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FORUM

Climate Factors Associated with Historic Spruce Beetle (Coleoptera: Curculionidae) Outbreaks in Utah and Colorado

ELIZABETH G. HEBERTSON[1] AND MICHAEL J. JENKINS[2]

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ABSTRACT This study investigated relationships between climate and historic spruce beetle, *Dendroctonus rufipennis* Kirby (Coleoptera: Curculionidae), outbreaks in northern and southeastern Utah and western Colorado between 1905 and 1996. A chronology of outbreak years was constructed from historic records, research papers, newspapers, and other sources of information. Historic climate data for the region included annual and mean monthly temperature and precipitation, in addition to Palmer drought severity index (PDSI) values estimated from tree rings. Classification and regression tree analysis (CART) was used to identify those climate factors most important for predicting historic spruce beetle outbreaks. The factors identified by the best CART model included mean December temperature, mean September temperature 1 yr before outbreak years, the mean estimated PDSI value of the 5-yr period before outbreak years, and mean October precipitation. The resulting model correctly classified nonoutbreak and outbreak years 67 and 70% of the time, respectively.

KEY WORDS spruce beetle, climate, Engelmann spruce, disturbance ecology, classification and regression tree analysis

The spruce beetle, *Dendroctonus rufipennis* Kirby (Coleoptera: Curculionidae), is a native insect that primarily infests Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in the intermountain region of the western United States (Furniss and Carolin 1977). Spruce beetles typically attack recently fallen, overmature, and weakened trees (Knight 1961, Schmid and Frye 1977, Schmid 1981, Hard 1985). Periodically, spruce beetle populations reach outbreak levels causing widespread tree mortality in susceptible spruce-fir forests. Bentz and Munson (2000) considered outbreak population levels when there were more than two clumps of at least five standing, infested trees for every 5 acres. In Utah, for example, recent spruce beetle outbreaks have resulted in the loss of >90% of the large spruce component in infested stands (Dymerski et al. 2001, Matthews et al. 2005). Similar levels of spruce mortality were reported for historic outbreaks on the White River Plateau in Colorado (circa 1940s) and on the Aquarius Plateau in Utah (circa 1920s) (Mielke 1950, Massey and Wygant 1954).

The initiation of historic spruce beetle outbreaks has been mainly attributed to blowdown, logging activities, and other disturbances that produce an abundance of suitable host material (Miller 1970, Schmid and Hinds 1974, Lister et al. 1976, Schmid and Frye 1977, Werner et al.1977, Schmid 1981, Veblen et al.1994, Hebertson and Jenkins 2007). As populations build in downed host material, spruce beetles may attack apparently healthy standing trees (Schmid 1981).

However, not all such disturbances result in outbreaks (Schmid 1981). Although the actual causes of outbreak remain unclear, population growth and spread has been associated with the ability of spruce beetles to exploit available resources (e.g., sufficient population levels), the abundance of parasites and predators, and stand conditions (Lister et al. 1976, Schmid and Frye 1976, Werner et al. 1977, Schmid 1981, Hard 1985, Paine et al. 1997, Jenkins et al. 1998, Holsten et al. 1999, Hebertson and Jenkins 2007). A few studies also suggest that climate factors may have an important role in spruce beetle population dynamics (Knight 1961, Dyer 1969, Werner and Holsten 1985, Hansen et al. 2001a).

As poikilotherms, the growth, development, and behaviors of spruce beetles are strongly influenced by temperature. For example, seasonal temperatures have been found to directly influence the rate and length of spruce beetle development. In the intermountain region, spruce beetles are typically semivoltine (2-yr life cycle), although univoltine (1-yr life cycle) and life cycles >2 yr are not uncommon (Massey and Wygant 1954, Knight 1961, Schmid and Frye 1977, Werner and Holsten 1985). Higher proportions of univoltine broods develop with higher air and subcortical temperatures, although the timing of thermal input seems most critical for this development (Dyer 1969, Werner and Holsten 1985, Hansen et al. 2001a). Air temperatures also govern spruce beetle dispersal with flight occurring at temperatures exceeding

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≈16°C (Dyer 1969). The early occurrence of flight during warm springs allows sufficient time for the development of univoltine broods (Hansen et al. 2001a). Conversely, lower summer temperatures often prolong spruce beetle life cycles (Knight 1961).

