

SPATIOTEMPORAL RELATIONSHIPS BETWEEN CLIMATE AND WHITEBARK
PINE MORTALITY IN THE GREATER YELLOWSTONE ECOSYSTEM

by

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DEDICATION

This thesis is dedicated to my mother, Jean Haughey Jewett (1945 – 2008). Thank you for providing a loving, nurturing environment where learning and education were both valued and expected. I hope I can emulate your perseverance in the face of adversity. Thank you for teaching me how to write, and probably more importantly, how to edit. I am sure this would have been better if you could have helped me edit it, Mom, but I did the best I could without you.

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ABBREVIATIONS USED

6S	Second Simulation of the Satellite Signal in the Solar Spectrum, a method of atmospherically correcting satellite imagery
ANUSPLIN	Spline-based method for interpolating climate data, used to create WorldClim climate dataset
ATCOR3	a method of atmospheric and topographic correction of satellite imagery
DDE	Dataset Deviance Explained, analogous to R^2 in linear regression
DEM	Digital Elevation Model
DOS	Dark Object Subtraction, a method of atmospheric correction
E1	Expectation 1, that warmer temperatures lead to increased whitebark pine mortality and negative EWDI values
E2	Expectation 2, that drier conditions lead to increased whitebark pine mortality and negative EWDI values
E3	Expectation 3, that previous mountain pine beetle activity in or near a cell decreases current mountain pine beetle activity, leading to positive EWDI values
ETM+	Landsat Enhanced Thematic Mapper Plus, found on Landsat 7
EWDI	Enhanced Wetness Difference Index, the difference in Tasseled Cap Wetness between two dates of imagery
GYA	Greater Yellowstone Area
GYE	Greater Yellowstone Ecosystem
LANDFIRE	Landscape Fire and Resource Management Planning Tools Project, used to delineate wildfire perimeters
MPB	Mountain Pine Beetle(s), (<i>Dendroctonus ponderosae</i>)
NDFI	Normalized Difference Forest Index
NDMI	Normalized Difference Moisture Index
NLCD	National Land Cover Database
NDVI	Normalized Difference Vegetation Index
NDVI _c	NDVI with a middle-infrared-based adjustment for forest canopy closure
PRISM	Parameter-elevation Regressions on Independent Slopes Model, a climate dataset
RMSE	Root Mean Square Error
SCP	Supercooling point, indicator of maximum cold-hardiness in MPB
SLC	Scan Line Corrector, a component of Landsat ETM+ that failed, leaving data gaps in imagery (“SLC-off”) after May 2003
SNOTEL	Snowpack Telemetry, automated weather stations, usually in remote/mountainous locations
TC _{Wet}	Tasseled Cap Wetness, the third component of the Tasseled Cap transformation of Landsat data, sensitive to soil/canopy moisture
TM	Landsat Thematic Mapper, found on Landsat 4 and Landsat 5

ABBREVIATIONS USED – CONTINUED

USFS	United States Forest Service
USGS	United States Geological Survey
USFWS	United States Fish and Wildlife Service
RSAC	Remote Sensing Applications Center, an office of the USFS
WAKII	Method of topographically correcting satellite imagery

ABSTRACT

Whitebark pine (*Pinus albicaulis*) serves as a subalpine keystone species by regulating snowmelt runoff, reducing soil erosion, facilitating the growth of other plants, and providing food for wildlife, particularly grizzly bears (*Ursus arctos horribilis*). Mountain pine beetle (*Dendroctonus ponderosae*) is an ideal bio-indicator of climate change, as its life cycle is entirely temperature dependent. Western North America is currently experiencing the largest outbreak of mountain pine beetle on record, and evidence suggests that a changing climate has accelerated the life-cycle of this bark beetle, allowing it to expand into new habitat. This study explored the relationships between climate, mountain pine beetles, and whitebark pine mortality in the Greater Yellowstone Ecosystem (GYE). A time-series of Landsat satellite imagery was used to monitor whitebark pine mortality in the GYE from 1999 to 2008. The patterns of mortality were analyzed with respect to monthly climate (temperature and precipitation) variations over the 9-year period. The impacts of topography and autocorrelation (both spatial and temporal) were also analyzed with respect to whitebark pine mortality. Whitebark pine mortality was assessed using the Enhanced Wetness Difference Index (EWDI), a Landsat-derived measure of canopy moisture. Regression tree models were built to predict yearly changes in EWDI. Thirty-eight percent of the deviance in whitebark pine was explained by a regression tree with 10 predictor variables. The most important predictor variables were autocorrelation terms, indicating a strong host-tree depletion effect, where mountain pine beetles were much less likely to attack recently attacked areas. Topographic variables (elevation, slope, aspect) were not useful in predicting whitebark pine mortality. Climate variables alone were used to construct a regression tree with 14 predictor variables which predicted 15% of the dataset deviance in whitebark pine mortality. Drier climatic conditions favored increased whitebark pine mortality, likely due to the decreased ability of whitebark pine to repel beetle attacks. Warmer climatic conditions also favored increased whitebark pine mortality, likely due to a decrease in winter mortality of mountain pine beetle. These results show for the first time a statistical link between climate variability and whitebark pine mortality, likely mediated by mountain pine beetles.

CHAPTER 1

INTRODUCTION

Climate change will be one of the most significant environmental processes of the twenty-first century. The impacts will be varied, and ecosystems will be affected in countless ways, many yet to be determined. Under current greenhouse gas emissions trends, global temperatures are predicted to increase 5.1 °C by the year 2100 (Sokolov *et al.*, 2009; Sokolov *et al.*, In-Press), with larger increases on the continental interiors and at higher latitudes. Precipitation patterns will shift, and sea levels will rise (Bernstein *et al.*, 2007). Biological responses to climate change are more challenging to predict, but some are already evident. Plants are blooming earlier in the spring, while migration patterns are being altered both in time and space (Bernstein *et al.*, 2007). Many species will continue to attempt to move poleward and uphill to maintain suitable habitat. One of the more complex questions regarding biological responses to climate change involves how interactions between species will be altered. It is unlikely that predator and prey, parasite and host, competitor and mutualist will be able to shift their habitat at the same rate or with the same level of success. New species will interact, and old interactions will change.

Mountain pine beetle (*Dendroctonus ponderosae*) (MPB) is an ideal bio-indicator of climate change (Logan and Bentz, 1999). Its life cycle is entirely temperature dependent, it has the ability to reproduce rapidly in response to an increasingly suitable habitat, and a large increase in its population is easy to monitor: whole forests turn

distinctively red as they are killed by the beetle. Western North America is currently experiencing the largest outbreak of MPB on record, affecting 1.6 million ha in the United States and 20 million ha in Canada (Gibson *et al.*, 2008). The damage wreaked on western pine forests by this beetle has converted British Columbia's forests from a carbon sink into a net carbon source, as decomposing trees release carbon dioxide into the air, further driving changes in climate (Kurz *et al.*, 2008). Mathematical models have predicted MPB will continue to expand its range as land that was formerly inhospitable due to cool summers and harsh winters becomes tolerable. These models predict an expansion of MPB northward and upslope over the next several decades, as well as possibly "jumping" into jack pine (*Pinus banksiana*) hosts and moving for the first time towards the eastern portion of North America (Carroll *et al.*, 2003; Hicke *et al.*, 2006).

Whitebark pine (*Pinus albicaulis*) is both ecologically critical and useful as a broader environmental monitoring tool. In the Northern Rockies of the United States, this five-needled pine grows at the highest forested elevation, surviving conditions too cold, dry, and windy for other tree species. Though a biologically suitable host tree, historically MPB were rare in whitebark pine, generally only affecting weak trees or having a mild outbreak during unusually warm and dry climatic periods, such as during the 1930s (Perkins and Swetnam, 1996; Logan and Powell, 2001). Whitebark pine is considered an ecological keystone species in the subalpine environment. It stabilizes soil, moderates snowfall runoff, facilitates the growth of shade-tolerant tree species, and provides an unparalleled wildlife food source, especially for birds, squirrels, and bears (Tomback, 2001). No other tree species in the subalpine zone provides a comparable

level of ecological services. Grizzly bears (*Ursus arctos horribilis*) in the Greater Yellowstone Ecosystem (GYE) use nutrient-rich whitebark pine seeds as a critical late summer pre-hibernation food source, and the availability of whitebark pine seeds is strongly connected to grizzly bear survival (Mattson *et al.*, 1992). The seeds of whitebark pine are so important for bear survival in the GYE that whitebark pine zones are considered “critical habitat” by the federal agencies monitoring recovery of the grizzly bear from the threatened species list (Tomback *et al.*, 2001). Slow-growing whitebark pine already lives at the tops of mountains, making climate-induced uphill migration difficult. Models of whitebark pine’s responses to a changing climate predict a 97% loss in climatically-suitable habitat by the end of the century (Warwell *et al.*, 2006).

Satellite imagery provides a unique tool for monitoring landscape-wide ecological change. The Landsat family of satellites has been providing a continuous record of the Earth’s landmasses since 1972 and is well suited for monitoring changes in forest health (Collins and Woodcock, 1996). Landsat imagery has been effective at detecting outbreaks of MPB, and the free distribution of Landsat data from the United States Geological Survey (USGS) makes time-series analysis very cost effective.

The goal of my research was to utilize the power of remotely-sensed imagery to investigate the interactions of two species sensitive to climate change: whitebark pine and mountain pine beetle. Mathematical models have *predicted* the responses of MPB to a changing climate (Logan and Powell, 2001; Bentz and Schen-Langenheim, 2006), and mathematical models have *predicted* the responses of whitebark pine to a changing climate (Weaver, 2001; Warwell *et al.*, 2006), but this is believed to be the first study to

analyze the *actual* response of whitebark pine and mountain pine beetle to changes in climate. In this study, I used Landsat imagery to detect whitebark pine mortality, likely caused by MPB, and analyzed this mortality with respect to the climatic conditions experienced by the whitebark pine forests and MPB populations. Chapter 2 of this study is a review of literature relevant to this study, including sections on whitebark pine ecology, MPB ecology, spatial interpolation of meteorological stations to generate climate datasets, processing of Landsat data with respect to conifer change detection, and the use of regression trees. Chapter 3 of this study presents the research methodology, results, and a discussion of these results. Chapter 4 summarizes the findings and implications of the research, and the appendix offers a more detailed look at the results from the regression tree modeling.

CHAPTER 2

LITERATURE REVIEW

Ecology of Whitebark Pine

Whitebark pine (*Pinus albicaulis*) grows at timberline and in subalpine forests of western North America, divided into two main ranges. The western range encompasses the Sierra Nevada in California northward to the Cascade and Coast ranges of Oregon, Washington, and British Columbia. This study focused on the more extensive eastern range, where whitebark pine grows in the northern Rocky Mountains of Wyoming, Montana, Idaho, Alberta and British Columbia, in particular the region surrounding Yellowstone National Park known as the Greater Yellowstone Ecosystem (GYE) (McCaughey and Schmidt, 2001). Over two-thirds of GYE whitebark pine forests exist in national park or designated wilderness areas (Keane, 2000; Logan *et al.*, 2009). Whitebark pine grows between 1,700 m and 3,200 m in this region, with the elevation decreasing with increasing latitude (Arno and Hoff, 1990).

In the Northern Rockies, whitebark pine occupies 10-15% of forested land, growing both as a climax species and a seral species in mixed stands, where it is eventually successional replaced primarily by shade-tolerant subalpine fir (*Abies lasiocarpa*), and less often by mountain hemlock (*Tsuga mertensiana*) and Engelmann spruce (*Picea engelmannii*) (Arno, 1986). The climax stands occur generally only at timberline, and are considered climax not because they outcompete other tree species but simply because other species are not able to survive the harsh conditions (Mattson and

Reinhart, 1989). Mean January minimum temperature for whitebark pine environments is -14 °C, with an absolute minimum of -34 °C. Maximum July mean temperature is 18 °C, with an absolute maximum of 29 °C. Yearly precipitation averages 931 mm, falling primarily as snow (Weaver, 1992a). Either a too-cool growing season or wind-induced drought are thought to exclude whitebark pine from higher elevations, while the lower elevational limit is controlled by competition from subalpine fir and lodgepole pine (realized limit) or drought (physiological limit) (Weaver, 1992b). In the Northern Rockies, whitebark pine is rarely found on limestone substrates, due primarily to limestone's low water retention, however in wetter regions near and north of the Canadian border, whitebark pine is found preferentially on well-drained substrates such as limestone (Arno, 2001).

A keystone species is one that “may determine the ability of large numbers of other species to persist in the community” (Tomback *et al.*, 2001). Many ecologists consider whitebark pine a subalpine keystone species due primarily to its use by wildlife as a food source, but also for facilitating ecological succession, reducing soil erosion, capturing wind-blown snow, and regulating spring run-off (Tomback, 2001; Tomback *et al.*, 2001). Windblown snow accumulates in areas with whitebark pine and remains longer into the spring than areas without these trees. The increased depth and duration of the snowpack provides both enhanced thermal protection for plants and animals below the snowpack as well as moderates heavy streamflows in the spring by spreading the meltwater “pulse” over a longer period. The broad, spreading canopies of whitebark pine

cover more ground per tree than canopies of other high-mountain conifers, enhancing their snow capturing and retention abilities (Tomback *et al.*, 2001).

Another factor in the status of whitebark pine as a keystone species is the role it plays in ecological succession. Whitebark pine prospers when and where no other trees can. Whitebark pine grows just below treeline in cold, windy, and generally harsh environments. It is often one of the first trees to establish after a wildfire or other disturbance in less extreme sites, securing the soil and beginning the subalpine successional process. The physical protection from the elements offered by whitebark pine on exposed sites creates microenvironments much more suitable to life. Whitebark pines often act as “nurse trees,” facilitating the growth of more shade-tolerant competitor species such as subalpine fir and Engelmann spruce (Mattson and Reinhart, 1989; Arno and Hoff, 1990; Tomback *et al.*, 2001).

As a wildlife food source, whitebark pine is unrivaled in its subalpine environment. No other plant in the subalpine zone provides a similar combination of large seeds packed with fat and protein. Whitebark pine seeds average 119 mg in mass, in comparison to 3 - 13 mg for other conifer seeds found in the same range. The seeds are an important source of protein (21%) and the high fat content (52%) is vital for animals preparing to over-winter (Lanner and Gilbert, 1992; Mattson *et al.*, 2001; Tomback *et al.*, 2001). The wingless seeds in the indehiscent cones of whitebark pine require a foraging animal to free the seeds from the closed cones and then disperse them from the tree (Tomback, 2001).

While over 110 different wildlife species have been documented to eat whitebark pine seeds, only 2 species, the Clark's nutcracker (*Nucifraga columbiana*) and the red squirrel (*Tamiasciurus hudsonicus*), are responsible for harvesting 99% of the seeds from the trees (Hutchins and Lanner, 1982). Both of these animals store seeds in the ground (called caches or middens) for future use. The squirrel middens are prime sources of whitebark seeds for grizzly bears (*Ursus arctos horribilis*), as the bears are not known to eat seeds either directly from the whitebark pine tree or from fallen cones (Mattson and Reinhart, 1997). While squirrels deposit a great deal of whitebark pine seeds into the ground, there is no evidence of whitebark pine seedlings establishing on squirrel middens (Hutchins, 1992). Because whitebark pine seeds are not capable of being wind-dispersed, they are dependent upon the Clark's nutcracker for seed dispersal (Tomback, 2001). A single nutcracker is estimated to cache 35,000 whitebark pine seeds per season in approximately 9,000 caches of 3 - 4 seeds each. The nutcrackers use only about 55% of these seeds, so each bird leaves thousands of seeds in the ground for future whitebark pine germination (Tomback, 1982). Dispersal by nutcrackers confers an advantage to whitebark pine over wind-dispersed competitors such as spruce and fir. The nutcrackers carry the whitebark pine seeds much further than the wind carries competitors' seeds and can also carry them upwind. Whitebark pine regeneration has been documented over 8 km from the nearest seed source (Tomback, 2001). Because of its advantages in seed dispersal, large wildfires preferentially favor regeneration of whitebark pine over spruce and fir (Tomback *et al.*, 1989).

Whitebark pine seeds (via raided red squirrel middens) are a vital food source to many grizzly bear populations. In the moist maritime climate of northern Idaho and Montana, berries replace whitebark pine seeds in the grizzly bear diet, but in the drier continental climate of the GYE, whitebark pine seeds are critical to grizzly bear survival (Mattson and Reinhart, 1992; Mattson *et al.*, 2001). The “availability of whitebark pine seeds has the greatest potential of any food-related factor to impact behavior and demography of the Yellowstone bear population” (Mattson *et al.*, 1992). The high fat content of the seeds promotes winter survival and spring lactation in female grizzly bears, and whitebark seed consumption has a strong positive correlation with female reproductive success, which is likely why female grizzly bears eat twice as many whitebark pine seeds as do their male counterparts (Mattson *et al.*, 2001). Grizzly bears do not starve in years of low whitebark pine cone crop, but instead turn to other food sources, generally lower in elevation and in areas where contact with humans is more common (Mattson *et al.*, 1992). Humans are directly responsible for 70 - 90% of grizzly bear deaths in the GYE, so increasing human-bear interaction leads to increased grizzly bear mortality, with twice as many bears being killed in poor cone crop years compared to mast years when a great deal of cones are produced (Pease and Mattson, 1999).

Threats to Whitebark Pine

Whitebark pine is in decline across much of its range, due to a combination of factors including fire suppression, mountain pine beetle outbreaks, blister rust infestations

and global climate change. All of these threats are either exacerbated or caused entirely by human influence.

In its seral habitat, whitebark pine competes with Engelmann spruce and especially subalpine fir. Over several hundred years, the more shade-tolerant spruce and fir will successionaly replace whitebark pine. Historically, periodic wildfire (every 50 - 400 years, depending on the local climate) maintained whitebark pine on the landscape, as whitebark pine is both more fire-resistant than spruce and fir and better colonizes burned landscapes, thanks to seed dispersal by the Clark's nutcracker (Sala *et al.*, 2001; Tomback *et al.*, 2001). Aggressive wildfire suppression over the last 75 years has significantly increased the natural fire return interval to at least 10 times the natural lengths, and even in a wilderness area with a "let-burn" policy the fire return interval was found to be 1.7 times that of pre-settlement times (Arno, 1986; Brown *et al.*, 1994). Fire exclusion has led to an increase of fir and spruce at the expense of whitebark pine (Murray *et al.*, 2000; Kendall and Keane, 2001). Succession has shrunk the vertical range of whitebark pine by 240 m in western Montana, thus removing about 50% of the original habitat area (Arno, 2001). The combination of succession and beetle attacks led to a change in forest composition in the Bitterroot National Forest. In 1900, whitebark pine made up 39% of the forest between 2100 and 2300m of elevation, while subalpine fir was only 13%. By 1995, these numbers had nearly reversed, with whitebark pine reduced to only 11%, and subalpine fir up to 32% (Arno, 2001).

Continued fire exclusion will allow seral whitebark stands to be overtaken by subalpine fir within 100 - 400 years (depending on local climate), according to computer

models (Kendall and Keane, 2001). Whitebark pine declines more rapidly when fire exclusion is paired with blister rust infections (Keane and Morgan, 1992; Keane, 2001). In pure whitebark pine climax stands, computer models predict that fire exclusion will maintain dominance for at least 500 years, and will actually triple the whitebark pine basal area (Keane, 2001). Add blister rust infections to these sites, however, and a permanent shift to shrub-herb cover is predicted, as no other trees are able to establish on these climatically severe sites (Keane *et al.*, 1989). In contrast, returning to historic fire intervals (with natural variation of 10 - 30% from the mean) maintains whitebark pine on the landscape. Fires between 300 – 30,000 ha best utilize the colonization advantage of whitebark pine over wind-dispersed competitors like subalpine fir (Keane, 2001).

The successional effects of fire suppression are amplified by the endemic mountain pine beetle (*Dendroctonus ponderosae*) (MPB), which can kill healthy mature trees as the beetle larvae invade the tree. These mature trees are also the most reproductively active, so the death of these trees can have a disproportionately large impact on stand seed production (Kendall and Keane, 2001). Twentieth century beetle outbreaks are responsible for massive whitebark pine mortality in Idaho and Montana, especially in Glacier National Park (Tomback *et al.*, 2001). Historically, fire would refresh beetle-killed forests, as whitebark pine prospers in post-fire environments (Keane, 2000). Fire suppression leads to increased competition for whitebark pines from spruce and fir, which leads to whitebark pines that are less able to repel beetle attacks, as well as removes the competitive advantage whitebark pine has in seed dispersal (Keane, 2000).

Compounding the plight of whitebark pine is global climate change. Annual mean temperature in the Northern Rockies is projected to increase 3 - 10 °C by the end of the century (Bartlein *et al.*, 1997; Bradley *et al.*, 2004). Climate change will likely shrink the range of whitebark pine. Temperature increases of 1 - 5 °C are predicted to lead to a successional replacement of whitebark pines by Douglas-fir (*Psuedotsuga menziesii*) and lodgepole pine (*Pinus contorta*) (Romme and Turner, 1991). The range of the whitebark pine is projected to retreat northward by 50 - 300 km and upslope by 500 m. The vertical retreat alone would result in a 90% loss of habitat for the whitebark pine in the GYE (Weaver, 2001). A United States Forest Service (USFS) bioclimatic model for western North America predicts a 70% decline in suitable habitat for whitebark pine by 2030 and a 97% decline by 2100 (Warwell *et al.*, 2006).

The invasive fungus white pine blister rust (*Cronartium ribicola*) kills the top, cone-producing portions of trees first, so even a non-lethal infection cuts off reproduction. Native to Eurasia, this tree-killing fungus has spread to all five-needled pines in western North America after its introduction around 1922 (McDonald and Hoff, 2001). In the moist climates of northern Idaho and northwestern Montana that blister rust prefers, up to 50% of whitebark pine trees have already been killed by blister rust, and 80-100% of the remaining live trees are fatally infected (Kendall and Keane, 2001). The cold, dry continental climate common to the eastern side of the continental divide and the GYE has slowed the spread of blister rust. The GYE historically had one of the lowest rates of blister rust infection in whitebark pine due to its cold, dry climate, but a 2006 survey indicates an average infection rate of 25% across the ecosystem, double the

infection rate from a decade earlier (Kendall *et al.*, 1996; Reinhart *et al.*, 2007). In addition to direct mortality, blister rust infection in whitebark pine leads to both preferential selection and increased infection by MPB, yielding synergistic mortality (Kendall and Keane, 2001; Bockino, 2007a; Bockino, 2007b). Finally, while wildfire normally leads to a post-fire increase of whitebark pine, blister rust infection on unburned trees severely reduces post-fire whitebark pine regeneration (Tomback *et al.*, 1995).

In general, computer models of future ecological succession in whitebark pine forests have yielded similar results as field studies of past events: fire exclusion causes subalpine fir to replace whitebark pine, and this process is accelerated by MPB outbreaks and blister rust infestations (Keane, 2001). Overall, whitebark pine cover has declined 45% in the last century in the Interior Columbia River Basin and the Bob Marshall Wilderness Complex, and the ecologically vital seral stands have decreased 98% (Kendall and Keane, 2001).

Threat to Whitebark Pine from Mountain Pine Beetle

Perhaps the most imminent threat to whitebark pine populations in the GYE is an epidemic of mountain pine beetle (*Dendroctonus ponderosae*) (MPB). The United States had 1.6 million hectares of pine infested with MPB as of 2007, which is the most widespread in at least 70 years (Carroll *et al.*, 2003; Gibson *et al.*, 2008). The outbreak was even larger in Canada, where 20 million hectares of pine were infested, an order of magnitude larger than any previous Canadian outbreak (Gibson *et al.*, 2008; Kurz *et al.*, 2008). The Canadian outbreak has caused so much pine mortality that the forests of British Columbia have been converted from a small carbon dioxide sink to a large net

carbon source (Kurz *et al.*, 2008). The MPB outbreak in whitebark pine has not received the same level of attention as it has in lodgepole, perhaps because 85% of this infestation is in lodgepole pine, but also because whitebark pine is not a common timber species (Gibson *et al.*, 2008). The US Forest Service's Aerial Detection Survey uses fixed-wing aircraft to monitor current-year forest mortality due to insect and disease. It often does not include national park or wilderness areas, nor does it cover all areas every year. Despite these limitations, it can still provide a useful assessment of MPB population dynamics. The Aerial Detection Survey of the GYE recorded only 217 ha of MPB-infested whitebark pine in 1999, increasing nearly every year to 69,433 ha in 2007, a 320-fold increase (Gibson *et al.*, 2008; Logan *et al.*, 2009).

MPB is the most damaging insect to adult pines in western North America, where it ranges from northern Mexico (latitude 31 °N) to northwestern British Columbia (latitude 56 °N) (Wood, 1963; Amman *et al.*, 1989; Safranyik *et al.*, 1999). All native pines (and many exotics) are possible hosts for MPB, but the principle hosts are lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), western white pine (*Pinus monticola*), and sugar pine (*Pinus lambertiana*) (Amman *et al.*, 1989; Safranyik *et al.*, 1999). After spending 1-3 years developing as eggs, larvae, and pupae in the host tree phloem, adult MPB emerge from their tree in mid-summer and fly to a new host tree where eggs can be deposited for the next life cycle. Adult emergence peaks when air temperature is between 20 - 32 °C, and generally takes place over roughly a week-long period at the end of July or early August, but it has occurred up to a month earlier after an unusually warm spring or early summer (Safranyik *et al.*, 1999). MPB dispersal is poorly

understood, but it is believed most adults choose a new host within 100 m of their emergence site, save for a small percentage (~ 3%) that catch wind currents for upwards of 100 km (Robertson *et al.*, 2007; Heavilin and Powell, 2008). During an epidemic, hundreds of beetles aggregate on the same tree to form a “mass attack” that overwhelms host tree defenses. Attacked pines increase sap output in an attempt to “pitch-out” attacking beetles, but this defense is compromised by drought and when overwhelmed by a beetle mass-attack (Raffa and Berryman, 1987; Powell and Bentz, In Press) .

Larvae of MPB feed in the phloem of the host tree, eventually girdling it and killing the tree (Amman *et al.*, 1989). MPB carry blue-stain fungi (*Ophiostoma clavigerum* and *Ophiostoma montium*) spores that infect the tree and cut off water transport, inhibiting the pitch-out defense of the host tree and providing another mechanism of tree death (Safranyik *et al.*, 1975; Carroll and Safranyik, 2004). Attacked trees generally die within two weeks of attack (known as the “green-attack” or “fader” stage), and within a year of initial attack, host trees develop a noticeably red canopy due to dead needles, known as the “red-attack” stage (Safranyik, 2004). Within three years after attack, most trees will be defoliated, known as the “gray-attack” stage (Wulder *et al.*, 2006a).

