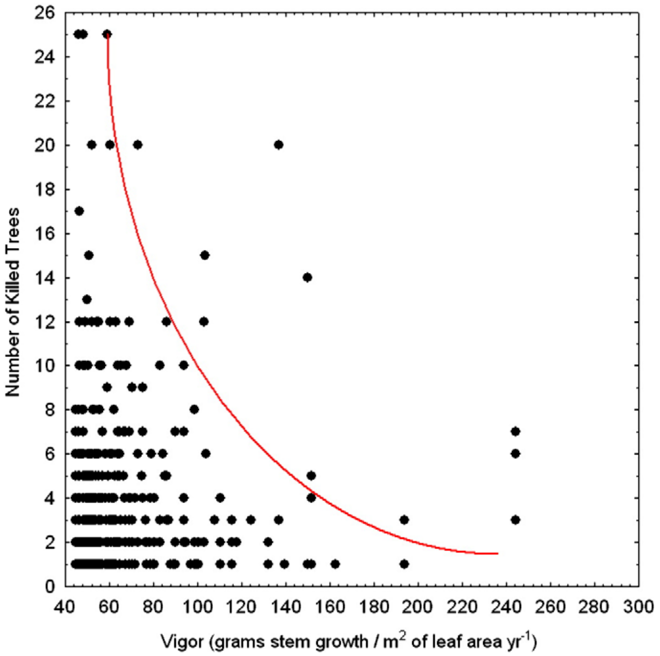

Fig. 6. Relationship between number of observed red-attack trees from the heli-GPS surveys, and 2001 vigor as predicted from the Landsat imagery. The regression line is a power relationship fit to the maximum vigor observed for different levels of tree mortality ($r^2 = 0.43$, $p < 0.01$).

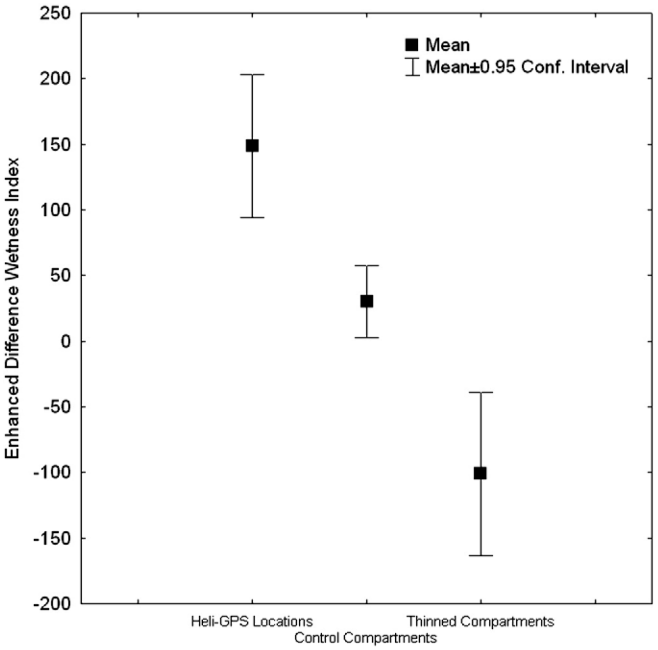

Fig. 7. The enhanced difference wetness index (EWDI) derived from Landsat imagery discriminates between those sites with the highest mortality (mapped via helicopter observations), unthinned control units, and compartments in which stands were heavily thinned before the bark beetle infestation.

In the context of assessing vigor, age is an important variable to consider since, as all yield tables show, volume increment decreases with age. In lodgepole pine stands that are older than 80 years, trees are likely to have approached their maximum height and basal area (Dahms, 1964; Cole & Edminster, 1985). When lodgepole pine regenerates after a fire, the stocking density may often well exceed 10,000 trees ha^{-1}. Under such competition for resources, few trees are able to achieve dominance. As a result, the growth of such overstocked stands stagnates. In these stand conditions, thinning may provide an opportunity for trees to grow to a size susceptible to bark beetle attack, without the commensurate increase in vigor that would increase the tree's resistance to attack. Likewise, trees that have been mechanically injured, burned, or subjected to previous attack by insects or disease may not respond to the extent predicted by the model. Similarly, no response from thinning should be expected during a prolonged drought (Kolb et al., 2007). When a thinning treatment is imposed, it is important to provide even spacing around those trees marked to remain. Otherwise, wood production is not likely to be evenly distributed and beetles may be successful at strip attacks — where the beetles make inoperative a portion of the water conducting sapwood, as observed by Waring and Pitman (1983).

5. Conclusion

The results presented in the paper demonstrate that changes in LAI in response to thinning are observable on Landsat imagery, at the forest management scale, and that the values predicted match those reported in previous studies (White et al., 1997). Similarly over a landscape, using polygons of forest stands derived from standard forest inventory it is possible to estimate what the maximum LAI is of the region for a given species and age combination. Using these two pieces of information we have demonstrated it is possible to compute the LAI as a function of the maximum LAI of the species in the region and then apply existing functions which relate the relative proportion of stand LAI to maximum possible LAI to stand vigor. In turn, we believe vigor is a very useful indicator of the likely response of a forest stand to insect infestation, as demonstrated here using the mountain pine beetle infestation as an example. We acknowledge the challenges of, at the individual stand level, acquiring validation data on LAI, vigor, and mortality rates, pre- and post-infestation and thus validation is exceedingly difficult. As a result we were limited to using historical data from a very small number of stands collated as part of reviews by Whitehead and Russo (2005) and other disparate datasets such as heli-GPS and differenced Landsat imagery. We hope however in this paper that demonstrating the use of Landsat imagery to predict vigor may allow additional studies to be undertaken to further test the utility and generality of these types of relationships at different sites and under different conditions. The lack of field data also highlights the needs for these types of remotely sensed image-based approaches, which could potentially be useful for extrapolating vigor and predicting stand responses to events such as insect infestations, at the landscape level.

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