During winter, temperatures less than −34°C are sufficiently low to kill large proportions of overwintering spruce beetles (Massey and Wygant 1954, Frye et al. 1974). In response to cold temperatures, prepupa of semivoltine populations undergo cold-hardening processes including the production of glycerol and other cryoprotectants important for winter survival (Miller and Werner 1987 cited in Bentz and Mullins 1999, Hansen et al. 2001b). The onset of cold temperatures also provides the necessary cues for brood adults to complete reproductive diapause (Hansen et al. 2001b). A portion of brood adults may also migrate to the base of host trees and enter hibernal diapause (Knight 1961).

Climate may indirectly affect spruce beetle populations by predisposing host trees to attack (Mattson and Haack 1987). Water stress associated with drought adversely affects host tree vigor by compromising or inhibiting important physiological processes including photosynthesis, the movement of gases, the flow of latex and oleoresins, and the absorption of water and ions (Kozlowski 1982). This can increase bark beetle survival and growth through elevated nutrient levels especially nitrogen, lowered plant defenses, and by providing a more suitable physical environment (Kozlowski 1982, Mattson and Haack 1987, Lorio et al. 1995, Paine et al. 1997). The current extensive spruce beetle outbreak on the Kenai Peninsula in Alaska, for example, has been in part attributed to the occurrence of atypically hot, dry weather in recent years with moisture-stressed spruce less resistant to attack (Snyder 2006).

Drought has been implicated in causing outbreaks of other bark beetle species as well. An unprecedented epidemic of pinyon engraver beetles, *Ips confusus* Leconte (Coleoptera: Curculionidae), triggered by drought beginning in 2000 resulted in widespread pinyon mortality in pinyon-juniper woodlands in the southwestern United States (Breshears et al. 2005, Shaw et al. 2005). During this same drought episode, mountain pine beetles have killed >2.5 million lodgepole pine trees on the Sawtooth National Recreation Area and in neighboring forests in southern Idaho (Matthews et al. 2005).

Although these studies allude to potential relationships between climate, spruce beetle population dynamics, and host vigor, much evidence still remains circumstantial and/or anecdotal. The complex nature of these interactions certainly challenges our ability to acquire reliable knowledge. However, the development and implementation of ecologically appropriate strategies for spruce beetle management and sustaining valuable spruce resources necessitates greater understanding of these interactions. This will become even more important with anticipated shifts in the geographical distribution of subalpine forests, the intensification of bark beetle behavior, and the potential expansion of bark beetle populations into new habitats associated with projected climate change (Williams and Liebold 2002, Carroll et al. 2003, Logan et al. 2003, Rehfeldt 2004, Breshears et al. 2005, Littell and Peterson 2005).

The purpose of our study was to help elucidate the nature of spruce beetle/climate relationships in the intermountain region by identifying and quantifying climate factors associated with historic spruce beetle outbreaks documented in Utah and Colorado. The specific climate variables we examined included regional temperature, precipitation, and drought severity.

Materials and Methods

Study Area. The study area encompassed the Wasatch Range and the Uinta Mountains in northern Utah, portions of the Colorado Plateau in central and southern Utah and in western Colorado, and the southern Rocky Mountains in Colorado (Fig. 1). Elevations of the highest peaks in this area range from 3,000 to >4,200 m.

The majority of precipitation in the region results from low-pressure systems that originate over the eastern Pacific Ocean (Jensen et al. 1990). Most storms lose moisture as they move east over the Sierra Nevada or Cascade ranges, resulting in an arid or semiarid climate. Annual precipitation amounts to <20 cm at lower elevations. The highest elevations, however, may receive >65 cm of annual precipitation falling mainly as snow in winter months. Winter temperatures during extremely cold periods may fall to −45°C, with maximum summer temperatures reaching 32–35°C in the mountains. Engelmann spruce and subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] forests occur at elevations from 2,400 to 3,300 m and are often mixed with Douglas-fir [*Pseudotsuga menziesii* variety *glauca* (Beissn.) Franco.], lodgepole pine (*Pinus contorta* Dougl. ex Loud.), aspen (*Populus tremuloides* Michx.), and shrub meadows.