Successful MPB mass attacks require “adaptive seasonality”: synchronous MPB emergence (synchrony) from host trees during the proper season (seasonality), which is after the spring frosts and before the fall frosts (Logan and Powell, 2001; Powell and Logan, 2005; Hicke *et al.*, 2006). Voltinism refers to the number of generations of an organism per year (Jenkins *et al.*, 2001), and in MPB voltinism is entirely dependent

upon temperature (Logan and Bentz, 1999), with greater thermal input (warmer temperatures) leading to quicker life cycles. The thermal restrictions on adaptive seasonality result in discontinuous thermal habitat suitability. The combined needs of synchrony and seasonality create “Goldilocks-like” windows of adaptive seasonality: not too hot, and not too cold. If a population is adaptively semi-voltine (two-year life cycles), additional warmth will initially *decrease* MPB survival, as synchrony and/or seasonality is disrupted. Only when additional thermal input is sufficient to make the jump to univoltinism (one-year life cycles) will another adaptive window be found (Logan and Powell, 2001). One-and-a-half-year life cycles are not adaptive, for example, as these beetles would emerge in the depths of winter, with no chance of survival. These adaptive windows result in severely non-linear population dynamics for MPB in a changing climate. A small increase in temperature could *decrease* MPB population levels, while a larger increase in temperature could lead to a sudden and dramatic *increase* in MPB population (Logan and Powell, 2001). MPB is considered an ideal bio-indicator of changes in climate because of its thermally-controlled life cycles (Logan and Bentz, 1999).

Univoltinism is considered necessary for MPB survival in lodgepole pine forests, but evidence from whitebark pine stands suggests that strict univoltinism might not be required to sustain an epidemic (Bentz and Schen-Langenheim, 2006). Two-year life cycles (semivoltinism) and even 3-year life cycles have historically been the standard in the cooler whitebark pine zones. Life cycles longer than one year weaken the synchrony of adult MPB emergence, which historically have prevented MPB from being a major

presence in whitebark pine habitat (Bentz and Schen-Langenheim, 2006). A shift from semi-voltine to univoltine not only increases the reproductive rate of MPB, it also increases the success of mass-attacks, causing synergistic population increase effects.

MPB were historically rare in whitebark pine, as the harsh winters and cool summers common to whitebark pine zones do not provide favorable growth conditions for the beetle. The lack of coevolution between whitebark pine and epidemic levels of MPB is thought to have left the whitebark pine much more susceptible to MPB attacks than lower elevation pines (Powell and Logan, 2005; Hicke *et al.*, 2006; Logan *et al.*, 2009). Mathematical models of MPB lifecycles show that an average increase in host tree phloem temperature of only 2 - 3 °C would enable beetles to reproduce rapidly in whitebark pine zones by shifting from two or three-year life-cycles to univoltinism (Logan and Powell, 2001; Powell and Logan, 2005).

A MPB outbreak in Idaho whitebark pine stands during the late 1920s and early 1930s occurred during a decade-long warming of 2.5 °C above average as well as during a sustained drought (Perkins and Swetnam, 1996; Logan and Powell, 2001; Perkins and Roberts, 2003), consistent with the Logan and Powell life-cycle model. Biologists have observed the predicted warmer-climate MPB outbreaks in the Northern Rockies, even at whitebark pine sites above 3,000 m (Powell and Logan, 2005). The beetles now appear able to complete a lifecycle in one or two years in whitebark pine zones, while just 20 years ago this typically required three years (Amman, 1973; Bentz and Schen-Langenheim, 2006).

Temperature is vitally important for MPB survival as well as to voltinism. While many factors influence MPB population dynamics, including food availability and predation (especially by woodpeckers and clerid beetles), cold-induced mortality is considered the most important factor, especially at high elevations (Raffa, 1988; Regniere and Bentz, 2007). Due to the timing of cryoprotectant manufacture, MPB can often withstand colder temperatures in mid-winter than during spring or fall (Bentz and Mullins, 1999), indicating that the timing of cold snaps is perhaps as significant as the actual temperature. Lethal ice crystals form within the body of the beetle at temperatures below the supercooling point (SCP), even with cryoprotectants in place, and is considered an indicator of maximum cold-hardiness. Mean SCP ranged from -9.8 °C for non-cold-hardened beetles during the summer to -32.3 °C for fully cold-hardened beetles during mid-winter (Regniere and Bentz, 2007).

The current MPB outbreak in whitebark pine threatens the vital functional role whitebark pine plays in high-mountain ecosystems, most prominently as it affects grizzly bears. In the 2007 delisting of the GYE population of grizzly bears as a federally threatened species under the Endangered Species Act, dissenting scientists argued that the perilous future of whitebark pine meant that the security of the grizzly population was also threatened (Hall, 2007). In the delisting document, the US Fish & Wildlife Service (USFWS) argued in favor of delisting the grizzly by stating “...(only) 16 percent of the total area of whitebark pine found in the GYA [Greater Yellowstone Area]...has experienced some level of mortality due to mountain pine beetles” (Logan *et al.*, 2009). Recent evidence from satellite imagery suggests that current MPB activity is much higher

than the USFWS posits, with 79% of whitebark pine hectares in the GYE showing some level of canopy mortality, and 27% showing “moderate” or “high” canopy mortality (Goetz *et al.*, 2009). Climate changes are expected to increase MPB in whitebark pine zones for at least an additional 30 years, according to mathematical modeling of beetle life-cycles (Carroll *et al.*, 2003; Hicke *et al.*, 2006). If climate change is altering the habitat suitability of MPB in whitebark pine zones, then an entire subalpine ecosystem could be at risk of collapsing.

Processing of Remotely Sensed Imagery for Change Detection

Remotely sensed imagery provide a low-cost, practical method to monitor landscape wide changes in forest health, including MPB attacks. The steep topography of the GYE presents challenges for mapping land cover using remote sensing, however. Depending on slope, aspect, and sun angle illumination, some regions will reflect considerably more or less light than they would on flat terrain, confusing much smaller spectral differences between vegetation types. For instance, with a solar angle of 40°, Landsat TM band three pixel values were found to vary by up to 52 pixel values (out of 255 possible values), depending on slope aspect (Holben and Justice, 1980). Because of this, topographic correction is sometimes used to achieve more accurate land cover classification. Terrain-corrected Landsat images (USGS Level 1T) account for the elevation of a pixel, but not for slope and aspect effects (Williams, 2006). There are many possible terrain correction algorithms that do account for slope and aspect, but there is not a clear consensus on the best choice. Many of them, such as the Cosine

correction and Minnaert correction, tend to overcorrect, making shaded slopes too bright after correction (Tokola *et al.*, 2001; Riano *et al.*, 2003; Jensen, 2005). The C-correction, Civco's two-stage normalization technique and a slope-matching variant all refine the Cosine technique, reducing the overcorrection, and have shown adequate results (Civco, 1989; Riano *et al.*, 2003; Nichol *et al.*, 2006).

Very accurate land cover classifications (95%) were achieved in steep, mountainous, and forested terrain in New Zealand using a combination of the 6S absolute atmospheric correction (Vermote *et al.*, 1997) and the WAKII topographic correction (Dymond and Shepherd, 1999; Dymond and Shepherd, 2004). As the angle of incident light increases on forest canopy, so does the reflectance, in an exponential-type curve. This explains why Lambertian models overcorrect shadowed slopes and undercorrect sunny slopes. The WAKII model addresses this problem, and also accounts for diffuse slope irradiance in addition to direct irradiance (Dymond and Shepherd, 1999).

Unfortunately, the WAKII model is not applicable when a significant portion of bare ground is exposed, as is the case for prime whitebark pine habitat (Dymond *et al.*, 2001). The Civco model is scene-dependent, requiring a north aspect – south aspect slope comparison, and is based on leaf-off deciduous forests, which are quite different than the present study area (Civco, 1989). Other models similar to WAKII use the 6S (Second Simulation of the Satellite Signal in the Solar Spectrum) atmospheric correction code along with sky-view and terrain-view factors to compensate for topography, but overall classification accuracy was not impressive (Sandmeier and Itten, 1997). Hopefully a model similar to WAKII that is appropriate for the subalpine forests of the

Northern Rockies will be developed. Until then, it is not believed that topographic normalization would improve image classification accuracy for this whitebark pine study.

Radiometric correction is necessary when comparing imagery from different dates and/or different sensors and is considered vital for many types of change detection (Lu *et al.*, 2003; Coppin *et al.*, 2004; Hadjimitsis and Clayton, 2004). Converting imagery digital numbers to “top-of-atmosphere” (also known as “at-satellite”) reflectance compensates for differences between sensors, sun illumination angles, and earth-sun distance differences. Top-of-atmosphere conversions are a minimum first step for change detection purposes, reducing the inter-image differences at invariant features while minimizing distortions added to the dataset (Huang *et al.*, 2001).

Absolute atmospheric correction (a form of radiometric correction) attempts to model all effects of atmospheric interactions on the imagery, converting the data to “surface reflectance,” or what would be captured in the absence of any atmosphere. Methods such as 6S, and ATCOR 3 (Atmospheric and Topographic Correction) are highly parameterized, requiring extensive information about local atmospheric conditions on the date of image capture (Richter, 1997; Vermote *et al.*, 1997). This atmospheric parameterization is difficult for retrospective studies, especially in rural and mountainous areas like the GYE with complex microclimate effects and a low density of weather monitoring stations. While the ATCOR 3 program has the capability to adjust for both topographic and atmospheric variability at the same time, it is not suitable for terrain over 1500 m, and the atmospheric correction code needs further refinement (Richter, 1997; Hadjimitsis and Clayton, 2004).

Simpler techniques such as Dark Object Subtraction (DOS) work as well or better than more complicated methods like 6S that require inputs of meteorological data (Pax-Lenney *et al.*, 2001; Song *et al.*, 2001; Hadjimitsis and Clayton, 2004). DOS assumes that the darkest features in an image would have zero reflectance without atmospheric interference. The recorded level of reflectance for these darkest objects is subtracted from all pixel values to remove atmospheric effects. A modified DOS that compensates for Rayleigh scattering seems to provide increased accuracy by relying on image-derived estimates of atmospheric scattering (Song *et al.*, 2001; Hadjimitsis and Clayton, 2004).

Relative atmospheric correction (also known as normalization) attempts to match imagery to a base image, generally with a regression function. After a successful correction, it appears that all images were captured by the same sensor under the same atmospheric conditions, and the pixel value of an area with unchanged land cover (known as a “pseudo-invariant feature” will be as similar as possible in all images (Schott *et al.*, 1988; Hadjimitsis and Clayton, 2004). Relative atmospheric normalization through the use of pseudo-invariant features reduced the between-image differences more than 6S or DOS (Schroeder *et al.*, 2006). Relative atmospheric corrections account for both sensor degradation and differences in atmospheric conditions on the different dates of image capture (Huang *et al.*, 2001; Hadjimitsis and Clayton, 2004; Jensen, 2005). Absolute-normalization combines aspects of relative and absolute atmospheric correction, and involves converting a radiometric base image to surface reflectance, followed by matching all other images to the radiometric base image via regression-based normalizations. The absolute-normalization procedure has been shown to provide the best

radiometric normalization for multi-date imagery and was effective when used to detect MPB attacks with Landsat (Schroeder *et al.*, 2006; Goodwin *et al.*, 2008).

Detection of MPB attacks with Remote Sensing

Detecting and monitoring MPB activity has been the focus of many remote sensing studies since the 1960s (Wulder *et al.*, 2006a). High spatial resolution sensors such as Quickbird have been useful at detecting low levels of MPB infestation, but forest shadow regions make change detection difficult and are also not appropriate for use on an area as large as the GYE (Hicke and Logan, In-Press). The accuracy rate of detecting MPB attacks with satellite imagery increases with the increasing severity of MPB attack (Goodwin *et al.*, 2008). When MPB infestations reach epidemic levels, Landsat is an effective tool for measuring conifer mortality landscape-wide (Safranyik, 2004; Wulder *et al.*, 2006a). Most studies involve using one or more derived vegetation indices to distinguish “red-attack” stands. Using a vegetation index helps to remove effects of variable atmospheric conditions and illumination geometry between different dates of imagery (Cohen and Spies, 1992; Jin and Sader, 2005). Red-attack stands are spectrally distinguishable from healthy green vegetation through increased reflectance from 850-1100 nm (near-infrared) and from 600 - 700 nm (red), in addition to a decrease in green reflectance (500 - 600 nm) (Wulder *et al.*, 2006a). To detect subtle changes over time, such as a forest undergoing beetle attack, a multi-date series of images has been shown to be more effective than a pair of images (Brown de Calstoun *et al.*, 2003; Skakun *et al.*, 2003; Goodwin *et al.*, 2008).

Vegetation indices commonly used to detect MPB attack include the Normalized Difference Vegetation Index (NDVI) $((\text{Near Infrared} - \text{Red}) / (\text{Near Infrared} + \text{Red}))$, Normalized Difference Moisture Index (NDMI) $((\text{Near Infrared} - \text{Mid Infrared}) / (\text{Near Infrared} + \text{Mid Infrared}))$, the Red-Green Index (RGI) $(\text{Red}/\text{Green})$, and combinations of these, such as an average of NDVI and NDMI known as the Normalized Difference Forest Index (NDFI) (Jin and Sader, 2005; Wulder *et al.*, 2008; Goetz *et al.*, 2009). Though somewhat inferior to the other indices, the RGI is useful when infrared data is not available (Wulder *et al.*, 2008; Hicke and Logan, In-Press). NDMI is highly correlated to canopy water content, correlates better with plant biomass than NDVI, and was more effective at classifying land cover change than NDVI (Hardisky *et al.*, 1983; Jin and Sader, 2005). Regression equations relating field data from GYE whitebark pine stands to NDFI-detected red-attack stands had an R^2 of 0.51 (Goetz *et al.*, 2009).

The Enhanced Wetness Difference Index (EWDI), defined as the difference in Tasseled Cap Wetness (TC_{Wet}) for two or more dates of imagery, has been shown to be effective at detecting red-attack stands of lodgepole pine (67 - 78% overall accuracy), with greater accuracy in more heavily infested stands (Franklin *et al.*, 2001; Skakun *et al.*, 2003; Wulder *et al.*, 2006b). A decrease in TC_{Wet} over time (negative EWDI value) is the best overall indicator of conifer mortality (Collins and Woodcock, 1996). The Tasseled Cap transformation compresses the six reflected bands of Landsat into three components that represent physical landscape characteristics known as brightness, greenness, and wetness (Crist and Ciccone, 1984; Huang *et al.*, 2002). TC_{Wet} is a contrast between the sum of visible and near-infrared bands and the sum of shortwave infrared

bands (Crist and Ciccone, 1984). EWDI detects red-attack stands by contrasting the canopy moisture in live vegetation with the very dry canopy of red-attack stands, and has been shown to be less sensitive to topographic effects or viewing angle effects than both bandwise analysis and most other vegetation indices (Song and Woodcock, 2003; Wulder *et al.*, 2006b). As with other indices, EWDI still suffers from a considerable overlap in EWDI values between green stands (unattacked) and red-attack stands of pine (Cohen and Spies, 1992; Song and Woodcock, 2003; Wulder *et al.*, 2006b).

While EWDI has been effective at detecting red-attack stands in lodgepole pine, the efficacy of this method has not been shown in whitebark pine. The grassy meadows, rocky outcroppings and steep slopes that are common in whitebark pine forests make the use of this method potentially more problematic, as changes to the grasses and shrubs will affect EWDI values (Hicke and Logan, In-Press). The free archive of historical high-resolution imagery available on Google Earth (Google Inc., 2009) allows for the establishment of a relationship between red-attack in whitebark pine and Landsat-derived EWDI values. Google Earth provides high spatial resolution coverage of the entire GYE, often over multiple dates, from sources including the Quickbird satellite (2.4-m multispectral pixels or 0.7-m pan-sharpened pixels) and aerial imagery (1-m pixels) from the National Agriculture Imagery Program. This high spatial resolution dataset allows for the visual identification of individual whitebark pine trees under attack from MPB. This method is much quicker and less expensive than actual on-the-ground field verification of forest conditions, and is available for retrospective studies.

Environmental variables are often linked to MPB outbreak, and tend to be highly autocorrelated in both space and time. To spread to a new area, a MPB outbreak requires suitable host trees, the presence of an infectious agent (emergent adult beetles), and a favorable climate for beetle development. MPB adult dispersal distance will affect the rate of spread of MPB infestation, but this subject is poorly understood. The presence/absence of MPB red attack in the past is important in predicting the likelihood of its current presence/absence (Aukema *et al.*, 2008; Powell and Bentz, In Press). It is also important to know if there are or have been MPB attacks nearby, to know if both potential pine hosts and potential infectious agents are available (Aukema *et al.*, 2008). Both temperature and precipitation have been found to impact MPB outbreaks, but previous studies were performed at coarse spatial scales (12 x 12-km in Aukema *et al.*, and 800 x 800-m in Carroll *et al.*) and never in whitebark pine (Carroll *et al.*, 2003; Aukema *et al.*, 2008). The US Forest Service's Remote Sensing Applications Center (RSAC) performed a change analysis of whitebark pine habitat in the GYE, comparing Landsat imagery from circa 2000 to circa 2008. This is the only known use of Landsat imagery to map whitebark pine MPB attacks in the GYE, although no attempt was made to account for confounding forest mortality factors such as wildfire. The RSAC study used NDFI to detect relative conifer mortality, then subset this data to whitebark pine habitat using the Landenburger and Lawrence whitebark pine map, the best available map of GYE whitebark pine (Landenburger and Lawrence, 2006). Relative conifer mortality was converted to mortality condition classes of based on 357 field reference sites. The

RSAC study found 79% of the whitebark pine canopy in the GYE had some level of mortality, of which 9% was considered “high” mortality (Goetz *et al.*, 2009).

Climate Data

This study required both spatially and temporally continuous climate data. Automated climate monitoring stations such as SNOTEL (SNOWpack TELemetry) stations provide data only for exact measurement locations (Natural Resources Conservation Service, 2009). Various methods have been used to interpolate weather station data to provide a spatially continuous climate dataset. The Daymet dataset provided daily temperature and precipitation information interpolated to a continuous 1-km coverage that incorporated topography, but this dataset ended before the time period of the current study (Thornton *et al.*, 1997). The PRISM (Parameter-elevation Regressions on Independent Slopes Model) dataset is the only known spatially and temporally continuous climate dataset that covers the requisite area and time period. PRISM has been shown through jack-knifed cross-validation to be superior to kriging, detrended kriging, and cokriging for interpolating weather station data (Daly *et al.*, 1994). PRISM is a localized, simple regression algorithm that excels at mapping climate for mountainous terrain with sparse weather stations, which are exactly the conditions in the GYE. Of particular interest to the GYE, the PRISM method models rain shadow and temperature inversion effects much better than other climate models (Daly *et al.*, 2008). PRISM was compared to the spline-based ANUSPLIN method (used to create the WorldClim global climate dataset) in Alaska, and was found to be superior (Simpson *et*

al., 2005). Comparisons to the Daymet (local-regression-based) and WorldClim climate datasets also showed PRISM to be superior at modeling precipitation and temperature, especially in areas of complex terrain (Daly *et al.*, 2008). Following extensive peer review by climate experts, the United States Department of Agriculture (USDA) has selected PRISM data as its official spatial climate dataset, and PRISM provided the first official update since 1968 to the previously manually-drawn Climate Atlas of the United States (Daly *et al.*, 2002).

The PRISM method creates an elevation-dependent regression equation for each pixel in the model, weighting data from local weather stations according to their distance, elevation, topographic facet, coastal proximity, and atmospheric layer, all relative to the pixel in question. The default for the regression includes at least 15 weather stations within 50 km horizontally and 1,500 m vertically of the pixel, but these values can be adjusted either manually or automatically using cross-validation (Daly *et al.*, 2002). Nationwide, nearly 13,000 weather stations were used for estimating precipitation, and almost 10,000 were used for temperature (Daly *et al.*, 2008). The 30-year climate normal data produced by PRISM were at 800-m resolution, while the monthly climate datasets were at 4000-m spatial resolution. Lack of funding for this program has led to a discontinuation of the PRISM product, making follow-up studies with future climatic information difficult (PRISM Group and Oregon State University, 2004).

Decision Trees

Classification and Regression trees (known collectively as “decision trees”) are non-parametric in nature, handle non-linear datasets, and can automatically select the most useful predictor variables from a suite of reasonable predictor variables (Breiman *et al.*, 1984; Lawrence and Ripple, 2000; Lawrence and Wright, 2001; Rogan *et al.*, 2003). Decision trees function by analyzing all input predictor variables to determine what binary split in one predictor variable will most reduce total dataset deviance. More splits are made until the remaining groups (terminal nodes) are acceptably homogeneous. The resulting series of binary splits make up the regression tree, with each terminal node assigned a response variable value (Breiman *et al.*, 1984; Venables and Ripley, 1997). Decision trees are built to minimize total dataset deviance, so are sensitive to the relative size of classes in the training data (Lawrence and Wright, 2001). Unlike many competing statistical methods, decision trees are non-parametric and allow the incorporation of categorical data alongside continuous data (Lawrence and Wright, 2001). Regression trees were found to explain a greater portion of response variable deviance than any combination of variables using multiple linear regression (Lawrence and Ripple, 2000). Decision trees are much better at modeling complex interactions between predictor variables than methods such as multiple linear regression (Lawrence and Ripple, 2000). Similar to a linear regression model with too many variables, a too-large regression tree will be overly specified to the training data (known as “over-fit”), and might perform worse on a separate, independent set of data than a smaller tree or simpler model would (Breiman *et al.*, 1984). Decision trees must be simplified (“pruned”) both to avoid over-

fitting as well as to simplify them enough to allow interpretation of the splits for ecological significance. Ten-fold cross-validation of tree residual deviance can be used to inform the tree-pruning process, which randomly splits the dataset into ten parts, builds trees out from nine parts, and tests the trees on the tenth part (Venables and Ripley, 1997). Pruning can leave trees with above-minimum deviance, but minimum-deviance trees are often far too large for interpretation.

Classification trees are similar in structure to regression trees, but output categorical classes rather than a continuous response. Classification trees have been highly successful at mapping whitebark pine habitat from Landsat and topographic data, both in the GYE and at Canada's Waterton National Park, with accuracy rates over 90% (Landenburger and Lawrence, 2006; Landenburger *et al.*, 2008; McDermid and Smith, 2008). Ensemble methods of decision trees, such as boosting and bagging, generate multiple decision trees using different criteria, and the resultant trees vote on an output value or class. Ensemble tree methods have been shown to improve the accuracy of decision trees, but as they can create hundreds of separate trees they greatly decrease the interpretability of the output, making these methods inappropriate for studies where the primary goal is insight into relationships between variables (Savage, 2005; Landenburger and Lawrence, 2006).

Summary of Research Needs

A review of the literature indicates the need for additional research to address several questions regarding whitebark pine. First, can whitebark pine mortality be

effectively monitored with Landsat using tools such as EWDI? Second, does whitebark pine mortality have a spatial and/or temporal autocorrelation component? Third, are climatic links to whitebark pine mortality evident? Finally, is there evidence of voltinism shifts in MPB populations that inhabit whitebark pine habitat? Chapter 3 of this thesis details efforts to address these questions.

CHAPTER 3

SPATIOTEMPORAL RELATIONSHIPS BETWEEN CLIMATE AND WHITEBARK
PINE MORTALITY IN THE GREATER YELLOWSTONE ECOSYSTEMIntroduction

Whitebark pine (*Pinus albicaulis*) serves as a subalpine keystone species by regulating snowmelt runoff, reducing soil erosion, facilitating the growth of other plants, and providing food for wildlife, particularly grizzly bears (*Ursus arctos horribilis*) (Tomback *et al.*, 2001). This tree is vitally important to a diverse assortment of species yet is in dire peril from a variety of threats, including direct and indirect effects of climate change.

Whitebark Pine

Whitebark pine is a five-needled, high-elevation pine found near upper tree line primarily in the northern Rocky Mountains of the United States and Canada (Wyoming, Idaho, Montana, British Columbia, and Alberta). Nearly all whitebark pine in the United States is found on federal land, nearly half in national parks or designated wilderness areas (Keane, 2000). Occupying 10-15% of forested land in the Northern Rockies, whitebark pine grows both as a climax species and as a seral species in mixed stands (Arno and Hoff, 1990), where it is often successional replaced by subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). Arguably, the most important role whitebark pine plays in its ecosystem is as a food source for birds, bears, and small mammals. The seeds of the whitebark pine are far larger and more nutritious than nearly

any other available plant food source and their high fat content makes the seeds exceptionally valuable as a pre-winter food source (Mattson and Reinhart, 1997). The importance of whitebark pine to bears, especially grizzly bears, cannot be overstated. When given an opportunity to eat whitebark pine seeds, grizzly bears will eat little else (Mattson and Reinhart, 1997). In the Greater Yellowstone Ecosystem (GYE), grizzly bears obtain between 25 – 66% of their energy from whitebark pine seeds (Mattson *et al.*, 2001). Because of the importance of whitebark pine to the grizzly bear, whitebark pine communities have been designated as “critical habitat” for grizzly bear recovery in the GYE (Tomback *et al.*, 2001).

Threats

Populations of whitebark pine have been declining in the last 90 years across its range in the northern Rockies. Whitebark pines are slow-growing and slow to reach sexual maturity, giving population declines long-lasting effects to the ecosystem (Keane, 2000). Wildfire suppression has led to wide-scale successional replacement by more shade-tolerant conifers, and attacks by the invasive fungus white pine blister rust (*Cronartium ribicola*) have killed or weakened many whitebark pines (Arno, 1986; Brown *et al.*, 1994; Kendall and Keane, 2001; McDonald and Hoff, 2001). The GYE historically had one of the lowest rates of blister rust infection in whitebark pine due to its cold, dry climate, but a 2006 survey indicates an average infection rate of 25% across the ecosystem, double the infection rate from a decade earlier (Kendall *et al.*, 1996; Reinhart *et al.*, 2007). In addition to direct mortality, blister rust infection in whitebark pine leads to both preferential selection and increased infection by mountain pine beetle

(*Dendroctonus ponderosae*) (MPB), yielding synergistic mortality (Kendall and Keane, 2001; Bockino, 2007a). Finally, warming global temperatures are projected to reduce suitable habitat for whitebark pine. A bioclimatic model for western North America predicts a 70% decline in suitable habitat for whitebark pine by 2030 and a 97% decline by 2100 (Warwell *et al.*, 2006). Although blister rust is a serious threat to whitebark pine survival, blister rust generally requires more than a decade to kill a mature tree by itself, making it a more long-term rather than imminent concern to whitebark pine populations (Kendall and Keane, 2001).

Mountain Pine Beetles

The most immediate threat to whitebark pine is an epidemic of MPB, which currently is the most widespread in at least 70 years, and climate change has been suggested as a contributing factor to this outbreak (Carroll *et al.*, 2003). The United States had 1.6 million hectares of pine infested with MPB as of 2007, and the outbreak was even larger in Canada, where 20 million hectares of pine were infested, an order of magnitude larger than any previous Canadian outbreak (Gibson *et al.*, 2008; Kurz *et al.*, 2008). The MPB outbreak in whitebark pine has not received the same level of attention as it has in lodgepole, perhaps because 85% of this infestation is in lodgepole pine, whitebark pine habitat is more removed from common human interaction, and also because whitebark pine is not a common timber species (Gibson *et al.*, 2008). The US Forest Service's Aerial Detection Survey of the GYE recorded only 535 acres of MPB-infested whitebark pine in 1999, increasing nearly every year to 171,572 acres in 2007, a 320-fold increase (Gibson *et al.*, 2008; Logan *et al.*, 2009). While the US Forest Service

argues that similar conditions existed in the 1930s, entomologist Jesse Logan states that “Nothing comparable to what is occurring today has been observed in recorded history or exists in the disturbance legacy of this long-lived species” (Gibson *et al.*, 2008; Logan *et al.*, 2009).

MPB were historically rare in whitebark pine, as the harsh winters and cool summers common to whitebark pine zones do not provide favorable growth conditions for the beetle. MPB growth rates are entirely temperature-dependent, with warmer temperatures leading to quicker life-cycles (Logan and Bentz, 1999). Mathematical models of MPB lifecycles show that an average increase in host tree phloem temperature of only 2-3 °C would enable beetles to reproduce rapidly in whitebark pine zones by shifting from two or three-year life-cycles to one-year life-cycles, known as univoltinism (Logan and Powell, 2001; Powell and Logan, 2005). This change in thermal habitat suitability is distinctly non-linear: warming temperatures initially *decrease* MPB habitat suitability (by disrupting the ability of MPB to synchronously “mass attack” host trees), until the univoltinism threshold is met, which in turn causes a rapid *increase* in habitat suitability (Logan and Powell, 2001; Powell and Logan, 2005). This non-linearity yields the potential for sudden changes in beetle population dynamics resulting from gradual temperature changes. A MPB outbreak in Idaho whitebark pine stands during the late 1920s and early 1930s occurred during a decade-long warming of 2.5 °C above average as well as during a sustained drought (Perkins and Swetnam, 1996; Logan and Powell, 2001; Perkins and Roberts, 2003), consistent with the Logan and Powell life-cycle model. Biologists have observed the predicted warmer-climate MPB outbreaks in the Northern

Rockies, even at whitebark pine sites above 3,000 m (Powell and Logan, 2005). The beetles now appear able to complete a lifecycle in one or two years in whitebark pine zones, while just 20 years prior this typically required three years (Amman, 1973; Bentz and Schen-Langenheim, 2006). In addition to affecting growth rates, temperature is vitally important for MPB survival. Cold-induced mortality is the most important factor in MPB population dynamics (Regniere and Bentz, 2007). Due to the timing of cryoprotectant manufacture, MPB can often withstand colder temperatures in mid-winter than during spring or fall (Bentz and Mullins, 1999), indicating that the timing of cold snaps is perhaps as significant as the actual temperature.

The current MPB outbreak in whitebark pine threatens the vital functional role that whitebark pine plays in the high-mountain ecosystem, most prominently as it affects grizzly bears. In the 2007 delisting of the GYE-population of grizzly bears as a federally threatened species under the Endangered Species Act, dissenting scientists argued that the perilous future of whitebark pine meant that the security of the grizzly population was also threatened (Hall, 2007). In the delisting document, the US Fish & Wildlife Service (USFWS) argued in favor of delisting the grizzly by stating “...(only) 16 percent of the total area of whitebark pine found in the GYE...has experienced some level of mortality due to mountain pine beetles” (Logan *et al.*, 2009). Recent evidence suggests that current MPB activity is much higher than the USFWS posits, with 79 percent of whitebark pine hectares in the GYE showing some level of canopy mortality, and 27 percent showing “moderate” or “high” canopy mortality (Goetz *et al.*, 2009). Climate changes are expected to increase MPB in whitebark pine zones for at least an additional 30 years,

according to mathematical modeling of beetle life-cycles (Hicke *et al.*, 2006). If climate change is altering the suitability of whitebark pine zones as MPB habitat, then an entire subalpine ecosystem could be at risk of collapsing.

Detection with Remote Sensing

Detecting and monitoring MPB activity has been the focus of many remote sensing studies since the 1960s (Wulder *et al.*, 2006a). Landsat is an effective tool for measuring landscape-wide changes, although it is not very sensitive to sub-epidemic levels of MPB infestation (Safranyik, 2004; Wulder *et al.*, 2006a). Most studies involve using one or more derived spectral vegetation indices to distinguish “red-attack” stands. Red-attack stands are spectrally distinguishable from green vegetation through increased reflectance from 850-1100 nm (near-infrared) and from 600 - 700 nm (red), in addition to a decrease in green reflectance (500 - 600 nm) (Wulder *et al.*, 2006a). These spectral response changes are caused by the loss of needle moisture followed by the destruction of photosynthetic pigments and cellular structures in the needles (Wulder *et al.*, 2006a).

To detect subtle changes over time, such as a forest undergoing beetle attack, a multi-date series of images has been shown to be more effective than a pair of images (Skakun *et al.*, 2003; Goodwin *et al.*, 2008). The Enhanced Wetness Difference Index (EWDI), defined as the difference in Tasseled Cap Wetness (TC_{Wet}) for two or more dates, has been shown to be effective at detecting red-attack stands of lodgepole pine (67-78% overall accuracy), with greater accuracy in more heavily infested stands (Franklin *et al.*, 2001; Skakun *et al.*, 2003; Wulder *et al.*, 2006b). TC_{Wet} (Equation 3.1) is determined largely by reflectance in the middle-infrared portion of the electromagnetic spectrum

(Landsat bands 5 and 7 at 1.55 – 1.75 μm and 2.08 – 2.35 μm , respectively) (Huang *et al.*, 2002). Leaves with low water content reflect much more strongly in middle-infrared than moist leaves (Crist and Ciccone, 1984; Carter, 1991).

Equation 3.1 (Huang *et al.*, 2002)

$$\text{TC}_{\text{Wet}} = 0.2626(\text{Band 1}) + 0.2141(\text{Band 2}) + 0.0926(\text{Band 3}) + 0.0656(\text{Band 4}) \\ - 0.7629(\text{Band 5}) - 0.5388(\text{Band 7})$$

EWDI detects red-attack stands by contrasting the canopy moisture in live vegetation with the very dry canopy of red-attack stands, and has been shown to be less sensitive to topographic effects or viewing angle effects than both bandwise analysis and most other vegetation indices (Cohen and Spies, 1992; Song and Woodcock, 2003). A decrease in TC_{Wet} over time (negative EWDI value) is the best overall indicator of conifer mortality (Collins and Woodcock, 1996).

While EWDI has been effective at detecting red-attack stands in lodgepole pine, the efficacy of this method has not previously been shown in whitebark pine. The grassy meadows and rocky outcroppings that are common in whitebark pine forests make the use of this method potentially more problematic, as changes to grasses and shrubs will affect EWDI values. The free archive of historical high-resolution imagery available on Google Earth (Google Inc., 2009) allows for the establishment of a relationship between red-attack in whitebark pine and Landsat-derived EWDI values. Google Earth provides high-resolution coverage of the entire GYE, often over multiple dates, from sources including the Quickbird satellite (2.4-m multispectral pixels or 0.7-m pan-sharpened pixels) and aerial imagery (1-m pixels) from the National Agriculture Imagery Program.

This high-resolution dataset allows for the visual identification of individual whitebark pine trees under attack from MPB. This method is much quicker and less expensive than actual on-the-ground field verification of forest conditions, and is available for retrospective studies.

Environmental variables such as temperature and precipitation are often linked to MPB outbreak, and tend to be highly autocorrelated in both space and time. To spread to a new area, a MPB outbreak requires suitable host trees, the presence of an infectious agent (emergent adult beetles), and a favorable climate for beetle development. Adult MPB dispersal distance is poorly understood, with estimates ranging from less than 30 m occasionally over 100 km, but might be of importance when modeling MPB outbreak spread (Robertson *et al.*, 2007). The presence/absence of MPB red attack in the past is important in predicting the likelihood of its current presence/absence. The relationship between past and current MPB activity is likely non-linear, but high levels of recent MPB activity decrease the likelihood of current attack, evidently because potential host trees have been depleted (Aukema *et al.*, 2008; Powell and Bentz, In Press). These impacts from past MPB activity are also important in adjacent areas, as host depletion effects have been noted 18 km away (Aukema *et al.*, 2008). Both temperature and precipitation have been found to impact MPB outbreaks, but it has previously been documented only at coarse spatial scales and never before in whitebark pine (Carroll *et al.*, 2003; Aukema *et al.*, 2008).

Current Study Goals

The connection between climate and whitebark pine mortality was explored. MPB has been the predominant non-fire cause of whitebark pine mortality in the GYE for the last decade, therefore evaluations of climatic impacts on whitebark pine mortality focused on the response of MPB to changing climatic conditions. MPB life-cycles are entirely dependent upon phloem temperature in their host trees (which in turn is controlled by air temperature); it was expected, therefore, that drier and warmer climatic conditions would be favorable to beetle survival, resulting in an observed increase in whitebark pine mortality (Powell and Logan, 2005). A time-series of Landsat imagery was used to monitor whitebark pine mortality in the GYE from 1999 to 2008. The patterns of mortality were analyzed with respect to monthly climate variations (climate anomalies) over the 10-year period. The impacts of topography and autocorrelation (both spatial and temporal) were also analyzed with respect to whitebark pine mortality. Various subsets of predictor variables were combined in predictive models in order to best elucidate relationships among variables. Given previously modeled changes in MPB voltinism due to climate change (Logan and Powell, 2001; Hicke *et al.*, 2006), it was also predicted that towards the end of the study period (2008), climate conditions from one and two years prior to the image date would become relatively more important to MPB survival than they were at the beginning of the study period (2003). The use of spatially and temporally explicit climate data across an ecosystem combined with spatially and temporally explicit conifer mortality data generated from the Landsat imagery allowed

the investigation, at a landscape scale, of questions regarding climate change, MPB life-cycles, and whitebark pine mortality.

Methods

Overview of Methods

Nine Landsat images of the GYE from 1999 to 2008 were geometrically and radiometrically processed to a vegetation index (EWDI) suitable for detecting conifer mortality over time. Spatially explicit monthly temperature and precipitation data were compared to long-term average temperature and precipitation data to create climate anomaly datasets. A digital elevation model (DEM) was acquired and used to create slope and aspect datasets. Wildfires were a confounding source of abrupt conifer mortality, so areas that experienced a wildfire during the study period were removed from the area of analysis. Climate, topographic, and conifer mortality data were extracted from approximately 40,000 randomly-selected points across the study area. The data from these points were used to create and test regression tree models. Twenty-four separate regression trees were built using various subsets of predictor variables in order to analyze relationships between climate, topography, and the response variable EWDI, a measure of conifer mortality. These regression trees were compared with respect to the amount of dataset deviance explained and analyzed for the strength and direction of variable relationships. Separate from the above analysis, high-resolution aerial and satellite imagery available on Google Earth was used to confirm the relationship between EWDI and MPB-caused red-attack stands of whitebark pine.

Study Area

The study area encompassed 345,757 ha of previously mapped (Landenburger and Lawrence, 2006; Landenburger *et al.*, 2008) whitebark pine habitat in the core of the GYE, imaged by the Landsat satellites (Path 38, Row 29) (Figure 3.1). Yellowstone National Park comprised the center of the study area, and the vast majority of the federally-designated Greater Yellowstone Grizzly Bear Primary Conservation Area was also included. The study area also included sections of the Gallatin, Custer, Shoshone, Bridger-Teton, and Beaverhead-Deerlodge National Forests. Elevation within the study area ranged from 2,410 m – 3,681 m, with a mean elevation of 2,816 m. Mean January minimum temperature for whitebark pine environments throughout its range is -14 °C, with an absolute minimum of -34 °C. Maximum July mean temperature is 18 °C, with an absolute maximum of 29 °C. Yearly precipitation averages 931 mm, with 85% generally falling as snow (Weaver, 1990; Weaver, 1992a).

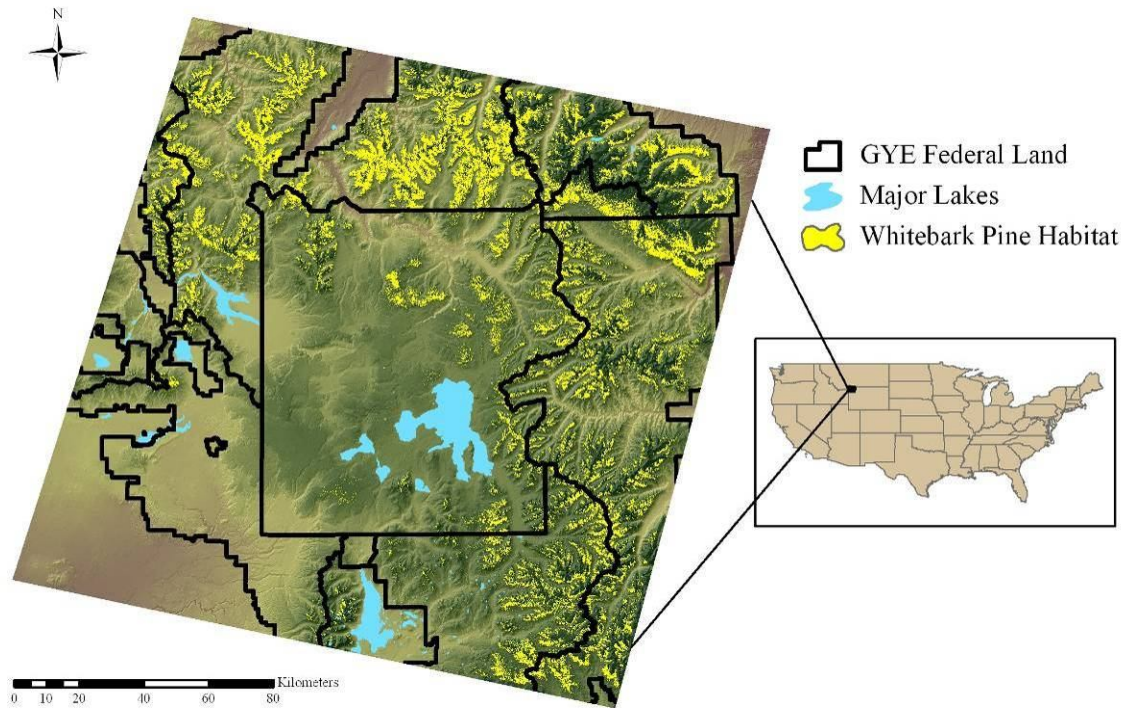


Figure 3.1: Study area map displayed over a shaded relief map of the GYE. Whitebark pine habitat is taken from Landenburger and Lawrence, 2006.

The Landenburger and Lawrence map was used to restrict the study area to whitebark pine habitat because this map provided a highly accurate (95.8% accuracy) guide to whitebark pine habitat in the GYE, and was mapped at the same scale as the current research (30-m pixels). One shortcoming of this map is a 20% overprediction of whitebark pine at the highest elevations (Landenburger *et al.*, 2008). Whitebark pine grows in sparse stands at the highest elevations that can be hard to classify as “forest.” To compensate for this known issue with low-cover, high elevation areas, the National Land Cover Database’s 2001 Percent Cover map (accuracy ranged from 78 – 93%) was used to further restrict the study to only those areas with greater than 0% canopy cover (Homer *et al.*, 2004).

Analysis of Relationship between Whitebark Pine Mortality and Climate

Imagery: Near-anniversary Landsat Enhanced Thematic Mapper Plus (ETM+) and Thematic Mapper (TM) imagery (pixel size $30 \times 30 \text{ m} = 0.0009 \text{ km}^2$) was obtained for all years from 1999 to 2008, except for 2000, which was unavailable due to persistent cloud and smoke cover (Table 3.1). The 2007 and 2008 images were ETM+ imagery with the scan-line corrector (SLC) off, leaving significant data gaps for those years. Late summer and early fall (ranging from 9 August to 6 October) images were chosen to minimize the effects of snow, snowmelt, and understory green-up on TC_{Wet} . All images were geometrically registered to a base Landsat image (September 15, 1999 ETM+) to within 0.5 pixels Root Mean Squared Error (RMSE).

Table 3.1: Landsat imagery used in this study

Landsat Imagery		
Date	Sensor	Notes
15 September 1999	ETM+	Geometric base image
20 September 2001	ETM+	Radiometric base image
23 September 2002	ETM+	
4 October 2003	TM	
6 October 2004	TM	
7 September 2005	TM	
9 August 2006	TM	
21 September 2007	ETM+	Scan-line-corrector OFF
22 August 2008	ETM+	Scan-line-corrector OFF

Climate Data: Spatially and temporally explicit climate data was obtained from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) group at Oregon State University (PRISM Group and Oregon State University, 2004) (Table 3.2).

Nationwide datasets for monthly average minimum temperature (October – March), monthly average maximum temperature (April – September), 30-year-average monthly temperature (April – September: maximum, October – March: minimum), monthly average precipitation, and 30-year-average monthly precipitation were acquired in raster format. Each month's average maximum temperature values were subtracted, by pixel, from the 30-year-average monthly temperature to create temperature anomaly datasets. Each month's precipitation values were subtracted, by pixel, from the 30-year-average monthly precipitation to create precipitation anomaly datasets. Degree day and spring precipitation anomaly datasets were created based on MPB climate suitability factors from Safranyik *et al.* (Safranyik *et al.*, 1975; Carroll *et al.*, 2003). The degree day dataset represented cumulative temperature suitable for MPB growth. This was calculated by determining the number of degrees in excess of 5.5 °C from monthly average temperatures for July, August, and September of the image year, multiplying these excesses by the number of days in the month, then summing all three months. The spring precipitation anomaly was the sum of the precipitation anomalies for April, May, and June for the image year and one year prior. The nationwide climate datasets were clipped to the study area. All climate datasets were resampled to 30-m pixels for analysis.

Table 3.2: Climate datasets. In the variable names, Y indicates the year of the satellite image, and X indicates the number of years prior to the image year. For example, panY-XJan represents four different variables: panY-0Jan, panY-1Jan, panY-2Jan, and panY-3Jan. The variable panY-2Jan would indicate the precipitation anomaly from January for two years prior to the date of the imagery, so January 2006 for 2008 imagery, January 2005 for 2007 imagery, etc.

Climate Dataset	Dates	Variable Abbreviations (Y-X = Image year minus 0, 1, 2, 3, or 4 years)	Native Spatial Resolution
Maximum temperature (monthly Average)	4/2000 – 9/2007 April – September (Summer)	-	4000 m
Minimum temperature (monthly average)	10/1999 – 3/2007 October – March (Winter)	-	4000 m
Minimum temperature anomaly (monthly)	4/2000 – 9/2007 April – September (Summer)	ano _{Y,X} Oct, ano _{Y,X} Nov, ano _{Y,X} Dec, ano _{Y,X} Jan, ano _{Y,X} Feb, ano _{Y,X} Mar	4000 m
Maximum temperature anomaly (monthly)	10/1999 – 3/2007 October – March (Winter)	ano _{Y,X} Apr, ano _{Y,X} May, ano _{Y,X} Jun, ano _{Y,X} Jul, ano _{Y,X} Aug, ano _{Y,X} Sep	4000 m
1971-2000 average maximum temperature (monthly)	April - September (Summer)	avgApr, avgMay, avgJun, avgJul, avgAug, avgSep	800 m
1971-2000 Average minimum temperature (monthly)	October – March (Winter)	avgOct, avgNov, avgDec, avgJan, avgFeb, avgMar	800 m
Summer temperature anomaly	April - September (Summer)	y _X sum	4000 m
Winter temperature anomaly	October – March (Winter)	y _X win	4000 m
Degree days		Degday	4000 m
Precipitation (monthly average)	10/1999 – 6/2008 January – December	-	4000 m
Precipitation anomaly (monthly)	January – December	pan _{Y,X} Jan, pan _{Y,X} Feb, pan _{Y,X} Mar, pan _{Y,X} Apr, pan _{Y,X} May, pan _{Y,X} Jun, pan _{Y,X} Jul, pan _{Y,X} Aug, pan _{Y,X} Sep, pan _{Y,X} Oct, pan _{Y,X} Nov, pan _{Y,X} Dec	4000 m
Water-year anomaly	October – September	y _X wttryr	4000 m
Spring precipitation anomaly	April – June	Spr-pano	4000 m
1971-2000 Average precipitation (monthly)	January – December	pavgJan, pavgFeb, pavgMar, pavgApr, pavgMay, pavgJun, pavgJul, pavgAug, pavgSep, pavgOct, pavgNov, pavgDec	800 m

Ancillary Data: A digital elevation model (DEM) was obtained from the National Elevation Dataset, at 30-m horizontal resolution (United States Geological Survey, 2009). The DEM was used to create slope and aspect datasets using a 3x3 moving window (90m x 90m) applied to the DEM. Aspect was binned into a 9-value factor dataset, representing north, northeast, east, southeast, south, southwest, west, northwest, and flat.

Perimeters of wildfires in the study area were obtained from three sources: US Forest Service Region 1 Fire History Layer (Smail and Tanke, 2008), Yellowstone National Park Fire History Layer (Spatial Analysis Center, 2005), and the federal Landscape Fire and Resource Management Planning Tools Project's (LANDFIRE) Rapid Refresh product, which is derived from MODIS satellite imagery (LANDFIRE, 2007). These three fire history datasets were rasterized to 30-m pixels and combined so that a fire in any layer resulted in a fire in the combined raster. Fire perimeters were separately calculated for each individual year, 1999 - 2008. Cumulative fire history masks were created for each year of imagery (i.e., the 2005 fire mask included fires from 1999, 2000, 2001, 2002, 2003, 2004, and 2005, while the 2004 mask did not include 2005 fires).

Image Processing: All images were converted to top-of-atmosphere reflectance, which has been shown to partially compensate for atmospheric and illumination differences between scenes (Huang *et al.*, 2001). Absolute-normalization involves converting a radiometric base image to surface reflectance, followed by matching all other images to the radiometric base image via regression-based normalizations. The absolute-normalization procedure has been shown to provide the best radiometric normalization for multi-date imagery (Schroeder *et al.*, 2006). Dark Object Subtraction

(DOS) was used to provide the first half of the absolute-normalization process, an absolute atmospheric correction to surface reflectance for the radiometric base image (September 20, 2001 ETM+). DOS effectively removes atmospheric effects in TC_{Wet} (Song and Woodcock, 2003). Cloud, smoke, and snow masking on all images was performed using manual digitizing. From 2003 – 2006, cloud, smoke, and snow masking removed no more than 13.4% of the study area from any one image. The SLC-off data gaps in the 2007 and 2008 ETM+ images caused more portions of the study area to be removed for those years, 18.7% and 23.5%, respectively.

A Tasseled Cap transformation was performed using Huang's ETM+ coefficients (Huang *et al.*, 2002). For the second half of the absolute-normalization procedure, TC_{Wet} components were normalized to the absolutely-corrected radiometric base image wetness using pseudo-invariant targets to build normalization regression equations. Paired T-tests comparing both the fitted points and the uncorrected points with the 2001 radiometric base image showed that the regression (fitted points) improved the match for all dates except 2003 ($p < 0.001$). Despite having a p -value = 0.2285, the regression-based correction for the 2003 image was used because it reduced the Sum of Squared Errors by 62% from the uncorrected image, indicating that the inter-date variation was being reduced with the regression. All images were clipped to intersecting areas only, excepting the data gaps in the SLC-off images. The images were further masked to areas mapped as whitebark pine by Landenburger and Lawrence (2006).

Areas that experienced a wildfire during the study period were removed from analysis, using the fire history masks. Extensive logging was an unlikely source of

substantial forest change because the majority of the study area was relatively inaccessible, high-elevation terrain and because 2/3 of GYE whitebark pine was found in protected designated wilderness areas or national parks (Logan *et al.*, 2009). While blister rust was present in the study area, it kills over decadal time periods and so was unlikely to cause detectable changes in EWDI over a yearly basis, especially when looking at 30-m pixels that would have many trees in one pixel (Tomback *et al.*, 2001). With wildfires removed, logging unlikely, and change due to blister rust likely too slow to be detectable, I assumed that the only likely source of widespread and substantial decreases in EWDI in the study area was mortality from MPB attacks.

EWDI was calculated for each date versus the initial year (EWDI-to-99), as well as for each date versus the previous year (EWDI-yearly). 1999 was chosen as the initial year because it was before the current MPB epidemic began in the GYE. Spatial autocorrelation terms were created by using circular moving windows of various radii to calculate average neighborhood values of EWDI-to-99 and EWDI-yearly. The window sizes were chosen to encompass what is known (and not known) about MPB dispersal distances, and extended 30 m, 90 m, and 150 m from the edge of the center pixel, which was excluded from the window (Robertson *et al.*, 2007). An additional temporal autocorrelation term was generated (minEWDI99) to measure the minimum EWDI-to-99 value at that pixel for all years prior to the image date. This term measures the maximum recent impact of MPB on that pixel, to offset possible increases in TC_{Wet} caused by recently-exposed understory vegetation under a dead canopy (Table 3.3).

Table 3.3: Autocorrelative predictor variables used

Autocorrelation Term	Definition
EWDI_{Y-1}	EWDI-yearly for the same pixel one year prior to the image
$\text{EWDI}_{Y-2\text{to}99}$	EWDI-to-99 value from 2 years before the image
$3 \times 3_{Y-1}$	Average of EWDI-yearly in 30 m neighborhood from one year prior to the image
$7 \times 7_{Y-1}$	Average of EWDI-yearly in 90 m neighborhood from one year prior to the image
$11 \times 11_{Y-1}$	Average of EWDI-yearly in 150 m neighborhood from one year prior to the image
$3 \times 3_{\text{to}99_{Y-2}}$	Average of EWDI-to-99 value in 30 m neighborhood from 2 years before the image
$7 \times 7_{\text{to}99_{Y-2}}$	Average of EWDI-to-99 value in 90 m neighborhood from 2 years before the image
$11 \times 11_{\text{to}99_{Y-2}}$	Average of EWDI-to-99 value in 150 m neighborhood from 2 years before the image
minEWDI_{99}	Minimum EWDI-to-99 value from all years prior to image

Data Extraction and Compilation: For each year 2003 – 2008, a different set of 10,000 random points was generated. Using a different set of points for each year allowed locations that were obscured by clouds/smoke/snow in one year but not in others to still be included in the analysis, maximizing the area of study. These random points were used to extract the pixel value for all variables for that year. Data points where any variable contained missing data (null) were removed from the analysis. Points where the NLCD forest canopy cover equaled zero (non-forested) were also removed from the analysis, leaving 40,639 total points for analysis. All years 2003 - 2008 were treated equally in the

analysis. For example, for the variable “ano_{Y-3Feb}” (representing the temperature anomalies from the February three years prior to the image date), these temperature anomalies would come from 2005 climate data for the 2008 image, but from 2000 climate data for the 2003 image. Similarly, the EWDI dataset came from a compilation of year-over-year changes from 2003 through 2008. One-third of the points were randomly selected and used to create a validation data set ($n = 13,527$), which was not used in building regression trees. The remaining two-thirds of the data points ($n = 27,112$) formed a training data set used to build regression trees to model the relationship between climate and whitebark pine mortality. Exploratory scatter plots and correlations between the response variable (EWDI-yearly) and various subsets of predictor variables were examined.

Regression Tree Analysis: This analysis utilized regression trees containing climatic, topographic, and autocorrelation variables to predict EWDI. In this way the connections between climate and whitebark pine mortality across the GYE were investigated. Regression trees were chosen for the analysis because they are non-parametric in nature, handle non-linear datasets, and can automatically select the most useful predictor variables from a suite of reasonable predictor variables (Lawrence and Wright, 2001; Rogan *et al.*, 2003). Regression trees were built in S-Plus (Version 8.0) with 5 minimum observations before a split, a minimum of 10 observations in a node, and minimum node deviance of 0.01. Trees were pruned both to avoid over-fitting and to simplify them in order to allow interpretation of the splits for ecological significance. Ten-fold cross-validation of tree residual deviance was used to inform the tree-pruning

process. This pruning generally left trees with more than minimum deviance, but minimum-deviance trees would have been far too large for interpretation.

Twenty-four regression trees were built using different subsets of the available predictor variables in order to examine different potential relationships with EWDI (Table 3.4). All predictor variables were included in the first tree to determine if any statistical relationship existed. The predictor variables (especially the climate terms) were highly correlated, so subsequent regression trees were built from a variety of variable subsets in an attempt to avoid ecologically spurious conclusions. For example, if the only winter temperature variable included in a regression tree was a February temperature anomaly, would a different tree that used December or January temperature perform nearly as well, indicating that “winter temperature” was really the ecologically important consideration, more so than February in particular? All climate terms were used to investigate whether whitebark pine mortality could be predicted solely based on recent climate. Due to the large number of climate terms (120), another regression tree was built using only the twelve seasonal climate summary terms, in an attempt to predict mortality with a smaller suite of climate variables. Regression trees were built using only temperature data and only precipitation data, to further investigate climatic relationships. Topographic variables have been suggested as important factors in insect outbreaks (Perkins and Roberts, 2003), especially as they impact incident solar radiation, so a regression tree was built solely from slope, aspect, and elevation. The autocorrelation terms were used to build a regression tree in an attempt to better understand the effect of prior MPB attack, and the neighborhood autocorrelation terms by themselves were used

in another regression tree to investigate MPB dispersal. In order to better understand potential changes in MPB voltinism, three regression trees were built using only climate data from one year prior to the image (Y-1), two years prior to the image (Y-2), and three years prior to the image (Y-3), respectively. These trees did not have 30-year-average climate data included. Finally, regression trees were built (with and without autocorrelation terms) for each year (2003 – 2008) of data, to investigate potential changes in the impact of climate on whitebark pine mortality during the course of the study period.

Table 3.4: Summary of regression tree analyses performed.

Tree Name	Predictor Variable Categories	# Input Predictor Variables	Ecological Question Addressed:
Full	All	129	Can EWDI be predicted with climate, topographic, and autoregressive terms?
All Climate	Precipitation anomaly, average precipitation, temperature anomaly, average temperature, seasonal climate summaries	117	Can climate alone predict EWDI?
Climate Summaries	Climate summaries	12	Can climate summaries alone predict EWDI?
Autocorrelation	Autocorrelation terms	9	What portion of EWDI predictive power is due to autocorrelation only?
Spatial autocorrelation	Spatial (neighborhood) autocorrelation terms	6	How important is area surrounding pixel to prediction? What is important distance for MPB dispersal?
Topographic	Topographic terms	3	Do slope, aspect, and elevation impact EWDI?
Temperature	Temperature anomaly, average temperature, seasonal temperature summaries	55	What portion of predictive power of climate variables is due to temperature alone?
Precipitation	Precipitation anomaly, average precipitation, seasonal precipitation summaries	62	What portion of predictive power of climate variables is due to precipitation alone?
Y-1 Climate	Precipitation anomaly, average precipitation, temperature anomaly, average temperature, seasonal climate summaries from one growth year before the image only	28	What is relative importance of climate variables from one growth year prior to image?
Y-2 Climate	Precipitation anomaly, average precipitation, temperature anomaly, average temperature, seasonal climate summaries from two growth years before the image only	27	What is relative importance of climate variables from two growth years prior to image?
Y-3 Climate	Precipitation anomaly, average precipitation, temperature anomaly, average temperature, seasonal climate summaries from three growth years before the image only	27	What is relative importance of climate variables from three growth years prior to image?
Yearly Full (6 trees)	All variables, but both predictor and response variables subset by image year (one tree for each year: 2003, 2004, 2005, 2006, 2007, 2008)	129	Did the variables included in each yearly tree change, either by season or growth year?
Yearly Climate Only (6 trees)	Precipitation anomaly, average precipitation, temperature anomaly, average temperature, seasonal climate summaries, but both predictor and response variables subset by image year (one tree for each year: 2003, 2004, 2005, 2006, 2007, 2008)	117	Did the variables included in each yearly tree change, either by season or growth year, when only climate data is used?

After each regression tree was built and pruned, the tree was used to predict EWDI values from the independent validation data set. These predicted EWDI values were compared to the observed EWDI values, generating a Sum of Squared Errors (SSE). The total deviance in the validation data set EWDI values was calculated (Total Sum of Squares, SST). The SSE was subtracted from the SST then divided by the SST to provide a measure of total dataset deviance explained (DDE) by the regression tree, a value analogous to R^2 in a linear regression model.

A partial DDE was calculated for each binary split in order to evaluate the relative importance of each variable in the regression tree. This was done by calculating the amount of deviance reduced by that split, then dividing this reduction by the root deviance. The amount of deviance reduced by a split was determined by subtracting the sum of the deviance remaining in the two daughter nodes from deviance extant in the parent node. All partial DDE values for that variable were summed if a variable was used in more than one split per tree. In order to better understand the contribution of each variable in the tree, a relative partial DDE value was calculated (Partial DDE_{Rel}). Partial DDE_{Rel} was calculated by dividing the amount of deviance explained by each variable by the total DDE for the regression tree, as opposed to the root deviance as in the standard DDE value. Partial DDE for a tree will sum to total DDE for that tree, and partial DDE_{Rel} for any tree will sum to one.

Mapping the Regression Tree: The pruned, full-variable regression tree (22 terminal nodes, called “final tree”) was applied to the full suite of climate and image data to create a predicted EWDI map for each year, 2003 – 2008. These were then compared

to maps of observed EWDI for each year, after the observed EWDI values had been binned into the same 22 value classes (nodes) according to the closest node value to the observed EWDI value. Residual maps were created by subtracting the EWDI class value in the observed yearly maps from the predicted EWDI maps. These residual maps were used to investigate spatial patterns in the regression tree models.

Google Earth-Based Evaluation of EWDI Response to Red-Attack

High-resolution aerial and satellite imagery available in Google Earth (Google Inc., 2009) was used to evaluate the relationship between Landsat-derived EWDI values and visible MPB-affected red-attack stands of whitebark pine. Locations were randomly generated across the study area ($n = 238$), stratified by the 2006 EWDI values. Stratification was done using the 2006 EWDI values because it contained a large range of EWDI values and was the most recent image without the data gaps from Landsat SLC failure. All locations were identified in Google Earth, and the high-resolution imagery was used to classify the 30-m radius area around each point as green, red-attack, or gray-attack for each year in which suitable high-resolution imagery was available. The “measure” tool in Google Earth was used to delineate the 30-m radius. Thirty-five locations had high-resolution imagery available for multiple years during the study period. These classifications were compared to Landsat-derived EWDI values for the appropriate year to determine if EWDI was an effective measure of the presence/absence of red-attack in whitebark pine.

Results

Google Earth Analysis

In the Google Earth analysis, green (unattacked by MPB) stands of whitebark pine had a higher EWDI value than red-attack stands, when comparing both mean and median values (Table 3.5, Figure 3.2a). Gray-attack stands had much higher EWDI values than either green stands or red-attack stands, although the sample size ($n = 8$) was very low for gray-attack stands (Figure 3.2b). The range of EWDI values in green stands (1,573) was also much greater than the range for red-attack (202) or gray-attack stands (288).

Table 3.5: Summary statistics comparing Landsat EWDI response between green (unattacked), red-attack, and gray-attack stands of whitebark pine.

	Green Stands EWDI (n = 195)	Red-Attack Stands EWDI (n = 43)	Gray-Attack Stands EWDI (n = 8)
Mean	-21.4	-46.7	87.9
Median	-8	-55	71
Maximum	608	62	260
Minimum	-965	-140	-28

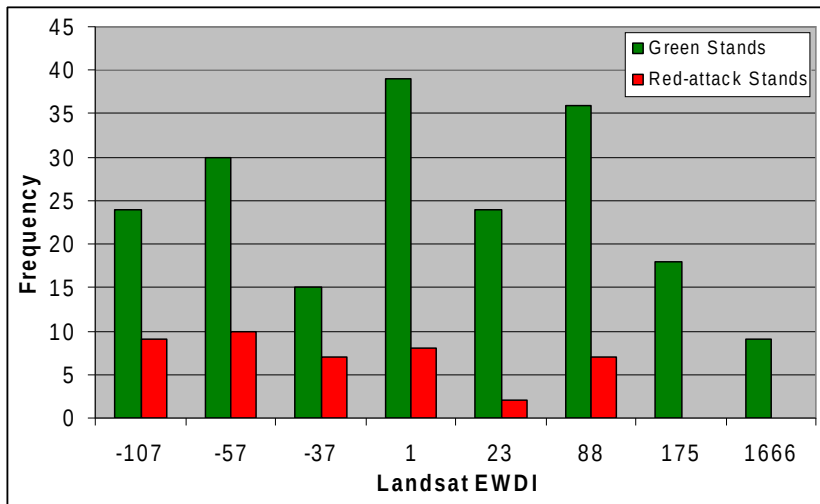


Figure 3.2a: Landsat EWDI response for red-attack and green (unattacked) whitebark pine stands, generated from interpretation of high-resolution Google Earth imagery.

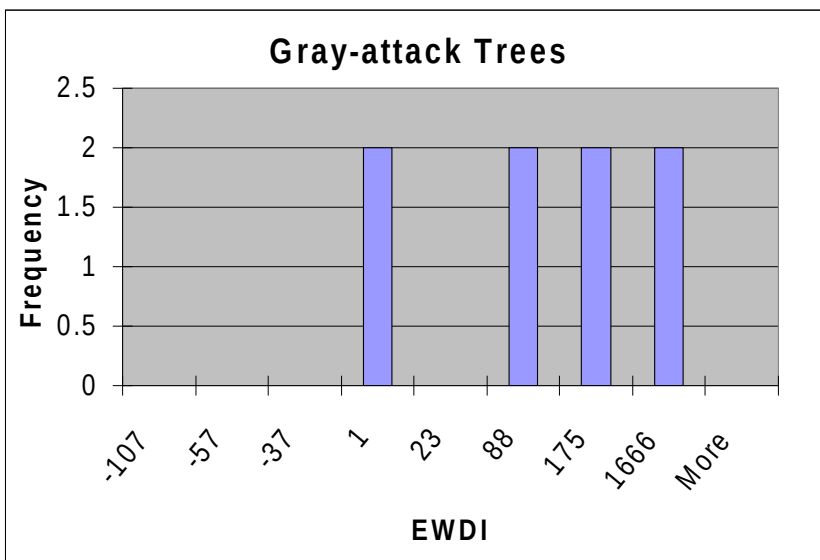


Figure 3.2b: Landsat EWDI response for gray-attack (post-attack) whitebark pine stands, generated from interpretation of high-resolution Google Earth imagery.

Landsat Analysis

Visual exploratory data analysis of scatter plots of predictor variables in the full tree versus EWDI-yearly (“EWDI” in the plots) were examined (Figure 3.3). EWDI_{Y-1} has the strongest correlation with EWDI, a negative correlation that is likely non-linear. MinEWDI99 might also have a negative, non-linear correlation with EWDI, although the “fish-tail” appearance of the scatter plot might indicate a binary or threshold-type response. None of the other predictor variables in the final all-variable regression tree show any clear pattern in their scatter plots against EWDI.

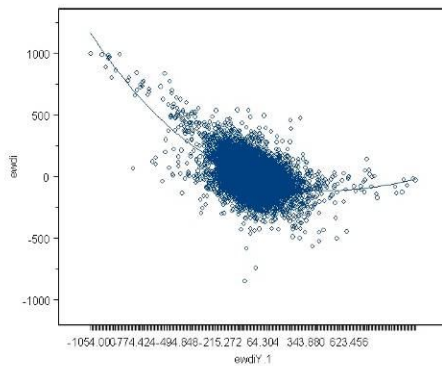


Figure 3.3a: EWDI_{Y-1}

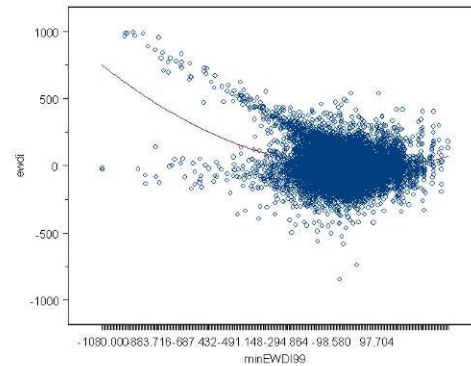
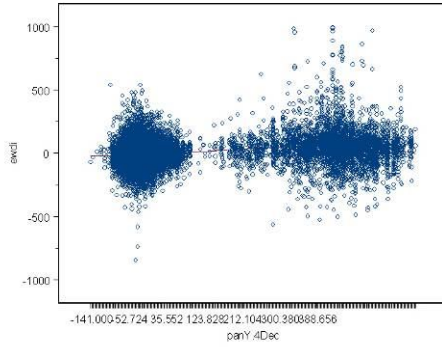
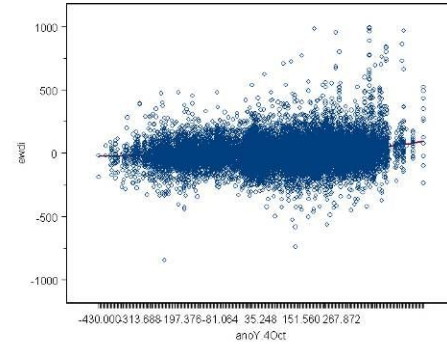
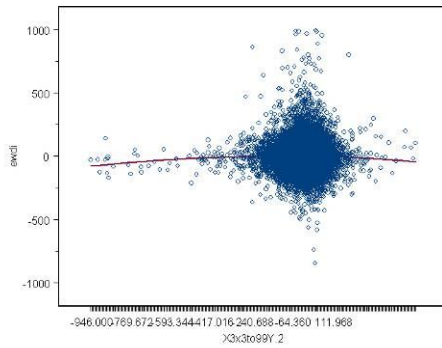
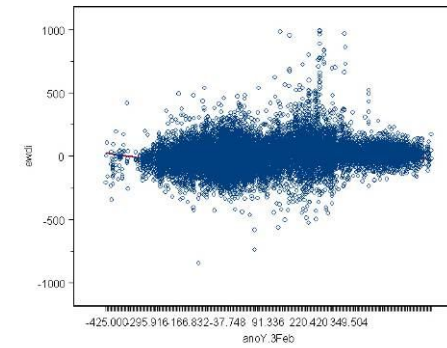
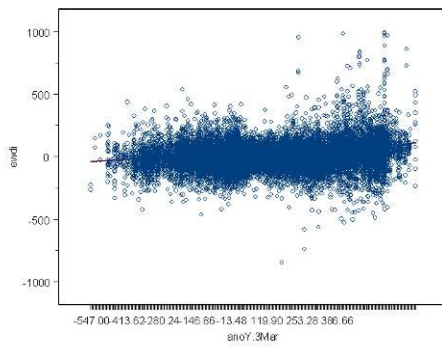
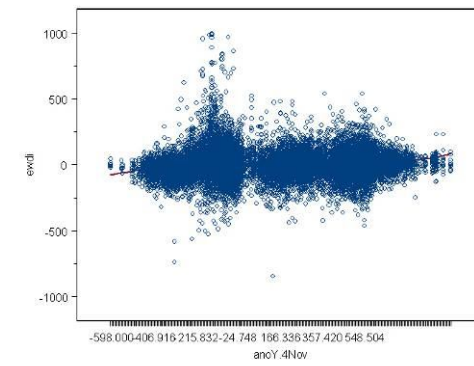


Figure 3.3b: minEWDI99

Figure 3.3c: panY_4Dec Figure 3.3d: anoY_4Oct Figure 3.3e: $3x3\text{to}99Y_2$ Figure 3.3f: anoY_3Feb Figure 3.3g: anoY_3Mar Figure 3.3h: anoY_4Nov

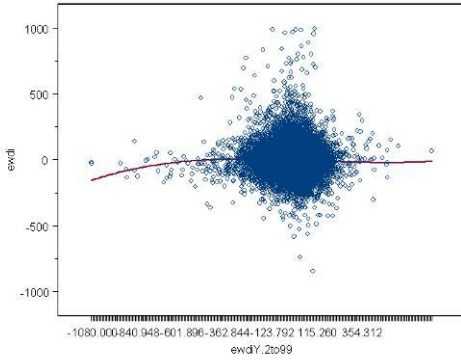
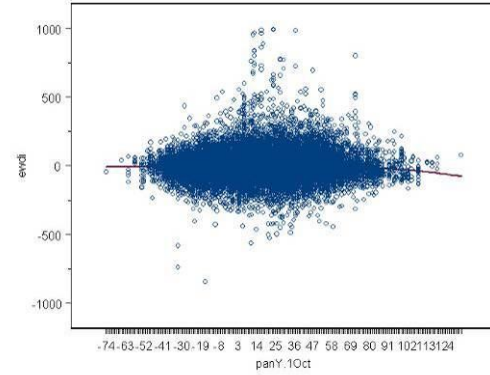
Figure 3.3i: ewdi_{Y-2to99}Figure 3.3j: panY_{-1Oct}

Figure 3.3: Correlations of predictor variables (X-axis) vs. EWDI-Yearly (Y-axis). Fitted curves are 3rd order linear polynomials.

A correlation analysis was performed between the variables in the final tree (Table 3.6). Again, the strongest correlation with EWDI, at almost twice the strength of the next most important relationship, is EWDI_{Y-1}, with a correlation of -0.474. This means that a highly positive EWDI value predicts a negative EWDI value for the same pixel in the following year, and vice versa. The strongest climate variable correlation with EWDI was panY_{-4Dec} at 0.2448, indicating that drier conditions in the December four years prior to the image date tend to associate with negative EWDI values and thus increased conifer mortality. Other important predictor correlates for EWDI are anoY_{-3Feb}, anoY_{-3Mar}, minEWDI99, and anoY_{-4Oct}. The three temperature anomaly predictor variables all indicate a positive correlation with EWDI, so that warmer temperatures indicate higher EWDI values, and thus decreased conifer mortality. Many of the predictor variables are also highly correlated with each other.

Table 3.6: Correlation matrix for variables included in final 22-node regression tree. The response variable EWDI-yearly is highlighted in green. Predictor variables with a correlation to EWDI-yearly greater in magnitude than 0.15 are bolded.

	ano _{Y-4} Oct	ano _{Y-3} Feb	ano _{Y-3} Mar	ano _{Y-4} Nov	pan _{Y-1} Oct	pan _{Y-4} Dec	ewdi _{Y-1}	minEWDI99	3x3to99 _{Y-2}	ewdi _{Y-2} to99
ewdi	0.1544	0.2042	0.1796	0.0486	0.0099	0.2448	-0.474	-0.1651	-0.0062	-0.02746
ano _{Y-4} Oct	1	0.5615	0.276	-0.0764	0.0515	0.4626	-0.0392	0.0669	0.088	0.071
ano _{Y-3} Feb		1	0.343	0.391	-0.2128	0.3555	-0.0203	-0.058	-0.0399	-0.0283
ano _{Y-3} Mar			1	-0.4238	-0.0326	0.6524	-0.0531	-0.3038	-0.0956	-0.0737
ano _{Y-4} Nov				1	-0.2349	-0.2879	-0.0978	0.3052	0.1109	0.0912
pan _{Y-1} Oct					1	0.3294	0.05157	-0.2065	-0.1341	-0.106
pan _{Y-4} Dec						1	-0.1315	-0.2402	-0.0652	-0.0466
ewdi _{Y-1}							1	-0.041	-0.4188	-0.5348
minEWDI99								1	0.3748	0.4198
3x3to99 _{Y-2}									1	0.7345
ewdi _{Y-2} to99										1

No clear pattern exists to the DDE values for each yearly regression tree (Table 3.7, although they cannot be *directly* compared due to their being based on different datasets. There is also no clear pattern to which variables were included in each yearly tree. Yearly regression trees from only climate data demonstrate the same lack of distinct patterns (Table 3.8). Additionally, the DDE values are generally low with the exception of 2007.

Table 3.7: Summary of regression trees using yearly subsets of data points, using all predictor variables. DDE = Dataset Deviation Explained, analogous to R^2 .

YEAR	DDE Training	DDE Validation	Root Variance (x 10,000)	Terminal Nodes	Temperature Terms	Precip. Terms	Topographic Terms	Autocorrelation Terms
2003	0.1655	0.1230	1127	10	ano _{Y-2} Dec avg30Nov			ewdi _{Y-1}
2004	0.2457	0.1930	1457	15	ano _{Y-1} Jun ano _{Y-4} Oct avg30Oct		aspect slope	ewdi _{Y-1} 7x7to99 _{Y-2} 3x3 _{Y-1}
2005	0.2957	0.2718	4619	7				ewdi _{Y-1} 7x7 _{Y-1}
2006	0.1723	0.0900	3512	14	ano _{Y-3} Feb ano _{Y-2} Jul avg30Feb		slope	3x3to99 _{Y-2} ewdi _{Y-1} ewdi _{Y-2} to99 3x3 _{Y-1} 7x7 _{Y-1}
2007	0.6901	0.6498	8715	15				ewdi _{Y-1} minEWDI99 ewdi _{Y-2} to99
2008	0.4272	0.3739	2149	11	avg30Oct avg30Dec		aspect	ewdi _{Y-1} minEWDI99

Table 3.8: Summary of regression trees using yearly subsets of data points, using climate predictor variables only. DDE = Dataset Deviation Explained, analogous to R^2 .

YEAR	DDE Training	DDE Validation	Root Variance (x 10,000)	Terminal Nodes	Temperature Terms	Precipitation Terms
2003	0.0195	0.0081	1127	2	ano _{Y-2} Dec	
2004	0.0494	0.0084	1457	8	avg30Jan ano _{Y-1} Feb avg30Aug avg30Apr	pan _{Y-2} Jun pan _{Y-1} Apr pan _{Y-2} May
2005	0.1528	0.0698	4619	14	ano _{Y-2} Oct ano _{Y-1} Mar ano _{Y-2} Feb ano _{Y-2} Jan avg30Jun avg30Feb ano _{Y-1} Jun ano _{Y-1} Apr avg30Oct ano _{Y-2} Dec	pan _{Y-4} Dec panYJun pan _{Y-3} Dec
2006	0.0140	0.0031	3512	2	ano _{Y-4} Oct	
2007	0.2695	0.1755	8715	16	avg30Aug _{Y-3} wtryr ano _{Y-1} Feb ano _{Y-2} Aug _{Y-2} sum	panYJul panYAug pan _{Y-1} Oct panYApr panYSep pavgFeb pavgMay pavgJun
2008	0.0568	0.0305	2149	4	ano _{Y-1} Mar	pan _{Y-1} Aug

The highly stochastic nature of the ecological processes being predicted yields DDE values far less than 1. The full 22-node tree had a DDE value of 0.3865 (Table 3.9). Most climate variables included in this tree were from three years before the date of imagery (measured in October – September MPB growing season years). Climate terms from one, two, and three growing seasons previous to the imagery are included in the all-climate tree (DDE = 0.1538). In the full tree and the all-climate tree, only one summer climate variable was included ($\text{ano}_{Y-1}\text{Jul}$), out of 20 climate variables used between the two trees. The seasonal climate summary tree (DDE = 0.1419) was almost as successful as the climate tree, using fewer predictor variables (9 versus 14) and far fewer potential predictor variables (12 versus 120). The autocorrelation tree (DDE = 0.3123) was able to explain 81% as much variation as the full 22-node tree did. It did not incorporate any of the spatial autocorrelation terms, only the temporal ones. Despite this, the tree built only on spatial autocorrelation terms (DDE = 0.1996) still performed better than any tree that did not include any autocorrelation terms. The 3x3 window (30-m radius), 7x7 window (90-m radius), and 11x11 window (150-m radius) autocorrelation terms were all included in the tree. No topographic variables were included in any tree except the tree that only used topographic variables, which had a DDE = 0.0015. Finally, for the trees that evaluated climate data from different growing season years, there was an increase from Y-1 (DDE = 0.1160) to Y-2 (DDE = 0.1414) to Y-3 (DDE = 0.1547).

Table 3.9: Summary of DDE and variables included in all regression trees. Root variance for all models is 236,800,000. Please see the appendix for further information and diagrams of these regression trees.

Model	DDE Training	DDE Validation	Nodes	Temperature Terms	Precipitation Terms	Topo. Terms	Autocorrelation Terms
Full 2008 22 node	0.4101	0.3865	22	ano _{Y-4} Oct ano _{Y-3} Feb ano _{Y-3} Mar ano _{Y-4} Nov	pan _{Y-4} Dec pan _{Y-1} Oct		EWDI _{Y-1} minEWDI99 3x3to99 _{Y-2} EWDI _{Y-2} to99
All Climate	0.1867	0.1538	17	ano _{Y-3} Feb ano _{Y-2} Mar avg30Dec ano _{Y-1} Mar ano _{Y-1} Apr ano _{Y-2} Dec ano _{Y-1} Jul ano _{Y-3} Apr	pan _{Y-3} Sep pan _{Y-1} May pan _{Y-1} Oct pan _{Y-2} Dec pan _{Y-4} oct pan _{Y-2} Sep		
Seasonal climate summary	0.1589	0.1419	19	_{Y-3} win _{Y-1} win _{Y-2} win _{Y-1} sum	_{Y-3} wtryr _{Y-1} wtryr spr-pano _{Y-2} wtryr _{Y-0} wtryr		
Autocorrelation	0.3412	0.3123	17				EWDI _{Y-1} minEWDI99 EWDI _{Y-2} to99
Spatial autocorrelation only	0.2090	0.1996	10				3x3 _{Y-1} 11x11 _{Y-1} 3x3to99 _{Y-2} 7x7 _{Y-1}
Topographic effects	0.0059	0.0015	4			aspect slope	
Temperature	0.1786	0.1505	18	ano _{Y-3} Feb ano _{Y-2} Mar Avg30Dec ano _{Y-1} Mar ano _{Y-3} Sep ano _{Y-2} Oct ano _{Y-3} Jun ano _{Y-3} Jan ano _{Y-1} Sep ano _{Y-3} Apr	ano _{Y-1} Apr ano _{Y-2} Dec ano _{Y-2} Feb		
Precipitation	0.1816	0.1482	19		pan _{Y-4} Dec pan _{Y-2} Jan pan _Y Mar pan _{Y-1} Aug pan _{Y-2} Sep pavgMay pan _{Y-3} Nov pavgMar pan _{Y-1} Nov pavgJun pan _{Y-3} Mar pan _{Y-2} Dec pan _{Y-3} Feb		
Y-1 Climate	0.1533	0.1160	17	ano _{Y-1} Mar ano _{Y-1} Sep ano _{Y-2} Oct ano _{Y-1} Apr	pan _{Y-2} Nov pan _{Y-1} Sep pan _{Y-1} Aug pan _{Y-1} Jun pan _{Y-1} Jan		
Y-2 Climate	0.1681	0.1414	18	ano _{Y-2} Mar ano _{Y-3} Nov ano _{Y-2} Sep ano _{Y-2} Feb ano _{Y-2} Apr ano _{Y-3} Dec	pan _{Y-2} Jan pan _{Y-2} Sep pan _{Y-2} Mar pan _{Y-2} Feb pan _{Y-2} Apr pan _{Y-2} Aug		
Y-3 Climate	0.1731	0.1547	18	ano _{Y-3} Feb _{Y-3} win ano _{Y-3} Sep ano _{Y-4} Nov ano _{Y-3} Mar ano _{Y-3} Apr ano _{Y-3} Aug	pan _{Y-3} Mar pan _{Y-3} Sep pan _{Y-4} oct pan _{Y-3} Jun		

Most of the ten variables in the tree (Figure 3.4; Table 3.10a) could be assigned a direction of relationship (positive or negative) with the response variable, EWDI. A positive relationship existed for precipitation anomalies $\text{pan}_{Y-4}\text{Oct}$ and $\text{pan}_{Y-1}\text{Oct}$, in addition to temperature anomaly $\text{ano}_{Y-3}\text{Mar}$. A negative relationship was demonstrated for EWDI with autocorrelation terms EWDI_{Y-1} , minEWDI99 , $3x3\text{to}99_{Y-2}$, and $\text{EWDI}_{Y-2\text{to}99}$, in addition to temperature anomaly $\text{ano}_{Y-4}\text{Nov}$. The direction of the relationships for $\text{ano}_{Y-4}\text{Oct}$ and $\text{ano}_{Y-3}\text{Feb}$ could not be determined, because terminal nodes on either side of the split were not consistently larger or smaller.

Eight of the fourteen variables in the climate-only tree could be assigned a direction of correlation (positive or negative) to EWDI (Figure 3.5, Table 3.10b). Precipitation anomaly variables $\text{Pan}_{Y-1}\text{Oct}$ and $\text{pan}_{Y-2}\text{Sep}$ had a positive correlation with EWDI. Precipitation anomaly $\text{pan}_{Y-2}\text{Dec}$, long-term average December temperature (Avg30Dec), and temperature anomalies $\text{ano}_{Y-1}\text{Mar}$, $\text{ano}_{Y-2}\text{Dec}$, $\text{ano}_{Y-1}\text{Jul}$, and $\text{ano}_{Y-3}\text{Apr}$ all showed a negative correlation with EWDI. The direction of correlation for the following six variables could not be determined given the nature of the regression tree: $\text{ano}_{Y-3}\text{Feb}$, $\text{ano}_{Y-2}\text{Mar}$, $\text{ano}_{Y-1}\text{Apr}$, $\text{pan}_{Y-3}\text{Sep}$, $\text{pan}_{Y-1}\text{May}$, and $\text{pan}_{Y-4}\text{Oct}$.

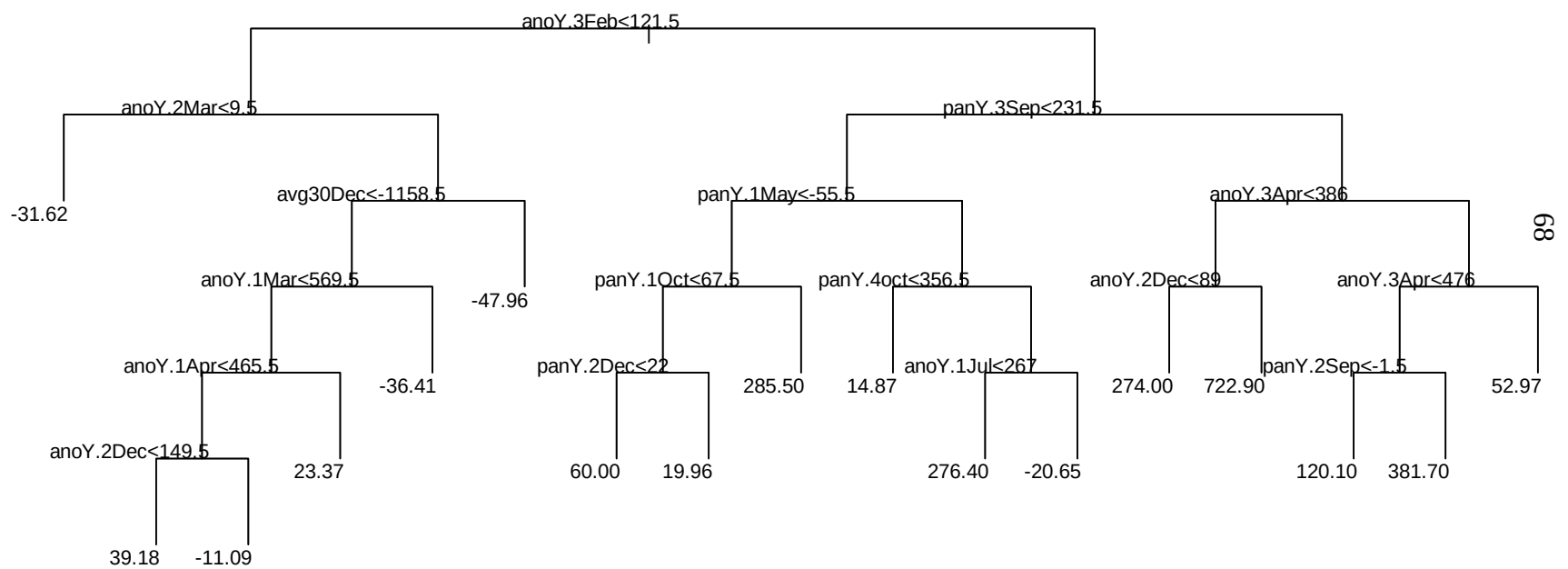


Figure 3.5: Diagram of climate-variables-only tree (17 nodes). Note that temperature values represent degrees of Celsius x 100, and precipitation variables are in millimeters (mm). Please see the appendix for diagrams of additional regression trees.

Table 3.10a: Interpretation of predictor variable relationships with response variable EWDI for 22-node final full-variable regression tree.

Final all-variable tree (22-node)			
Variable	Type of Variable	Response Direction with EWDI	Supports Expectation?
ano _{Y-4} Nov	Temperature	Negative	E1
pan _{Y-4} Oct	Precipitation	Positive	E2
pan _{Y-1} Oct	Precipitation	Positive	E2
EWDI _{Y-1}	Autocorrelation	Negative	E3
minEWDI99	Autocorrelation	Negative	E3
3x3to99 _{Y-2}	Autocorrelation	Negative	E3
EWDI _{Y-2} to99	Autocorrelation	Negative	E3
ano _{Y-3} Mar	Temperature	Positive	No
ano _{Y-3} Feb	Temperature	Not Clear	N/A
ano _{Y-4} Oct	Temperature	Not Clear	N/A

Expectation Codes

E1: Warmer temperatures decrease MPB mortality and/or increase MPB growth rates, leading to an increase in whitebark pine mortality, leading to a decrease in EWDI values.

E2: Drier conditions reduce ability of whitebark pine to repel attacks by MPB, leading to an increase in whitebark pine mortality, leading to a decrease in EWDI values.

E3: Previous MPB activity in a cell or neighboring cell decreases the likelihood of current MPB activity, due to depletion of potential host trees, leading to an increase in EWDI.

No: Does not support Expectation 1, Expectation 2, or Expectation 3.

N/A: Not applicable, due to lack of interpretability in variable relationship.

Table 3.10b: Interpretation of predictor variable relationships with response variable EWDI for 17-node climate variables only regression tree.

Climate variables only (17-node) Regression Tree			
Variable	Type of Variable	Response Direction with EWDI	Supports Expectations?
avg30Dec	Average Temperature	Negative	E1
ano _{Y-1} Mar	Temperature	Negative	E1
ano _{Y-2} Dec	Temperature	Negative	E1
ano _{Y-1} Jul	Temperature	Negative	E1
ano _{Y-3} Apr	Temperature	Negative	E1
pan _{Y-1} Oct	Precipitation	Positive	E2
pan _{Y-2} Sep	Precipitation	Positive	E2
pan _{Y-2} Dec	Precipitation	Negative	No
ano _{Y-3} Feb	Temperature	Not Clear	N/A
ano _{Y-2} Mar	Temperature	Not Clear	N/A
ano _{Y-1} Apr	Temperature	Not Clear	N/A
pan _{Y-3} Sep	Precipitation	Not Clear	N/A
pan _{Y-1} May	Precipitation	Not Clear	N/A
pan _{Y-4} Oct	Precipitation	Not Clear	N/A

Expectation Codes

E1: Warmer temperatures decrease MPB mortality and/or increase MPB growth rates, leading to an increase in whitebark pine mortality, leading to a decrease in EWDI values.

E2: Drier conditions reduce ability of whitebark pine to repel attacks by MPB, leading to an increase in whitebark pine mortality, leading to a decrease in EWDI values.

No: Does not support either Expectation 1 or Expectation 2.

N/A: Not applicable, due to lack of interpretability of variable relationship.

Partial DDE and Partial DDE_{Rel} values for the final all-variable regression tree are in Table 3.11a, and the same data for the climate-variables-only regression tree is presented in Table 3.11b. For the all-variable tree, $EWDI_{Y-1}$ was by far the most important variable, followed by $minEWDI99$. Taken together, these two autocorrelation terms accounted for over 71% of DDE_{Rel} of the dataset variation explained, while the next most important term ($ano_{Y-3}Feb$) accounted for only 9% of DDE_{Rel} . The autocorrelation variables were used frequently and accounted for over half of the splits in the regression tree. Climate variables from the Y-3 growth year (October Y-4 to September Y-3) accounted for a partial DDE_{Rel} of 0.2287, while all other growth years were represented entirely by $panY-1Oct$, with a $DDE_{Rel} = 0.0079$. See Table 3.12a for a summary of these relationships.

Table 3.11a: Analysis of dataset variation explained, by variable, in final, all-variable, 22-node regression tree.

Variable	Growth Year (Oct – Sep)	Variable Type	Partial DDE*	# Splits	Partial DDE_{Rel}
$ewdi_{Y-1}$	N/A	Autocorrelation	0.1792	8	0.4368
$minEWDI99$	N/A	Autocorrelation	0.1153	3	0.2811
$pan_{Y-4}Dec$	Y-3	Precipitation	0.0330	1	0.0805
$ano_{Y-4}Oct$	Y-3	Temperature	0.0087	1	0.0213
$3x3to99_{Y-2}$	N/A	Autocorrelation	0.0113	2	0.0274
$ano_{Y-3}Feb$	Y-3	Temperature	0.0367	1	0.0895
$ano_{Y-3}Mar$	Y-3	Temperature	0.0122	1	0.0298
$ano_{Y-4}Nov$	Y-3	Temperature	0.0031	1	0.0076
$ewdi_{Y-2}to99$	N/A	Autocorrelation	0.0074	2	0.0181
$pan_{Y-1}Oct$	Y-0	Precipitation	0.0033	1	0.0079
TOTAL =			0.4102		1.000

Table 3.11b: Analysis of dataset variation explained, by variable, in climate-only, 17-node regression tree.

Variable	Growth Year (Oct – Sep)	Variable Type	Partial DDE*	# Splits	Partial DDE_{Rel}
ano _{Y-3} Feb	Y-3	Temperature	0.0635	1	0.3401
ano _{Y-2} Mar	Y-2	Temperature	0.0078	1	0.0416
avg30Dec	N/A	Average Temperature	0.0043	1	0.0228
ano _{Y-1} Mar	Y-1	Temperature	0.0039	1	0.0208
ano _{Y-1} Apr	Y-1	Temperature	0.0043	1	0.0228
ano _{Y-2} Dec	Y-1	Temperature	0.0157	2	0.0842
pan _{Y-3} Sep	Y-2	Precipitation	0.0206	1	0.1101
pan _{Y-1} May	Y-1	Precipitation	0.0067	1	0.0357
pan _{Y-1} Oct	Y-0	Precipitation	0.0036	1	0.0192
pan _{Y-2} Dec	Y-1	Precipitation	0.0026	1	0.0140
pan _{Y-4} Oct	Y-3	Precipitation	0.0033	1	0.0179
ano _{Y-1} Jul	Y-1	Temperature	0.0058	1	0.0309
ano _{Y-3} Apr	Y-3	Temperature	0.0379	2	0.2030
pan _{Y-2} Sep	Y-1	Precipitation	0.0069	1	0.0367
TOTAL			0.1867		1.000

Table 3.12a: Cumulative impact of climate variables in full, all-variable tree by growth year.

Growth Year	# of variables	DDE_{Rel}	DDE_{Rel} Temp	DDE_{Rel} Precip
Y-0	1	0.0079	N/A	0.0079
Y-1	0	0	-	-
Y-2	0	0	-	-
Y-3	5	0.2287	0.1482	0.0805
		TOTAL →	0.1482	0.0884

In the climate-only regression tree, the most important variable was ano_{Y-3}Feb, with a partial DDE of 0.0635 (DDE_{Rel} = 0.34), but if this partial DDE is compared to the most important variable in the full tree (EWDI_{Y-1}, DDE = 0.1792), it explained roughly only one-third as much of the variation. Evaluating the impact of climate variables by growth year shows substantially more importance from the Y-3 growth year than any

other. Partial DDE_{Rel} , were summed by growth year to indicate the relative importance of each growth year: Y-0 growth year (only precipitation variables included) = 0.0192, Y-1 growth year = 0.2451, Y-2 growth year = 0.1517, and Y-3 growth year = 0.5610. Temperature variables account for nearly three-quarters of explained variation in the climate-only tree. See Table 3.12b for a summary of these relationships.

Table 3.12b: Cumulative impact of climate variables in climate-only tree by growth year.

Growth Year	# of variables	DDE_{Rel}	DDE_{Rel} Temp	DDE_{Rel} Precip
Y-0	1	0.0192	N/A	0.0192
Y-1	7	0.2451	0.1587	0.0864
Y-2	2	0.1517	0.0416	0.1101
Y-3	3	0.5610	0.5431	0.0179
		TOTAL→	0.7434	0.2336

The observed versus predicted EWDI-yearly values for years 2003 – 2008 are presented in Figure 3.6 and Figure 3.7. The overall trend in EWDI study-area-wide progressed from low whitebark pine mortality (highly positive EWDI values, shown in green) in 2003, and changing to much higher mortality (negative EWDI values show in orange/red) in 2004, 2005, and 2006. Low conifer mortality was observed in 2007 (positive EWDI, shown in green). 2008 had more mortality, especially in the Northwest portion of the study area (Gallatin National Forest) with many extremely negative EWDI values indicative of high rates of whitebark pine mortality. The predicted EWDI values also followed this trend, although more generally (appearing smoothed) and with fewer extreme values (observed EWDI values that appeared red might look orange on the predicted EWDI values, for instance).

Figure 3.7 shows a zoomed in portion of the study area from 2006 – 2008. The close-up is on the eastern border of Yellowstone National Park where it borders Shoshone National Forest, near Avalanche Peak in the Absaroka mountain range. These maps also demonstrate that the predicted maps generally followed the trend in EWDI values, but in a smoothed fashion, missing extremely high or low EWDI values, such as when a small area showed very negative EWDI values but was surrounded by more moderate values. One notable exception to this smoothing effect was noted in the 2007 maps of Figure 3.7, demarcated by the magenta oval. This extremely negative EWDI value clearly came through in the predicted map.

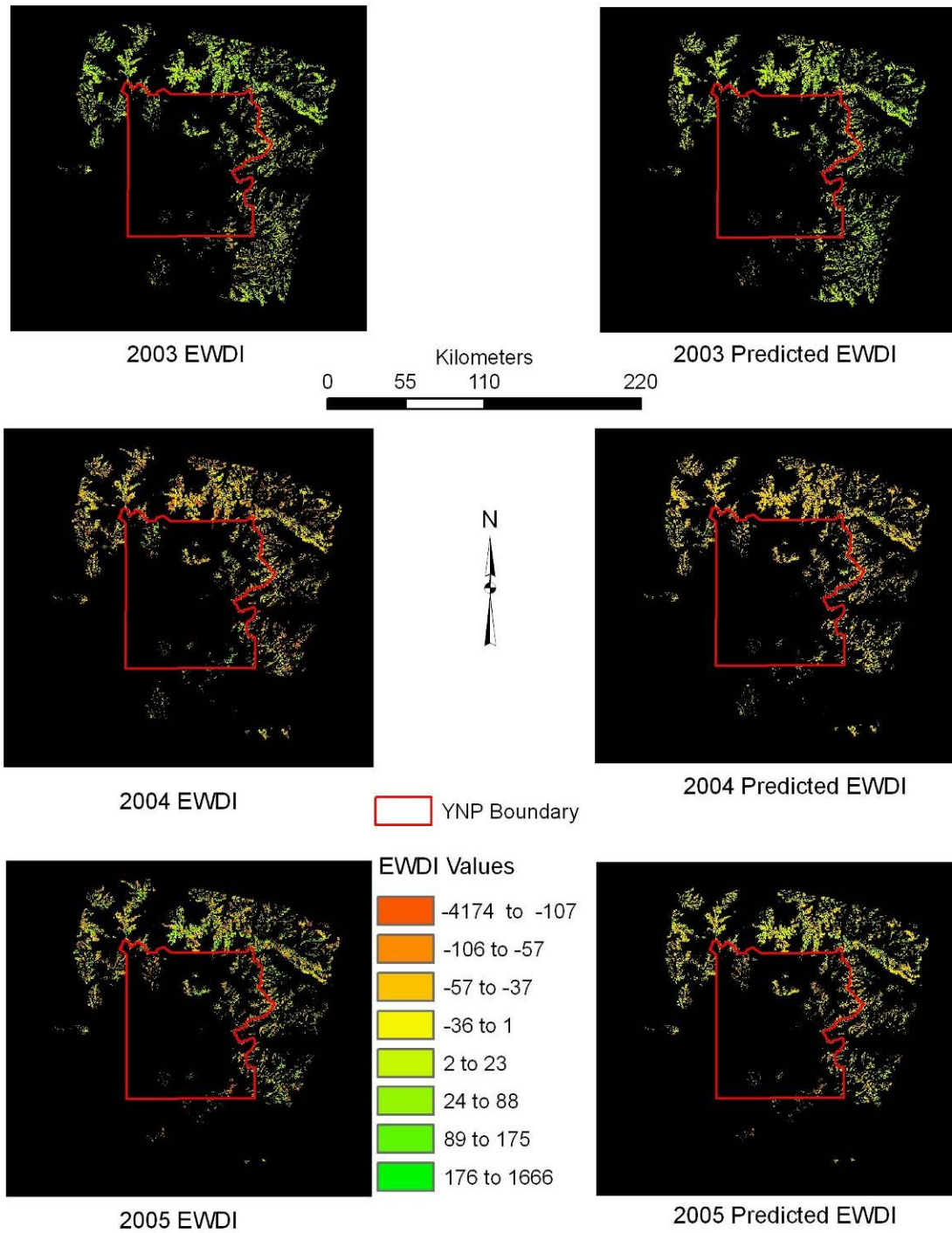


Figure 3.6a: EWDI-Yearly: Observed vs. Predicted 2003 – 2005

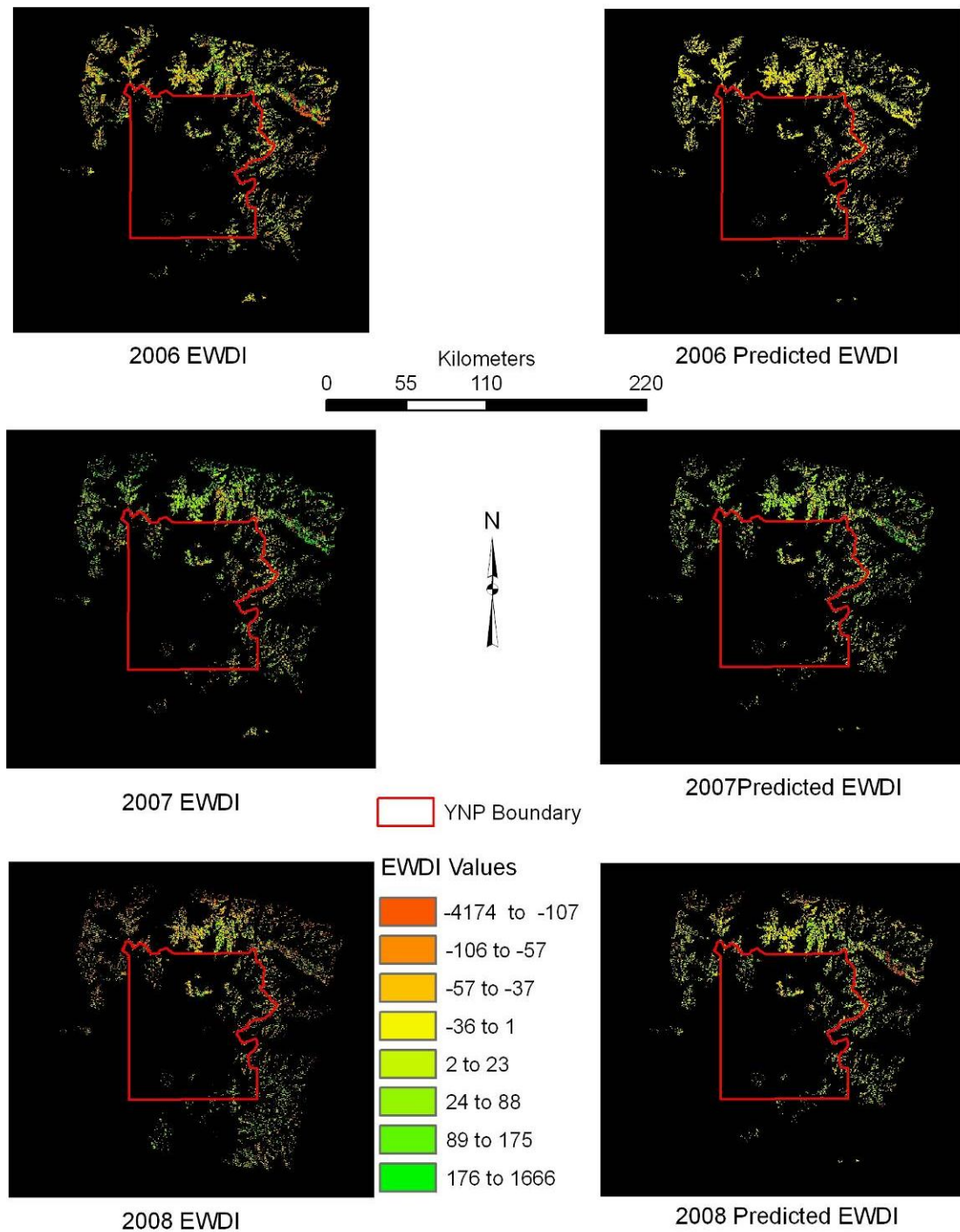


Figure 3.6b: EWDI-Yearly: Observed vs. Predicted 2006 – 2008

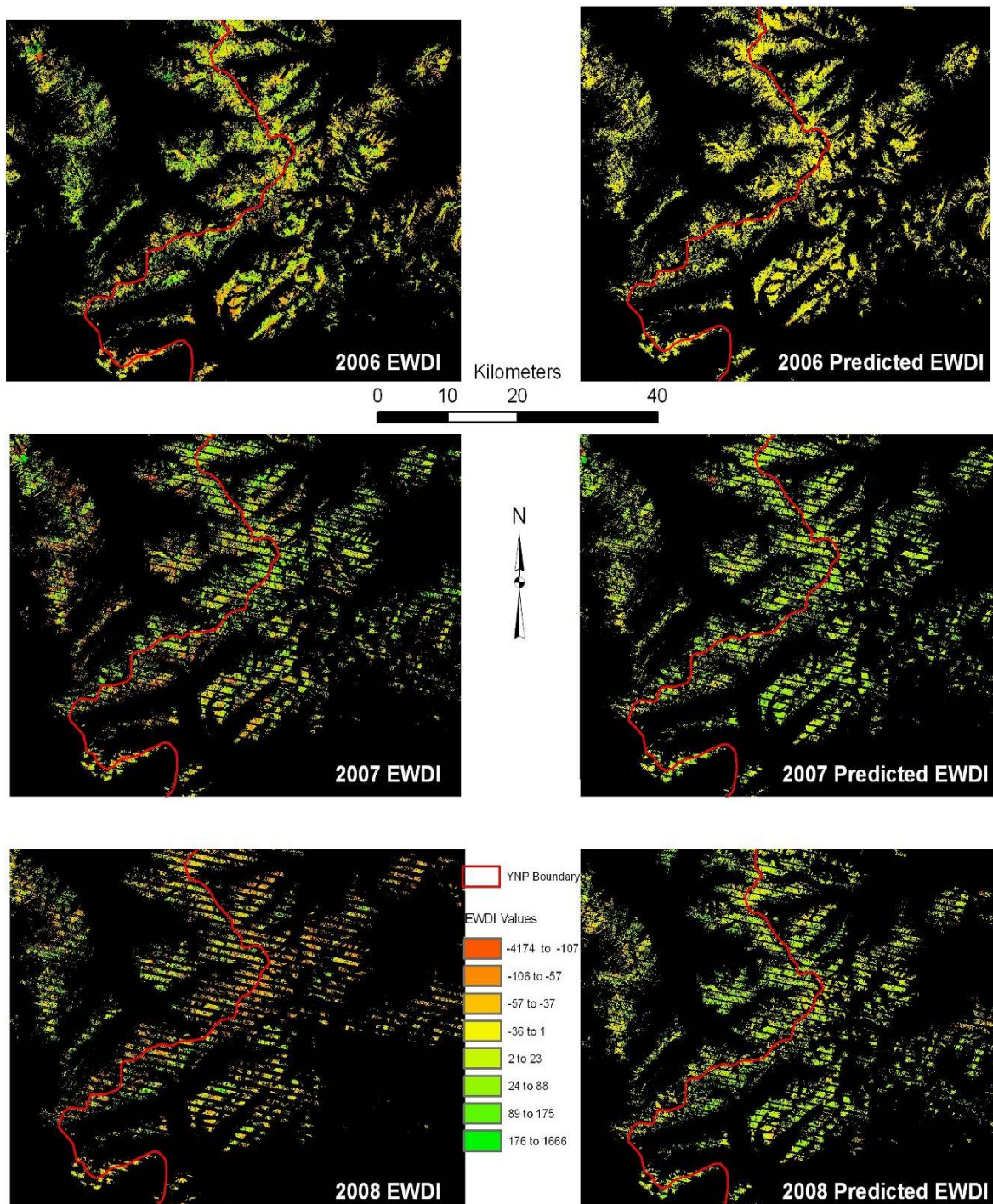


Figure 3.7: A close-up of EWDI observed values versus predicted values near Avalanche Peak, Yellowstone National Park, 2006 – 2008.

Discussion

Evaluation of EWDI Response to Red-Attack using Google Earth

In the high-resolution red-attack analysis, stands of green whitebark pine trees covered the widest spectrum of EWDI values, from very negative to very positive (Figure 3.2a). Red-attack stands covered a spectrum of values, but concentrated more on negative values. Gray attack stands had generally positive EWDI values (Figure 3.2b). These results corroborate other studies that show a relationship between MPB red-attack levels and EWDI values (Franklin *et al.*, 2001; Skakun *et al.*, 2003; Wulder *et al.*, 2006b). More negative EWDI values are generally found with MPB red-attack stands. Although the sample size of gray-attack stands was too small for strong conclusions, the results do support the hypothesis that positive EWDI values can occur after the MPB stage as a result of the exposure of the forest understory when needles fall off dead trees.

Regression Tree Analysis of Landsat and Climate Data

Yearly decreases in tasseled cap wetness (EWDI) in conifer forests are indicative of conifer mortality. Using a regression tree of only past climate anomalies and autocorrelation terms as predictor variables, mortality in whitebark pine habitat (measured by EWDI) can be predicted, with 38% of the dataset deviance explained. Using solely climate terms, 15% of the deviance in the dataset can be explained. Assuming that MPB were a primary cause of whitebark pine mortality during this study period allows these results to illuminate MPB population dynamics. These results support and expand on previous field studies and mathematical models that indicate climatic

drivers for shifts in MPB range and life-cycle. A deeper analysis of the relationships indicated by these results can inform the understanding of the future of both MPB and whitebark pine in the GYE.

Topographic Variable Analysis

Topographic data were not included in any regression tree model, which was an unexpected result because of the microclimate effects of slope and aspect, but might have been a function of the topographic effects occurring at finer scales than the available DEM. This finding does corroborate earlier analysis of the last major MPB outbreak in whitebark pine (during the 1930s), which also did not find topographic effects to be significant in predicting whitebark pine mortality (Perkins and Roberts, 2003).

Autocorrelation Variable Analysis

Autocorrelation terms were very important to these models in predicting yearly changes in EWDI. Seventy-six percent of the dataset deviance that could be explained (DDE_{Rel}) was explained by autocorrelation terms. All four autocorrelation terms in the full model support the expectation that there was a clear negative correlation between EWDI and any version of EWDI from prior years ($EWDI_{Y-1}$ most strongly, but also $minEWDI_{99}$, $3x3to99_{Y-2}$, $EWDI_{Y-2to99}$). This is strong support for the third expectation (E3) from Table 3.10a, that previous MPB activity in a cell or neighboring cell decreases the likelihood of current MPB activity, leading to an increase in EWDI (negative correlation). This negative correlation suggests that host tree depletion was more of a factor than availability of MPB in nearby pine trees for expanding the infestation, which

would have given a positive correlation between EWDI and $EWDI_{Y-1}$. After a very negative EWDI reading, positive EWDI values were expected in the future. Whitebark pine canopy is unlikely to recover on the time scale of this analysis, so this response might be due to exposing the understory grasses and shrubs to the satellite sensor after the needles fall off the whitebark pine in the gray-attack stage. The question of MPB dispersal distance is not well understood, and this study cannot shed much additional light on it. In the spatial-autocorrelation-terms-only regression tree, terms at all three distances (30 m, 90 m, and 150 m) were included in the tree, indicating that there is a dispersal effect at all three distances.

Climate Variable Analysis

Evaluating the regression trees built on climate data from different growth-years can inform questions of MPB voltinism in the whitebark pine zone. MPB historically required three-year life cycles in whitebark pine habitat, but recent field evidence suggests a shift to semivoltinism and even univoltinism (Bentz and Schen-Langenheim, 2006). Comparing the different growth-year regression trees, the Y-3 Climate tree explained the most dataset deviance ($DDE = 0.1547$), accounting for over twice as much deviance as any of the other growth-years, while the Y-1 Climate tree explained the least ($DDE = 0.1160$). When evaluating the variables included in the full tree, five out of six climate variables were from the Y-3 growth year, and the sixth term accounted for less than 1% of the deviance explained. These results indicate that a substantial portion of the MPB population in GYE whitebark pine are still on a three-year life-cycle. On the other hand, Y-1 and Y-2 growth years accounted for 0.25 and 0.15 of the deviance explained

(DDE_{Rel}). This could mean one or both of the following is true: (1) *some* populations of MPB in GYE whitebark pine are becoming semi- or univoltine, or (2) climate variations experienced by three-year life-cycle MPB populations in their second and third years of development affect MPB survival.

Temperature variables make up between 63-74% of the total contribution from climate variables in explaining dataset deviance (Tables 3.11a and 3.11b). The first expectation (E1) was that warmer temperatures (positive temperature anomalies) decrease MPB mortality and/or increase MPB growth rates, leading to an increase in whitebark pine mortality, in turn leading to a decrease in EWDI values. Therefore, a negative correlation between temperature anomalies and EWDI values would support this first expectation. In the full variable tree, one temperature variable supports E1, one does not support E1, and two are unclear. While that is not a resounding endorsement of the expectation that warmer temperatures yield increased whitebark pine mortality, the climate-only tree provides stronger evidence for this expectation. In the climate-only regression tree, five temperature variables support E1, none contradict it, while three are unclear. This is much stronger support. The second expectation (E2) states that drier conditions (negative precipitation anomaly) reduce the ability of whitebark pine to repel attacks by MPB, leading to an increase in whitebark pine mortality, and thus a decrease in EWDI values (positive correlation). In the full-variable tree, two precipitation variables support E2, while none are unclear or contradict it. For the climate-only tree, two precipitation variables support E2, one contradicts it, and three are unclear. Combining the evidence from these two trees leads to weak support of second

expectation that drier conditions lead to increased whitebark pine mortality, but further testing on this relationship is advisable. An analysis of the relationships between various predictor variables and changes in tasseled cap wetness (and thus conifer mortality) support the expectations that drier and warmer climatic conditions favor mountain pine beetle populations, leading to increased whitebark pine mortality.

Individual Variables: Inclusions and Omissions

Multi-collinearity among the climate predictor variables means that caution must be used when looking at the inclusion or omission of individual variables in the final regression trees. Still, there is some utility in this exercise. Spring and fall temperature variables ($\text{ano}_{Y-4}\text{Oct}$, $\text{ano}_{Y-4}\text{Nov}$, $\text{ano}_{Y-3}\text{Mar}$) were more prevalent in the full tree than winter temperature variables ($\text{ano}_{Y-3}\text{Feb}$), and no summer temperature variables were included at all. This yields support for the idea that cold-related mortality is the most important factor in MPB population dynamics (Regniere and Bentz, 2007), and that the seasonally-variable production of cryoprotectants by MPB makes them most vulnerable to cold in late fall and early spring (Bentz and Mullins, 1999).

The lack of seasonal summary terms in either the full or final tree is notable, especially considering the tree made from only seasonal climate summaries explained nearly as much deviance ($\text{DDE} = 0.1419$) as the all-climate tree ($\text{DDE} = 0.1483$). This might be related to field studies and mathematical models that indicate MPB respond to phloem temperature on hourly scales, not daily or monthly, so six- or twelve-month averages will miss a lot of detail (Logan and Bentz, 1999; Bentz and Schen-Langenheim, 2006). EWDI responds to changes in soil/canopy moisture, so it is also interesting that no

precipitation anomalies from the ten months prior to the image date were included in either the full or climate tree. Only one term (avg30Dec) from the 30-year-average temperature and precipitation datasets was included in either final model. This might indicate that within the narrow bioclimatic band that covers whitebark pine habitat, differences from slightly warmer or cooler sites are not very important. A similar study performed on a wider range of pine forests might find that this long-term climate data are important in stratifying the dataset. The lack of inclusion of 30-year-average climate data could also be due to the spatial scale of the data (800 m), which incorporates much variation of vegetation within a single climate pixel.

An analysis of yearly subsets of the dataset was not illuminating. There did not appear to be any pattern to differences in DDE between the different years. While very different predictor variables were included in the regression trees for each of these yearly subsets, there once again did not appear to be any pattern to these differences, such as coming from different seasons or different growth years.

Extensions and Implications

The current study fills a knowledge gap between mathematical models of expected MPB behavior given various climate parameters and field studies that intensively analyze temperature and MPB survival on a few hundred trees. The relationships between observed biophysical data that correlate with whitebark pine mortality and climate data were dissected. The spatial patterns of conifer mortality correspond well with predicted patterns based on our model, but the match could be improved. One shortcoming is the smoothing of data in the predicted EWDI maps and the general lack of extreme values that would indicate severe MPB outbreaks. This is likely due to the much coarser scale of the climate anomaly data (4000-m pixels) compared to the resolution of Landsat (30-m pixels) from which the EWDI values are derived. A map of residuals indicates this pattern (Figure 3.8). Fine-scale patterns of conifer mortality are not resolved by the model, and result in the bright orange/red patches in the residual map. These patches of highly negative residuals likely indicate severe outbreaks of MPB, but the climate in those patches is little different than in nearby areas, so the level of conifer mortality was underpredicted. Similar issues exist with highly positive values, shown in bright green. The predictive powers of the model would likely be improved with finer scale climate data. It is interesting to note that while the topographic variables (elevation, slope, and aspect) were originally at a similar spatial scale as EWDI, they were still not nearly as important in the predictive models as the much coarser climate data. In addition to reducing the spatial scale of the climate data, the temporal scale was also not ideal. MPB respond to hourly changes in tree phloem temperature, so monthly average data is

too coarse of a temporal scale. Future studies could either use more temporally explicit data (such as hourly data from SNOTEL stations) or generate a pseudo-daily climate data set from monthly data using stochastic climate models (Regniere and Bolstad, 1994). The regression trees created here could also be applied to forecasted future climate regimes to predict the impact of future climates on MPB in whitebark pine habitat.

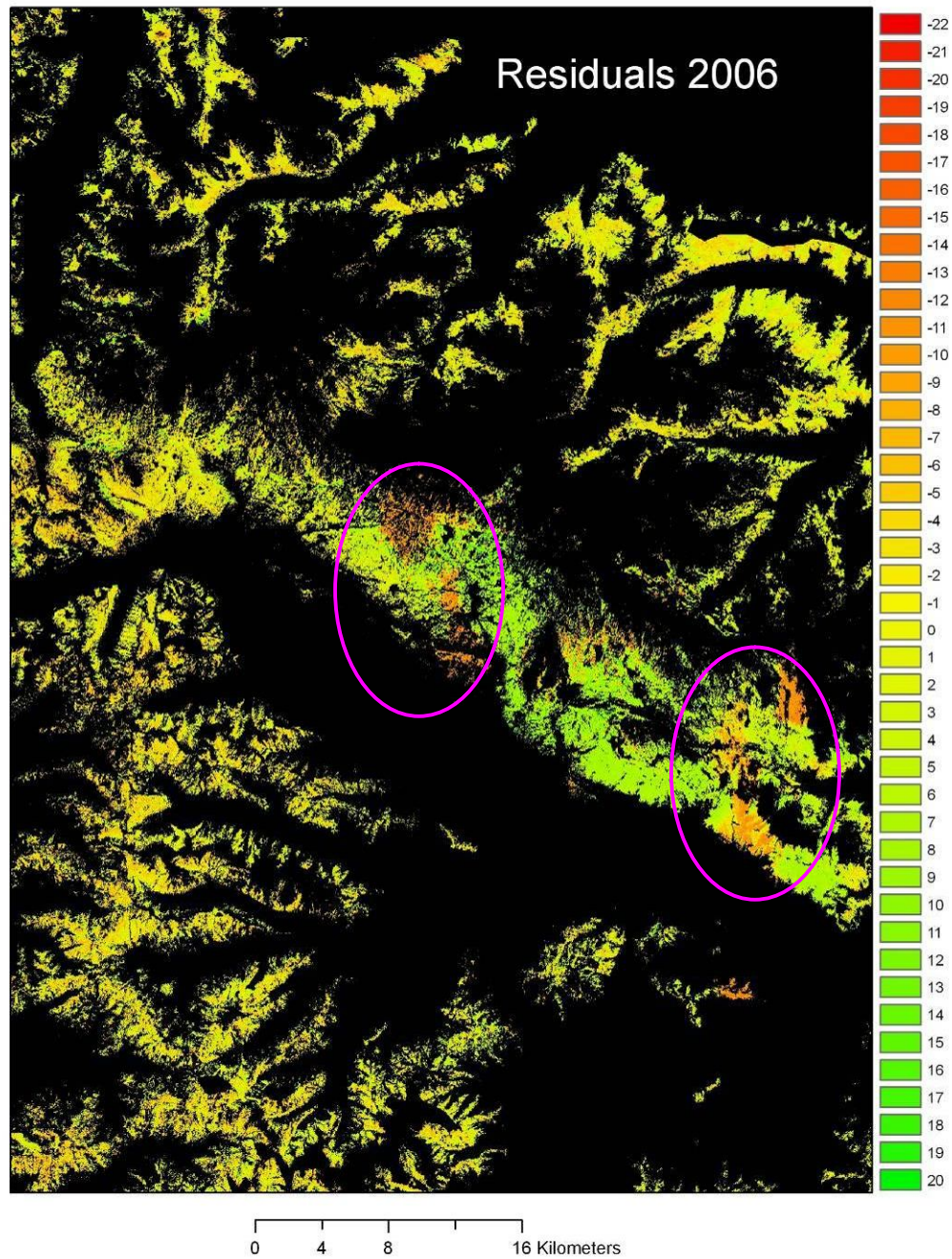


Figure 3.8: Class residuals for 2006 (Fitted EWDI class – Observed EWDI class) for the northeast portion of the study area, centered on the Beartooth Plateau. Magenta ovals indicate examples of areas with heavy spatial autocorrelation, likely caused in part by differences in spatial scale between predictive climate data (4,000-m pixels) and Landsat-derived EWDI response data (30-m pixels).

Finally, the results of this study are important to discussions of the future health of both whitebark pine and the entire high-mountain ecosystem that this keystone species supports. Middle-range climate change models predict average annual surface temperatures in the Northern Rockies to increase by 3.5 °C by 2100, with higher levels of warming occurring in the winter (Christensen *et al.*, 2007). This level of warming would likely shift MPB lifecycles in GYE whitebark pine towards epidemic-sustaining univoltinism, potentially devastating the whitebark pine. A severe decline in whitebark pine populations would also be cause for concern for the grizzly bear, recently removed from the federal threatened species list. Grizzly bear food sources were considered to be secure by the delisting agency (Hall, 2007), which is likely not the case if whitebark pine populations collapse due to mountain pine beetle.

This study provides the first evidence inferred from Landsat data of a direct link between climate and whitebark pine mortality at stand-level resolution across an ecosystem, showing evidence that drier and warmer climates lead to increased conifer mortality in whitebark pine habitat, likely due to increased mountain pine beetle activity. These links reinforce concerns of both the future viability of whitebark pine and the entire mountain ecosystem it supports.

CHAPTER 4

CONCLUSION

Through this project, I sought to shed light on an important biological aspect of climate change research: the potential impact of a changing climate on interactions between species. Whitebark pine (*Pinus albicaulis*) and mountain pine beetle (*Dendroctonus ponderosae*) (MPB) are both sensitive to changes in climate and have wide-ranging impacts on other species in their ecosystems. Historically, MPB were rare in whitebark pine habitat, but their recent population expansion suggests conditions have changed.

Beetle researchers have hypothesized that the current distribution of whitebark pine and other high-elevation pines was directly shaped by the avoidance of MPB. Unlike lodgepole pine (*Pinus contorta*), which coevolved with MPB and thus developed enhanced chemical defense mechanisms and short life cycles allowing easy regeneration from disturbance, high-elevation pine species have few defenses and slow-growing life cycles, an evolutionary path of beetle avoidance (Logan and Powell, 2001; Powell and Logan, 2005; Hicke *et al.*, 2006).

If the historic range of MPB has indeed shaped the current range of whitebark pine, this relationship is now out of balance. Life cycle timing of MPB is entirely temperature dependent, and one female can produce dozens of offspring in as little as a year (Safranyik *et al.*, 1999). These characteristics allow MPB to adapt to new climate conditions much more quickly than slow-growing whitebark pine (a classic K-selected

species (Logan and Powell, 2001)). The result is MPB are now moving rapidly into whitebark pine habitat and killing a large number of these trees with weak natural defenses. Over the long-term, changes in climate are projected to shift whitebark pine habitat northward and upslope, but this replacement habitat is far smaller than what it replaces. Long-lived, late reproducing species with specialized habitat and low mobility (such as whitebark pine) are expected to have the most difficult time adapting or migrating in response to climate change (Aitken *et al.*, 2008). Models predict a 97% reduction in climatically suitable whitebark pine habitat by the end of this century (Warwell *et al.*, 2006). The change in climate suitability is most likely to restrict regeneration more than directly kill adult trees (Warwell *et al.*, 2006). Whitebark pine trees can live many centuries, meaning that climate change alone would likely not *directly* cause the collapse of the whitebark pine ecosystem.

Synergies of other human-caused impacts cause more pressing threats to whitebark pine, however. Blister rust, an introduced pathogen, is still spreading, and it affects the cone-bearing crowns of trees first, compromising whitebark pine regeneration ability. The future warmer climate is expected to increase the number of large, stand-replacing wildfires, likely killing existing whitebark pines at a rate higher than normal (Bradley *et al.*, 1992; Westerling *et al.*, 2006). The most rapid impact is likely from MPB. It might not matter how many whitebark pine trees are able to resist blister rust in 2050 or how much habitat is suitable for whitebark pine regeneration in 2100 if the vast majority of the current whitebark pine population is decimated by MPB in the next ten years. Beetle researcher Jesse Logan predicted just such an “ecological extinction” of

whitebark pine from the GYE within 10 years due to MPB (Logan, 2007). Isolated pockets would remain, much as isolated pockets of giant sequoias remain in the Sierra Nevada, but whitebark pine could no longer serve its ecological role as a keystone species in the subalpine zone.

My results show for the first time a statistical link between climate variability and whitebark pine mortality, likely mediated by MPB. These results confirm earlier studies that used mathematical models to predict increasing MPB populations and shortened MPB life-cycles. Unlike previous studies, my results represent changes to whitebark pine observed across the landscape (measured with Landsat), rather than from mathematical models or from plot-based studies of MPB behavior, which might have been inadequately sampled for statistical interpolation across a landscape.

Climate information from one growth-year, two growth-years, and three growth-years prior to the image date were all important at predicting whitebark pine mortality. While the most important predictors were from three growth-years prior to the imagery, the importance of one and two growth-years prior supports earlier studies (Powell and Logan, 2005; Bentz and Schen-Langenheim, 2006) that suggest MPB in whitebark pine are shifting from three-year life cycles to two-year (semivoltinism) or even one-year life cycles (univoltinism). In lodgepole pine zones, MPB univoltinism allows for prolonged MPB epidemics, something that has not previously been seen in whitebark pine zones. MPB is expected to increase its habitat in whitebark pine zones for the next several decades under projected warming conditions (Hicke *et al.*, 2006). Requirements for adaptive seasonality forces MPB life-cycles into distinctly non-linear patterns. A

temperature increase of 1.5 °C might not increase habitat suitability (it could even decrease it), but a 2.0 °C increase could shift three-year life cycles to two year life cycles (semivoltine), or semivoltine to univoltine (Powell and Logan, 2005). The shift towards MPB univoltinism in whitebark pine zones could yield rapid, non-linear increases in MPB populations, in turn causing a dramatic reduction in whitebark pine populations over the course of a decade or less (Logan and Powell, 2001; Logan, 2007).

My regression models indicate that drier and warmer climatic conditions increase whitebark pine mortality. This increased mortality is likely due, at least in part, to increased MPB activity. The effects of warmer conditions were more pronounced than those for drier conditions. One likely mechanism for a drier climate increasing pine mortality is by reducing the ability of pines to repel attacking MPB, although drought might stress the whitebark pines in a variety of additional manners as well. Warmer conditions likely reduce MPB overwintering mortality as well as increase their growth rates, allowing more beetles to survive and reproduce to attack whitebark pine, causing increased pine mortality. The important temperature predictors were most commonly from the fall and spring, and never from summer months, indicating that cold-related MPB mortality is an important factor in whitebark pine mortality.

GYE grizzly bears (*Ursus arctos horribilis*) are dependent on whitebark pine seeds, and when grizzly bears were removed from the federal threatened species list, one rationale was that their whitebark pine food source was secure (Hall, 2007). My research shows an increase in whitebark pine mortality with increasing temperature, and middle-range forecasts predict that temperatures will increase 3.5 °C this century (Christensen *et*

al., 2007). Mathematical models of MPB life-cycles indicate this temperature increase is also enough to shift MPB into rapidly reproducing univoltine life-cycles (Logan and Powell, 2001), causing devastation to whitebark pine populations. These studies imply that the grizzly whitebark pine food source is *not* secure, and this issue requires close monitoring.

My study provides the first evidence inferred from Landsat data of a direct link between climate and whitebark pine mortality at stand-level resolution across an ecosystem. These results indicate that drier and warmer climates lead to increased conifer mortality in whitebark pine habitat, likely due to increased mountain pine beetle activity. This study reinforces concerns of both the future viability of whitebark pine and the entire mountain ecosystem it supports.

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APPENDIX A

REGRESSION TREE RESULTS AND MODEL DIAGRAMS

Seasonal Climate Summary Regression Tree Results**Nodes: 19****DDE Validation = 0.1419**

Regression tree:

```
snip.tree(tree = tree(formula = ewdi ~ degday + spr.pano + Y.0wtryr + Y.1wtryr +
```

```
+ Y.2wtryr + Y.3wtryr + Y.1win + Y.1sum + Y.2win + Y.2sum + Y.3win +
  Y.3sum, data = training.cnpycvr0, na.action = na.exclude, mincut = 5,
  minsize = 10, mindev = 0.01), nodes = c(19., 52., 8., 27., 24., 5.,
  18., 410., 28.))
```

Variables actually used in tree construction:

```
[1] "Y.3wtryr" "Y.3win" "Y.1win" "Y.1wtryr" "spr.pano" "Y.2win"
```

```
[7] "Y.0wtryr" "Y.1sum" "Y.2wtryr"
```

Number of terminal nodes: 19

Residual mean deviance: 7354 = 199200000 / 27090

Distribution of residuals:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
-8.268e+002	-4.237e+001	-7.818e-001	-3.812e-015	3.963e+001	9.494e+002

node), split, n, deviance, yval

* denotes terminal node

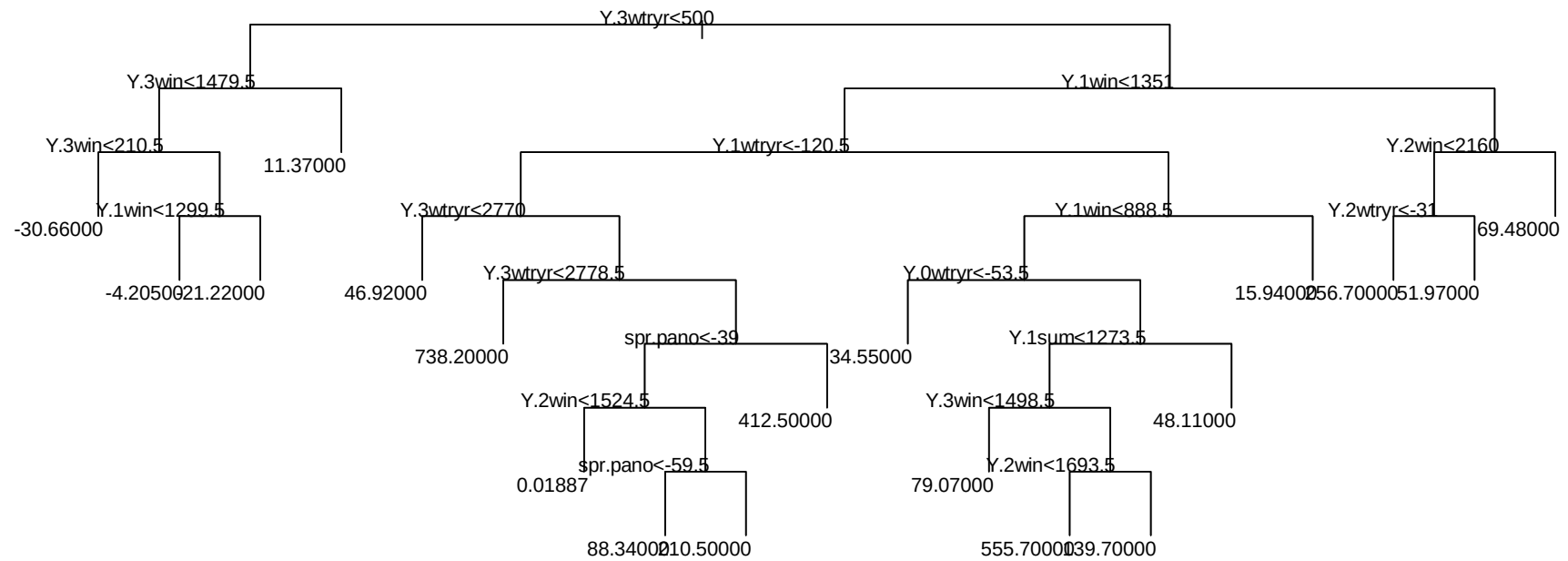
```
1) root 27112 236800000 -2.80400
 2) Y.3wtryr<500 22758 137000000 -12.91000
    4) Y.3win<1479.5 16611 107500000 -21.89000
      8) Y.3win<210.5 6879 32350000 -30.66000 *
      9) Y.3win>210.5 9732 74260000 -15.69000
        18) Y.1win<1299.5 3165 28940000 -4.20500 *
        19) Y.1win>1299.5 6567 44700000 -21.22000 *
    5) Y.3win>1479.5 6147 24490000 11.37000 *
  3) Y.3wtryr>500 4354 85390000 49.99000
    6) Y.1win<1351 4164 77980000 46.31000
      12) Y.1wtryr<-120.5 1683 33580000 64.96000
      24) Y.3wtryr<2770 1241 15750000 46.92000 *
      25) Y.3wtryr>2770 442 16300000 115.60000
        50) Y.3wtryr<2778.5 11 532500 738.20000 *
        51) Y.3wtryr>2778.5 431 11390000 99.72000
          102) spr.pano<-39 415 8352000 87.66000
            204) Y.2win<1524.5 53 778000 0.01887 *
            205) Y.2win>1524.5 362 7107000 100.50000
              410) spr.pano<-59.5 326 4721000 88.34000 *
              411) spr.pano>-59.5 36 1903000 210.50000 *
            103) spr.pano>-39 16 1415000 412.50000 *
      13) Y.1wtryr>-120.5 2481 43420000 33.67000
        26) Y.1win<888.5 1453 29190000 46.21000
          52) Y.0wtryr<-53.5 1167 20710000 34.55000 *
          53) Y.0wtryr>-53.5 286 7665000 93.79000
            106) Y.1sum<1273.5 155 5052000 132.40000
              212) Y.3win<1498.5 101 1197000 79.07000 *
              213) Y.3win>1498.5 54 3031000 232.10000
                426) Y.2win<1693.5 12 289500 555.70000 *
                427) Y.2win>1693.5 42 1127000 139.70000 *
            107) Y.1sum>1273.5 131 2108000 48.11000 *
          27) Y.1win>888.5 1028 13680000 15.94000 *
        7) Y.1win>1351 190 6110000 130.60000
          14) Y.2win<2160 97 3811000 189.20000
```

```
28) Y.2wtryr<-31 65 2442000 256.70000 *
29) Y.2wtryr>-31 32 470400 51.97000 *
15) Y.2win>2160 93 1619000 69.48000 *
```

Seasonal Climate Summary Regression Tree Model Diagram

Nodes: 19

DDE Validation = 0.1419



Autocorrelation Regression Tree Results**Nodes: 17****DDE Validation = 0.3123**

Regression tree:

```
snip.tree(tree = tree(formula = ewdi ~ ewdiY.2to99 + ewdiY.1 + X3x3to99Y.2 +
  X3x3Y.1 + X7x7to99Y.2 + X7x7Y.1 + X11x11to99Y.2 + X11x11Y.1 +
  minEWDI99, data = training.cnpycvr0, na.action = na.exclude, mincut =
  5, minsize = 10, mindev = 0.01), nodes = c(61., 26., 62., 22., 25.,
  41., 29., 24., 60., 27., 21., 23.))
```

Variables actually used in tree construction:

[1] "ewdiY.1" "minEWDI99" "ewdiY.2to99"

Number of terminal nodes: 17

Residual mean deviance: 5758 = 156000000 / 27100

Distribution of residuals:

	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
	-8.476e+002	-4.133e+001	2.699e+000	5.347e-013	4.265e+001	5.432e+002

node), split, n, deviance, yval

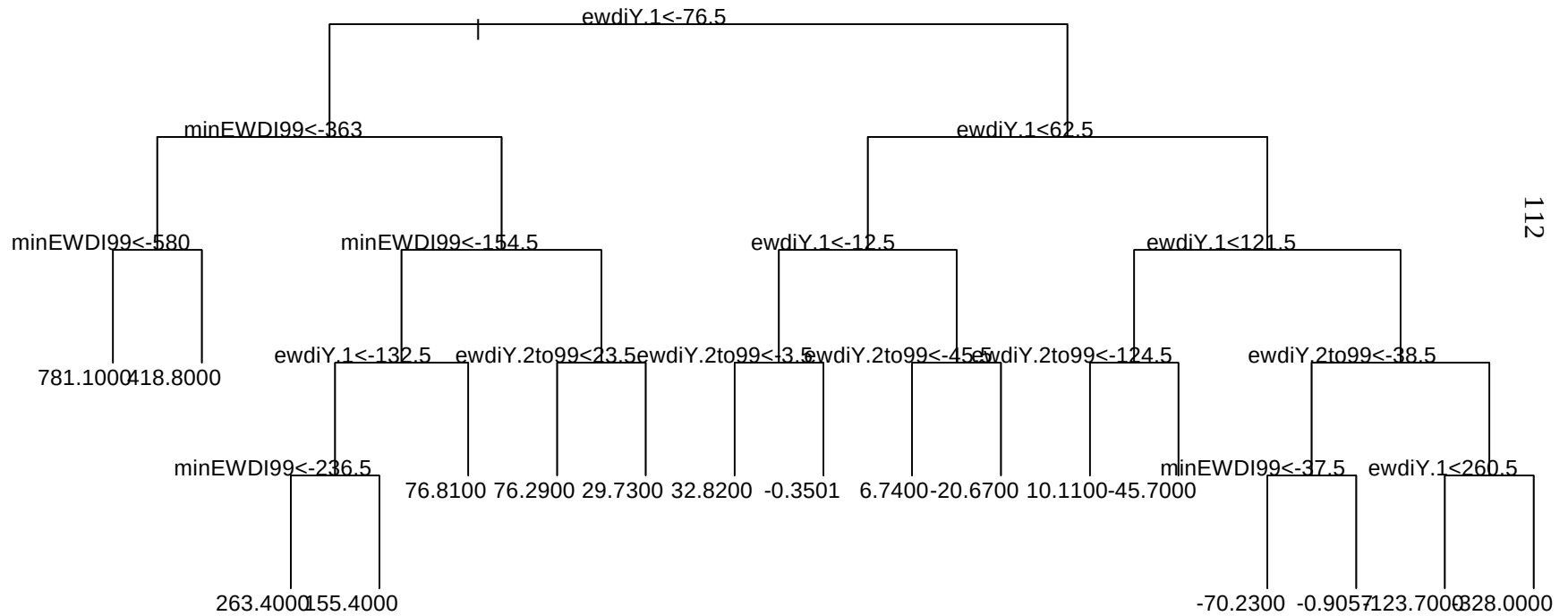
* denotes terminal node

- 1) root 27112 236800000 -2.8040
 - 2) ewdiY.1<-76.5 3765 71950000 74.4800
 - 4) minEWDI99<-363 97 4694000 538.3000
 - 8) minEWDI99<-580 32 557100 781.1000 *
 - 9) minEWDI99>-580 65 1322000 418.8000 *
 - 5) minEWDI99>-363 3668 45840000 62.2100
 - 10) minEWDI99<-154.5 591 9571000 150.6000
 - 20) ewdiY.1<-132.5 376 4791000 192.8000
 - 40) minEWDI99<-236.5 130 1336000 263.4000 *
 - 41) minEWDI99>-236.5 246 2463000 155.4000 *
 - 21) ewdiY.1>-132.5 215 2941000 76.8100 *
 - 11) minEWDI99>-154.5 3077 30770000 45.2400
 - 22) ewdiY.2to99<23.5 1025 9496000 76.2900 *
 - 23) ewdiY.2to99>23.5 2052 19790000 29.7300 *
 - 3) ewdiY.1>-76.5 23347 138800000 -15.2700
 - 6) ewdiY.1<62.5 18588 93880000 -5.6880
 - 12) ewdiY.1<-12.5 7296 41500000 9.6020
 - 24) ewdiY.2to99<-3.5 2189 14660000 32.8200 *
 - 25) ewdiY.2to99>-3.5 5107 25150000 -0.3501 *
 - 13) ewdiY.1>-12.5 11292 49570000 -15.5700
 - 26) ewdiY.2to99<-45.5 2102 11680000 6.7400 *
 - 27) ewdiY.2to99>-45.5 9190 36600000 -20.6700 *
 - 7) ewdiY.1>62.5 4759 36500000 -52.6800
 - 14) ewdiY.1<121.5 2956 16110000 -39.4100
 - 28) ewdiY.2to99<-124.5 333 2225000 10.1100 *
 - 29) ewdiY.2to99>-124.5 2623 12960000 -45.7000 *
 - 15) ewdiY.1>121.5 1803 19020000 -74.4400
 - 30) ewdiY.2to99<-38.5 1432 12600000 -57.4000
 - 60) minEWDI99<-37.5 1167 9146000 -70.2300 *
 - 61) minEWDI99>-37.5 265 2419000 -0.9057 *
 - 31) ewdiY.2to99>-38.5 371 4401000 -140.2000
 - 62) ewdiY.1<260.5 341 2743000 -123.7000 *
 - 63) ewdiY.1>260.5 30 506700 -328.0000 *

Autocorrelation Regression Tree Model Diagram

Nodes: 17

DDE Validation = 0.3123



Spatial Autocorrelation Regression Tree Results**Nodes: 10****DDE Validation = 0.1996**

Regression tree:

```
snip.tree(tree = tree(formula = ewdi ~ X3x3to99Y.2 + X3x3Y.1 + X7x7to99Y.2 +
  X7x7Y.1 + X11x11to99Y.2 + X11x11Y.1, data = training.cnpycvr0,
  na.action = na.exclude, mincut = 5, minsize = 10, mindev = 0.01),
  nodes = c(30., 25., 14., 62., 13.))
```

Variables actually used in tree construction:

[1] "X3x3Y.1" "X11x11Y.1" "X3x3to99Y.2" "X7x7Y.1"

Number of terminal nodes: 10

Residual mean deviance: 6910 = 187300000 / 27100

Distribution of residuals:

	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
-8.389e+002	-4.486e+001	-8.631e-001	-1.584e-013	4.214e+001	7.636e+002	

node), split, n, deviance, yval

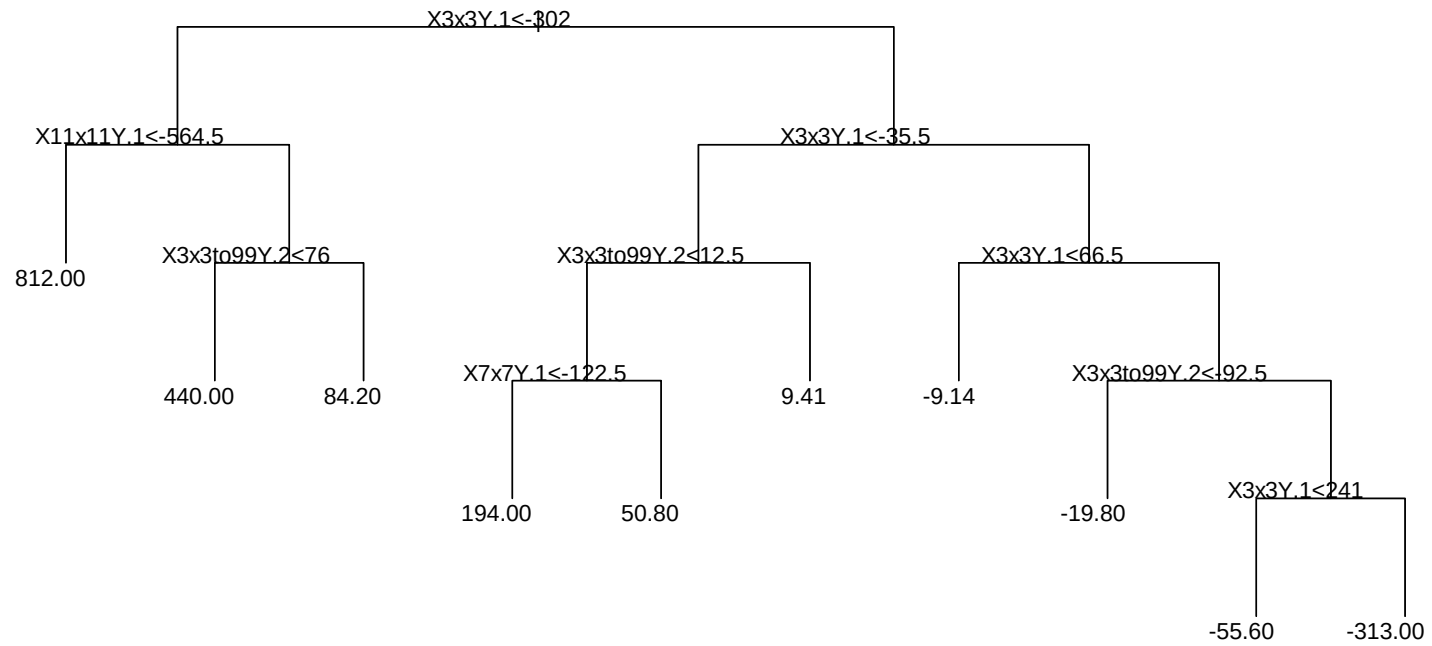
* denotes terminal node

- 1) root 27112 236800000 -2.804
- 2) X3x3Y.1<-302 114 7233000 456.100
 - 4) X11x11Y.1<-564.5 24 402300 812.300 *
 - 5) X11x11Y.1>-564.5 90 2975000 361.200
 - 10) X3x3to99Y.2<76 70 754100 440.300 *
 - 11) X3x3to99Y.2>76 20 248900 84.200 *
- 3) X3x3Y.1>-302 26998 205500000 -4.742
 - 6) X3x3Y.1<-35.5 6206 69550000 27.150
 - 12) X3x3to99Y.2<12.5 2292 27900000 57.460
 - 24) X7x7Y.1<-122.5 106 1939000 194.100 *
 - 25) X7x7Y.1>-122.5 2186 23880000 50.830 *
 - 13) X3x3to99Y.2>12.5 3914 38320000 9.406 *
 - 7) X3x3Y.1>-35.5 20792 127700000 -14.260
 - 14) X3x3Y.1<66.5 17879 97880000 -9.137 *
 - 15) X3x3Y.1>66.5 2913 26490000 -45.720
 - 30) X3x3to99Y.2<-92.5 984 9430000 -19.790 *
 - 31) X3x3to99Y.2>-92.5 1929 16070000 -58.950
 - 62) X3x3Y.1<241 1904 13960000 -55.610 *
 - 63) X3x3Y.1>241 25 465900 -313.000 *

Spatial Autocorrelation Regression Tree Model Diagram

Nodes: 10

DDE Validation = 0.1996



Topographic Regression Tree Results**Nodes: 4****DDE Validation = 0.0015**

Regression tree:

```
snip.tree(tree = tree(formula = ewdi ~ elev + slope + aspect, data =
  training.cnpycvr0, na.action = na.exclude, mincut = 5, minsize = 10,
  mindev = 0.01), nodes = c(11., 4., 10., 3.))
```

Variables actually used in tree construction:

[1] "aspect" "slope"

Number of terminal nodes: 4

Residual mean deviance: 8685 = 235400000 / 27110

Distribution of residuals:

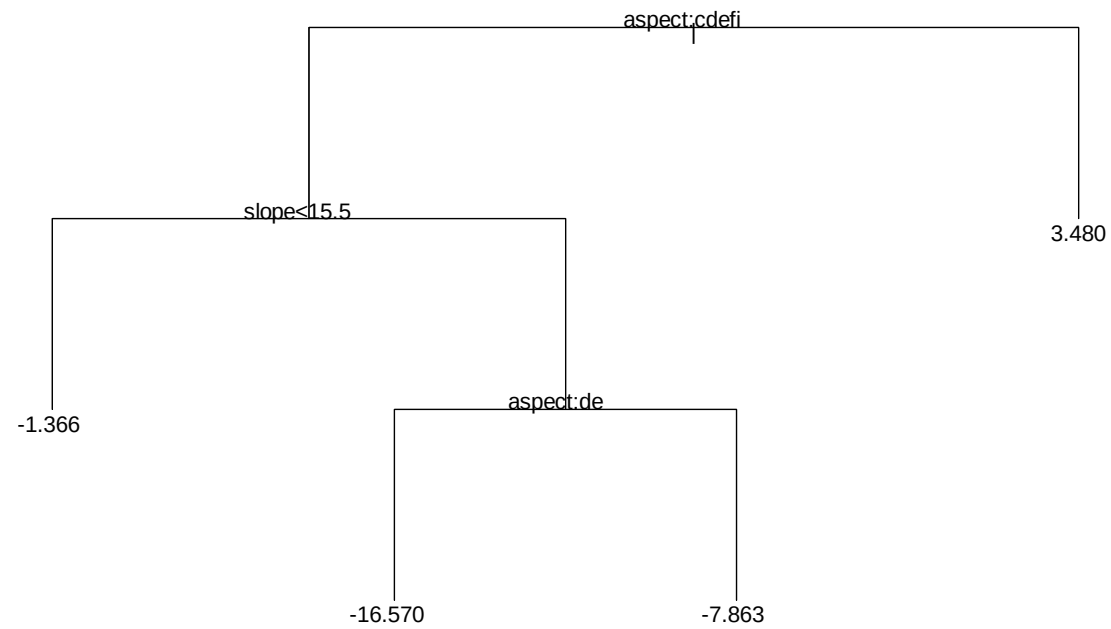
	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
	-8.466e+002	-4.948e+001	-4.480e+000	9.136e-013	4.252e+001	9.915e+002

- 1) root 27112 236800000 -2.804
- 2) aspect:3,4,5,6,9 15384 132300000 -7.595
- 4) slope<15.5 6230 55970000 -1.366 *
- 5) slope>15.5 9154 75900000 -11.830
- 10) aspect:4,5 4176 34510000 -16.570 *
- 11) aspect:3,6,9 4978 41220000 -7.863 *
- 3) aspect:1,2,7,8 11728 103700000 3.480 *

Topographic Regression Tree Model Diagram

Nodes: 4

DDE Validation = 0.0015



Temperature Regression Tree Results**Nodes: 18****DDE Validation = 0.1505**

Regression tree:

```
snip.tree(tree = tree(formula = ewdi ~ anoY.20ct + anoY.2Nov + anoY.2Dec +
  anoY.1Jan + anoY.1Feb + anoY.1Mar + anoY.1Apr + anoY.1May + anoY.1Jun +
  anoY.1Jul + anoY.1Aug + anoY.1Sep + anoY.30ct + anoY.3Nov + anoY.3Dec +
  anoY.2Jan + anoY.2Feb + anoY.2Mar + anoY.2Apr + anoY.2May + anoY.2Jun +
  anoY.2Jul + anoY.2Aug + anoY.2Sep + anoY.40ct + anoY.4Nov + anoY.4Dec +
  anoY.3Jan + anoY.3Feb + anoY.3Mar + anoY.3Apr + anoY.3May + anoY.3Jun +
  anoY.3Jul + anoY.3Aug + anoY.3Sep + avg30Jan + avg30Feb + avg30Mar +
  avg30Apr + avg30May + avg30Jun + avg30Jul + avg30Aug + avg30Sep +
  avg30Oct + avg30Nov + avg30Dec + Y.1win + Y.1sum + Y.2win + Y.2sum +
  Y.3win + Y.3sum, data = training.cnpycvr0, na.action = na.exclude,
  mincut = 5, minsize = 10, mindev = 0.01), nodes = c(21., 80., 123.,
  118., 62., 11., 41., 4., 58., 81., 12.))
```

Variables actually used in tree construction:

```
[1] "anoY.3Feb" "anoY.2Mar" "avg30Dec" "anoY.1Mar" "anoY.1Apr" "anoY.2Dec"
[7] "anoY.2Feb" "anoY.3Sep" "anoY.20ct" "anoY.3Jun" "anoY.3Jan" "anoY.1Sep"
[13] "anoY.3Apr"
```

Number of terminal nodes: 18

Residual mean deviance: 7180 = 194500000 / 27090

Distribution of residuals:

	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
-8.369e+002	-4.228e+001	-9.093e-001	-5.046e-015	4.044e+001	9.647e+002	

node), split, n, deviance, yval
* denotes terminal node

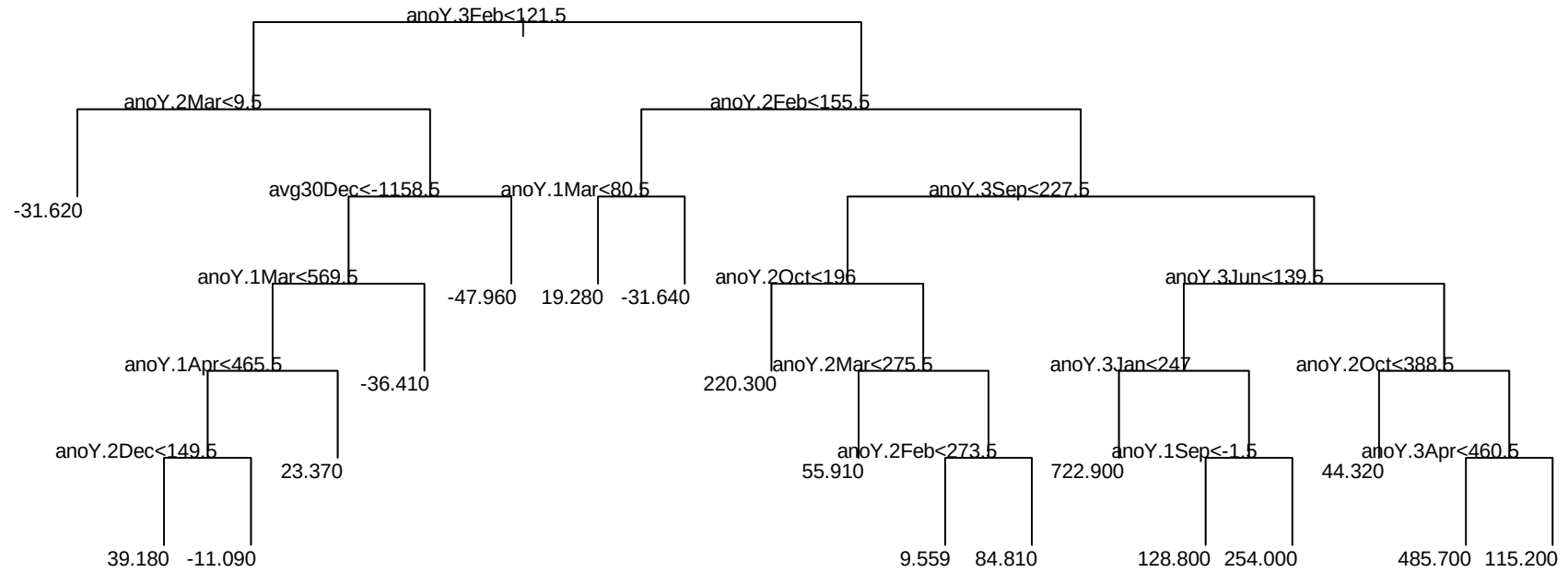
```
1) root 27112 236800000 -2.804
 2) anoY.3Feb<121.5 18245 123800000 -19.250
 4) anoY.2Mar<9.5 7181 27160000 -31.620 *
 5) anoY.2Mar>9.5 11064 94800000 -11.230
 10) avg30Dec<-1158.5 10365 88240000 -8.748
    20) anoY.1Mar<569.5 9282 80630000 -5.521
      40) anoY.1Apr<465.5 8215 67070000 -9.273
        80) anoY.2Dec<149.5 297 3735000 39.180 *
        81) anoY.2Dec>149.5 7918 62610000 -11.090 *
      41) anoY.1Apr>465.5 1067 12550000 23.370 *
    21) anoY.1Mar>569.5 1083 6691000 -36.410 *
 11) avg30Dec>-1158.5 699 5552000 -47.960 *
3) anoY.3Feb>121.5 8867 97960000 31.040
 6) anoY.2Feb<155.5 6026 36400000 17.170
 12) anoY.1Mar<80.5 5776 33590000 19.280 *
 13) anoY.1Mar>80.5 250 2187000 -31.640 *
 7) anoY.2Feb>155.5 2841 57940000 60.460
 14) anoY.3Sep<227.5 2099 29290000 44.740
    28) anoY.20ct<196 36 1133000 220.300 *
    29) anoY.20ct>196 2063 27030000 41.670
      58) anoY.2Mar<275.5 1168 15370000 55.910 *
      59) anoY.2Mar>275.5 895 11110000 23.090
        118) anoY.2Feb<273.5 734 8606000 9.559 *
        119) anoY.2Feb>273.5 161 1754000 84.810 *
 15) anoY.3Sep>227.5 742 26660000 104.900
    30) anoY.3Jun<139.5 168 11460000 260.400
      60) anoY.3Jan<247 21 739000 722.900 *
      61) anoY.3Jan>247 147 5590000 194.400
        122) anoY.1Sep<-1.5 70 1592000 128.800 *
```

123)	anoY.1Sep>-1.5	77	3423000	254.000	*
31)	anoY.3Jun>139.5	574	9951000	59.430	
62)	anoY.20Oct<388.5	504	6053000	44.320	*
63)	anoY.20Oct>388.5	70	2955000	168.200	
126)	anoY.3Apr<460.5	10	771800	485.700	*
127)	anoY.3Apr>460.5	60	1007000	115.200	*

Temperature Regression Tree Model Diagram

Nodes: 18

DDE Validation = 0.1505



Precipitation Regression Tree Results

Nodes: 19 nodes

DDE Validation = 0.1482

Regression tree:

```
snip.tree(tree = tree(formula = ewdi ~ panY.10oct + panY.1Nov + panY.1Dec +
  panY.Jan + panY.Feb + panY.Mar + panY.Apr + panY.May + panY.Jun + panY.2oct +
  panY.2Nov + panY.2Dec + panY.1Jan + panY.1Feb + panY.1Mar + panY.1Apr +
  panY.1May + panY.1Jun + panY.1Jul + panY.1Aug + panY.1Sep + panY.3oct +
  panY.3Nov + panY.3Dec + panY.2Jan + panY.2Feb + panY.2Mar + panY.2Apr +
  panY.2May + panY.2Jun + panY.2Jul + panY.2Aug + panY.2Sep + panY.4oct +
  panY.4Nov + panY.4Dec + panY.3Jan + panY.3Feb + panY.3Mar + panY.3Apr +
  panY.3May + panY.3Jun + panY.3Jul + panY.3Aug + panY.3Sep + pavg0oct +
  pavgNov + pavgDec + pavgJan + pavgFeb + pavgMar + pavgApr + pavgMay +
  pavgJun + pavgJul + pavgAug + pavgSep + spr.pano + Y.0wtryr + Y.1wtryr +
  Y.2wtryr + Y.3wtryr, data = training.cnpycvr0, na.action = na.exclude,
  mincut = 5, minsize = 10, mindev = 0.01), nodes = c(9., 21., 13.,
  8., 11., 50., 20., 24.))
```

Variables actually used in tree construction:

```
[1] "panY.4Dec" "panY.2Jan" "panY.Mar" "panY.1Aug" "panY.3oct" "panY.Apr"
[7] "panY.2Sep" "pavgMay" "panY.3Nov" "pavgMar" "panY.2Dec" "panY.3Feb"
[13] "panY.1Nov" "pavgJun" "panY.3Mar"
```

Number of terminal nodes: 19

Residual mean deviance: 7154 = 193800000 / 27090

Distribution of residuals:

	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
	-8.357e+002	-4.171e+001	-7.024e-001	3.870e-014	4.008e+001	8.680e+002

node), split, n, deviance, yval
 * denotes terminal node

```
1) root 27112 236800000 -2.804
 2) panY.4Dec<232.5 22816 136900000 -12.940
   4) panY.2Jan<-35.5 6632 26150000 6.693
     8) panY.Mar<-17.5 2225 12250000 -9.604 *
     9) panY.Mar>-17.5 4407 13010000 14.920 *
  5) panY.2Jan>-35.5 16184 107200000 -20.980
    10) panY.1Aug<8.5 8628 42450000 -28.590
      20) panY.3oct<46.5 5602 28660000 -21.710 *
      21) panY.3oct>46.5 3026 13040000 -41.330 *
      11) panY.1Aug>8.5 7556 63680000 -12.290 *
  3) panY.4Dec>232.5 4296 85090000 51.010
    6) panY.Apr<24.5 3846 59030000 40.180
      12) panY.2Sep<-5.5 2248 39420000 53.800
        24) pavgMay<107.5 843 15250000 31.250 *
        25) pavgMay>107.5 1405 23480000 67.340
          50) panY.3Nov<-25.5 1213 16300000 57.700 *
          51) panY.3Nov>-25.5 192 6355000 128.200
            102) pavgMar<84.5 124 1210000 76.490 *
            103) pavgMar>84.5 68 4208000 222.600
              206) panY.2Dec<5.5 8 452600 529.300 *
              207) panY.2Dec>5.5 60 2902000 181.700
                414) panY.3Feb<215 48 1619000 127.800 *
                415) panY.3Feb>215 12 586800 397.300 *
      13) panY.2Sep>-5.5 1598 18610000 21.020 *
    7) panY.Apr>24.5 450 21750000 143.600
      14) panY.1Nov<-13.5 157 9857000 296.900
        28) panY.3Feb<257 123 4088000 222.800
          56) pavgJun<66.5 65 1584000 312.700 *
```

```

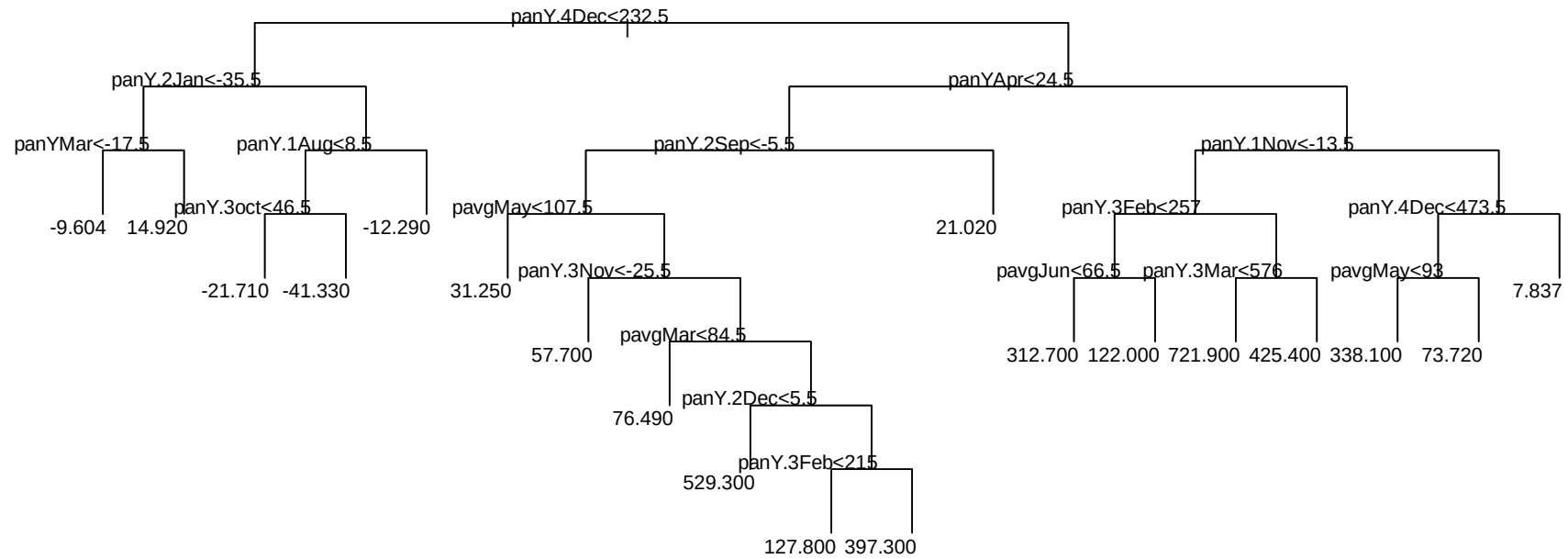
57) pavgJun>66.5 58 1390000 122.000 *
29) panY.3Feb>257 34 2651000 564.900
58) panY.3Mar<576 16 665500 721.900 *
59) panY.3Mar>576 18 1241000 425.400 *
15) panY.1Nov>-13.5 293 6224000 61.410
30) panY.4Dec<473.5 158 3909000 107.200
60) pavgMay<93 20 930500 338.100 *
61) pavgMay>93 138 1757000 73.720 *
31) panY.4Dec>473.5 135 1597000 7.837 *

```

Precipitation Regression Tree Model Diagram

Nodes: 19

DDE Validation = 0.1482



Growth Year Y-1 Climate Regression Tree Results

Nodes: 17

DDE Validation = 0.1160

Regression tree:

```
snip.tree(tree = tree(formula = ewdi ~ anoY.2Oct + anoY.2Nov + anoY.2Dec +
  anoY.1Jan + anoY.1Feb + anoY.1Mar + anoY.1Apr + anoY.1May + anoY.1Jun +
  anoY.1Jul + anoY.1Aug + anoY.1Sep + panY.2Oct + panY.2Nov + panY.2Dec +
  panY.1Jan + panY.1Feb + panY.1Mar + panY.1Apr + panY.1May + panY.1Jun +
  panY.1Jul + panY.1Aug + panY.1Sep + Y.1wtryr + Y.1win + Y.1sum, data
  = training.cnpycvr0, na.action = na.exclude, mincut = 5, minsize = 10,
  mindev = 0.01), nodes = c(95., 31., 6., 119., 122., 45., 60., 28.,
  4., 10.))
```

Variables actually used in tree construction:

```
[1] "anoY.1Mar" "panY.2Nov" "panY.1Sep" "panY.1Aug" "panY.1Jun" "anoY.1Sep"
```

```
[7] "anoY.2Oct" "anoY.1Apr" "panY.1Jan"
```

Number of terminal nodes: 17

Residual mean deviance: 7398 = 200500000 / 27100

Distribution of residuals:

	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
	-8.324e+002	-4.209e+001	-4.278e-001	-2.287e-013	4.034e+001	9.463e+002

node), split, n, deviance, yval

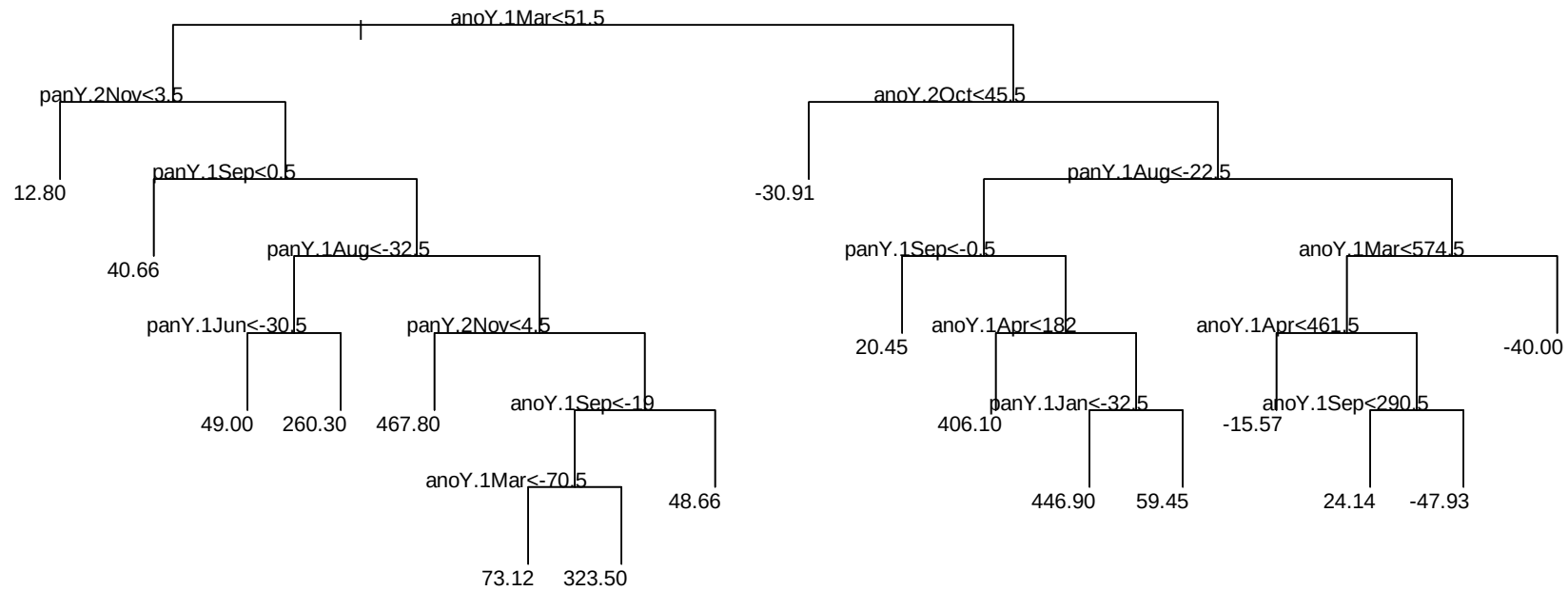
* denotes terminal node

- 1) root 27112 236800000 -2.804
- 2) anoY.1Mar<51.5 8551 83350000 28.190
 - 4) panY.2Nov<3.5 5248 18080000 12.800 *
 - 5) panY.2Nov>3.5 3303 62050000 52.660
 - 10) panY.1Sep<0.5 2644 42040000 40.660 *
 - 11) panY.1Sep>0.5 659 18110000 100.800
 - 22) panY.1Aug<-32.5 124 4533000 209.100
 - 44) panY.1Jun<-30.5 30 274200 49.000 *
 - 45) panY.1Jun>-30.5 94 3244000 260.300 *
 - 23) panY.1Aug>-32.5 535 11780000 75.690
 - 46) panY.2Nov<4.5 12 1250000 467.800 *
 - 47) panY.2Nov>4.5 523 8647000 66.690
 - 94) anoY.1Sep<-19 150 4495000 111.500
 - 188) anoY.1Mar<-70.5 127 1601000 73.120 *
 - 189) anoY.1Mar>-70.5 23 1674000 323.500 *
 - 95) anoY.1Sep>-19 373 3730000 48.660 *
 - 3) anoY.1Mar>51.5 18561 141500000 -17.090
 - 6) anoY.2Oct<45.5 6214 23060000 -30.910 *
 - 7) anoY.2Oct>45.5 12347 116600000 -10.130
 - 14) panY.1Aug<-22.5 932 19450000 43.730
 - 28) panY.1Sep<-0.5 715 8745000 20.450 *
 - 29) panY.1Sep>-0.5 217 9044000 120.400
 - 58) anoY.1Apr<182 27 1330000 406.100 *
 - 59) anoY.1Apr>182 190 5198000 79.840
 - 118) panY.1Jan<-32.5 10 681100 446.900 *
 - 119) panY.1Jan>-32.5 180 3095000 59.450 *
 - 15) panY.1Aug>-22.5 11415 94250000 -14.520
 - 30) anoY.1Mar<574.5 10420 87160000 -12.090
 - 60) anoY.1Apr<461.5 9071 70180000 -15.570 *
 - 61) anoY.1Apr>461.5 1349 16120000 11.320
 - 122) anoY.1Sep<290.5 1109 12930000 24.140 *
 - 123) anoY.1Sep>290.5 240 2166000 -47.930 *
 - 31) anoY.1Mar>574.5 995 6382000 -40.000 *

Growth Year Y-1 Climate Regression Tree Model Diagram

Nodes: 17

DDE Validation = 0.1160



Growth Year Y-2 Climate Regression Tree Results

Nodes: 18

DDE Validation = 0.1414

Regression tree:

```
snip.tree(tree = tree(formula = ewdi ~ anoY.3Oct + anoY.3Nov + anoY.3Dec +
  anoY.2Jan + anoY.2Feb + anoY.2Mar + anoY.2Apr + anoY.2May + anoY.2Jun +
  anoY.2Jul + anoY.2Aug + anoY.2Sep + panY.3Oct + panY.3Nov + panY.3Dec +
  panY.2Jan + panY.2Feb + panY.2Mar + panY.2Apr + panY.2May + panY.2Jun +
  panY.2Jul + panY.2Aug + panY.2Sep + Y.2wtryr + Y.2win + Y.2sum, data
  = training.cnpycvr0, na.action = na.exclude, mincut = 5, minsize = 10,
  mindev = 0.01), nodes = c(25., 441., 437., 2., 216., 24., 26., 440.,
  7.))
```

Variables actually used in tree construction:

[1] "anoY.2Mar" "panY.2Jan" "anoY.3Nov" "anoY.2Sep" "anoY.2Feb" "panY.2Sep"

[7] "panY.2Mar" "panY.2Feb" "anoY.2Apr" "panY.2Apr" "panY.2Aug" "anoY.3Dec"

Number of terminal nodes: 18

Residual mean deviance: 7270 = 197000000 / 27090

Distribution of residuals:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
-8.388e+002	-4.279e+001	-9.758e-001	8.481e-014	4.024e+001	8.980e+002

node), split, n, deviance, yval

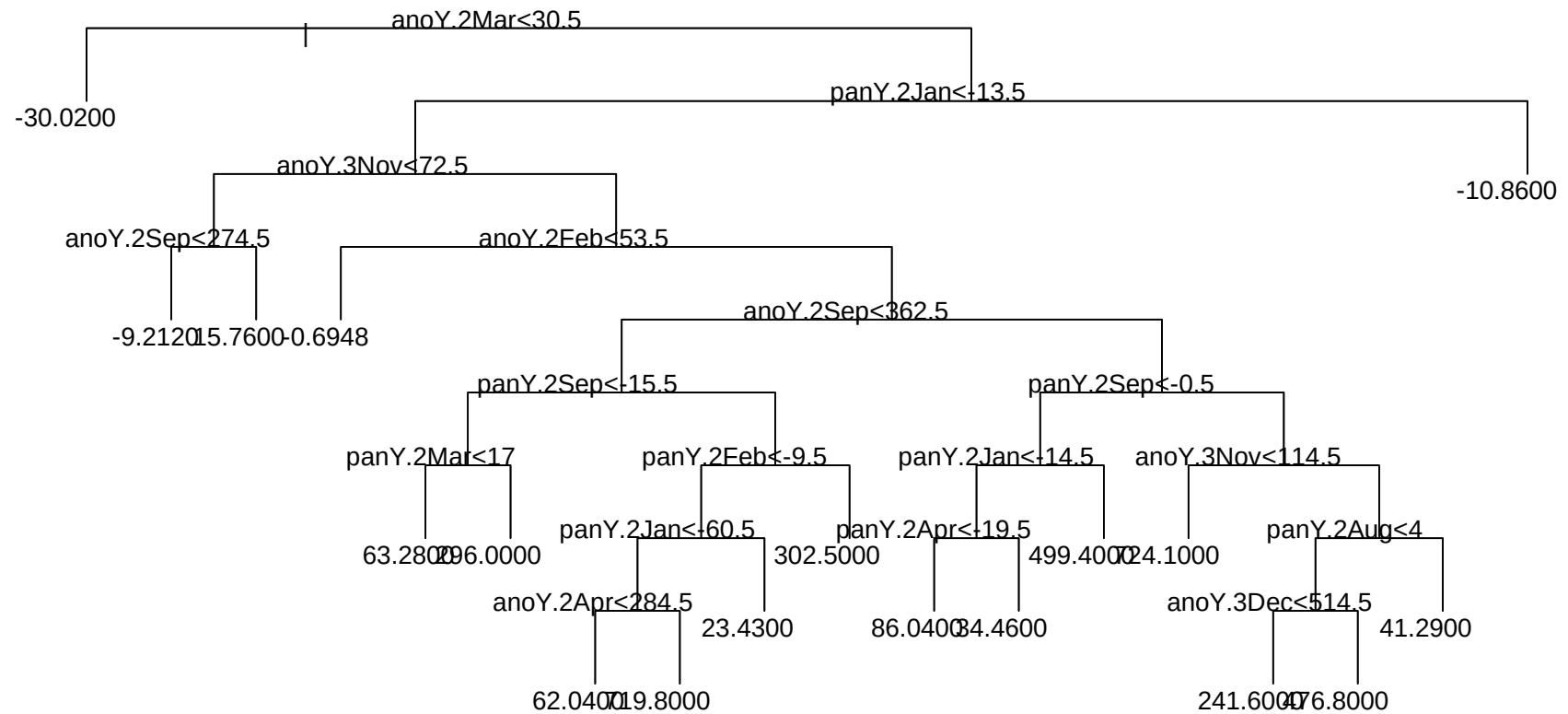
* denotes terminal node

- 1) root 27112 236800000 -2.8040
- 2) anoY.2Mar<30.5 7991 31360000 -30.0200 *
- 3) anoY.2Mar>30.5 19121 197100000 8.5710
- 6) panY.2Jan<-13.5 12391 128700000 19.1300
- 12) anoY.3Nov<72.5 8143 45400000 5.3310
- 24) anoY.2Sep<274.5 3400 26060000 -9.2120 *
- 25) anoY.2Sep>274.5 4743 18110000 15.7600 *
- 13) anoY.3Nov>72.5 4248 78790000 45.5700
- 26) anoY.2Feb<53.5 878 10130000 -0.6948 *
- 27) anoY.2Feb>53.5 3370 66290000 57.6200
- 54) anoY.2Sep<362.5 2457 35940000 43.7400
- 108) panY.2Sep<-15.5 795 11540000 68.8400
- 216) panY.2Mar<17 776 9491000 63.2800 *
- 217) panY.2Mar>17 19 1043000 296.0000 *
- 109) panY.2Sep>-15.5 1662 23660000 31.7300
- 218) panY.2Feb<-9.5 1647 22270000 29.2700
- 436) panY.2Jan<-60.5 147 4413000 88.8800
- 872) anoY.2Apr<284.5 141 1765000 62.0400 *
- 873) anoY.2Apr>284.5 6 158000 719.8000 *
- 437) panY.2Jan>-60.5 1500 17280000 23.4300 *
- 219) panY.2Feb>-9.5 15 282700 302.5000 *
- 55) anoY.2Sep>362.5 913 28600000 94.9900
- 110) panY.2Sep<-0.5 718 13680000 67.0100
- 220) panY.2Jan<-14.5 713 12130000 63.9700
- 440) panY.2Apr<-19.5 408 7315000 86.0400 *
- 441) panY.2Apr>-19.5 305 4347000 34.4600 *
- 221) panY.2Jan>-14.5 5 607800 499.4000 *
- 111) panY.2Sep>-0.5 195 12290000 198.0000
- 222) anoY.3Nov<114.5 15 580900 724.1000 *
- 223) anoY.3Nov>114.5 180 7216000 154.2000
- 446) panY.2Aug<4 85 3791000 280.4000
- 892) anoY.3Dec<514.5 71 2357000 241.6000 *
- 893) anoY.3Dec>514.5 14 786800 476.8000 *
- 447) panY.2Aug>4 95 861300 41.2900 *
- 7) panY.2Jan>-13.5 6730 64430000 -10.8600 *

Growth Year Y-2 Climate Regression Tree Model Diagram

Nodes: 18

DDE Validation = 0.1414



Growth Year Y-3 Climate Regression Tree Results

Nodes: 18

DDE Validation = 0.1547

Regression tree:

```
snip.tree(tree = tree(formula = ewdi ~ anoY.4Nov + anoY.4Dec + anoY.3Jan +
  anoY.3Feb + anoY.3Mar + anoY.3Apr + anoY.3May + anoY.3Jun + anoY.3Jul +
  anoY.3Aug + anoY.3Sep + panY.4oct + panY.4Nov + panY.4Dec + panY.3Jan +
  panY.3Feb + panY.3Apr + panY.3Mar + panY.3May + panY.3Jun + panY.3Jul +
  panY.3Aug + panY.3Sep + Y.3wtryr + Y.3win + Y.3sum, data =
  training.cnpycvr0, na.action = na.exclude, mincut = 5, minsize = 10,
  mindev = 0.01), nodes = c(8., 52., 24., 9., 55., 21., 216., 11., 20.,
  28., 60., 109., 31.))
```

Variables actually used in tree construction:

[1] "anoY.3Feb" "Y.3win" "anoY.3Sep" "panY.3Mar" "anoY.4Nov" "panY.3Sep"

[7] "panY.4oct" "panY.3Jun" "anoY.3Mar" "anoY.3Apr" "anoY.3Aug"

Number of terminal nodes: 18

Residual mean deviance: 7226 = 195800000 / 27090

Distribution of residuals:

	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
-8.243e+002	-4.181e+001	-8.696e-001	2.350e-013	3.919e+001	9.310e+002	

node), split, n, deviance, yval

* denotes terminal node

- 1) root 27112 236800000 -2.804
 - 2) anoY.3Feb<121.5 18245 123800000 -19.250
 - 4) Y.3win<210.5 6879 32350000 -30.660
 - 8) anoY.3Sep<-7.5 2103 9384000 -43.080 *
 - 9) anoY.3Sep>-7.5 4776 22500000 -25.190 *
 - 5) Y.3win>210.5 11366 89980000 -12.350
 - 10) panY.3Mar<171.5 10876 83550000 -14.050
 - 20) anoY.4Nov<216.5 4618 26080000 -23.730 *
 - 21) anoY.4Nov>216.5 6258 56720000 -6.916 *
 - 11) panY.3Mar>171.5 490 5699000 25.550 *
 - 3) anoY.3Feb>121.5 8867 97960000 31.040
 - 6) panY.3Sep<231.5 8062 64080000 23.640
 - 12) panY.4oct<155.5 5264 22990000 14.090
 - 24) anoY.3Sep<513.5 5034 21550000 15.930 *
 - 25) anoY.3Sep>513.5 230 1051000 -26.180 *
 - 13) panY.4oct>155.5 2798 39710000 41.590
 - 26) panY.3Jun<-93.5 247 4171000 89.090
 - 52) panY.3Sep<125.5 226 2572000 67.960 *
 - 53) panY.3Sep>125.5 21 412500 316.400 *
 - 27) panY.3Jun>-93.5 2551 34930000 36.990
 - 54) anoY.3Mar<572.5 2245 30370000 32.480
 - 108) anoY.4Nov<-96.5 989 15720000 46.010
 - 216) anoY.4Nov<-97.5 964 13720000 41.930 *
 - 217) anoY.4Nov>-97.5 25 1362000 203.300 *
 - 109) anoY.4Nov>-96.5 1256 14330000 21.820 *
 - 55) anoY.3Mar>572.5 306 4176000 70.100 *
 - 7) panY.3Sep>231.5 805 29010000 105.200
 - 14) anoY.3Apr<386 72 6384000 404.900
 - 28) anoY.3Feb<257 51 2648000 274.000 *
 - 29) anoY.3Feb>257 21 739000 722.900 *
 - 15) anoY.3Apr>386 733 15520000 75.740
 - 30) anoY.3Apr<476 124 4973000 187.600
 - 60) anoY.3Aug<197 101 2949000 149.300 *
 - 61) anoY.3Aug>197 23 1226000 355.700 *
 - 31) anoY.3Apr>476 609 8676000 52.970 *

Growth Year Y-3 Climate Regression Tree Model Diagram

Nodes: 18

DDE Validation = 0.1547