Historic Spruce Beetle Outbreaks. We constructed a chronology of historic spruce beetle outbreaks within the study area from various sources including U.S. Department of Agriculture (USDA) Forest Service, forest insect and disease reports and biological evaluations, research papers, and personal communications with professional entomologists and foresters. We considered spruce beetle populations to have reached outbreak levels in these historic locations because their associated impacts warranted reporting. The period of documented outbreaks for the study area extends from the 1870s to the present.

Historic Climate Data. We obtained historic climate data from the National Climate Data Center for divisions 4, 5, and 7 in Utah and division 2 in western Colorado. These climate divisions corresponded best with locations in which historic spruce beetle outbreak years were derived. The specific climate division data set was TD-9640, which consisted of sequential "time biased corrected" mean monthly temperatures and precipitation for each division

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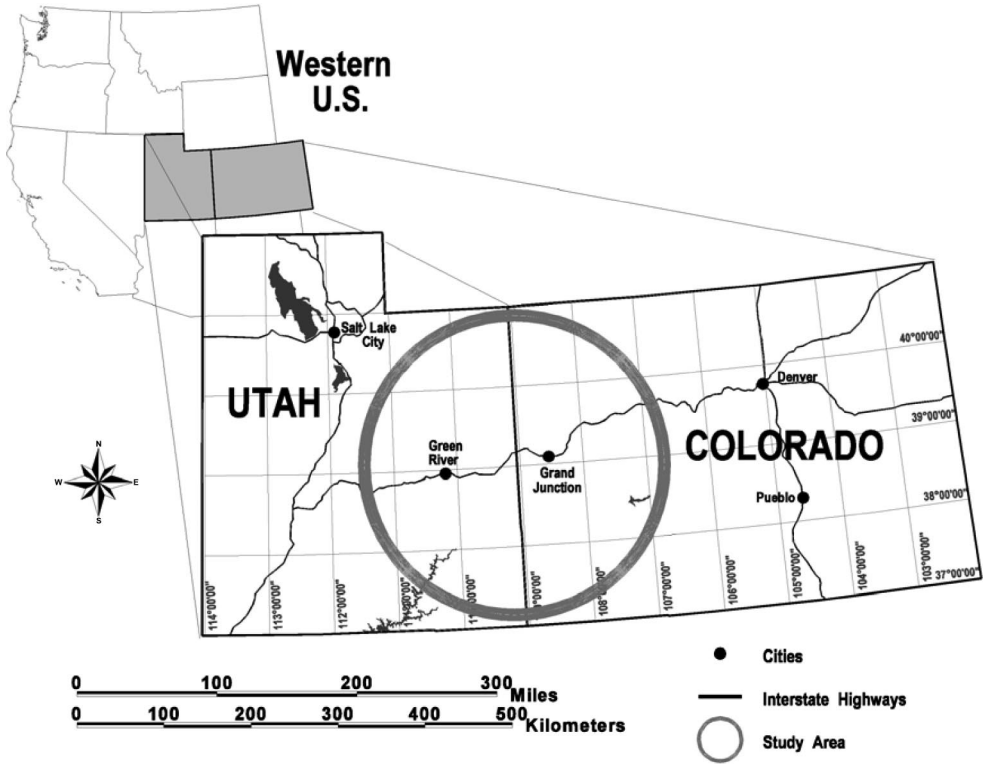


Fig. 1. The general study area.

(NCDC 1994). Monthly averages within each climate division in this data set were calculated giving cooperating stations that report both temperature and precipitation equal weight using the time bias model (Karl et al. 1986). This model adjusts the climate division monthly averages to rectify differences of the 24-h period over which observations from individual stations are gathered.

To study any seasonal influences on spruce beetle outbreaks, we used the mean monthly temperature and precipitation data to derive mean seasonal values for each climate division during the period of study. Fall included the months of September, October, and November. Winter included the months of December, January, and February. Spring included the months of March, April, and May. Summer included the months of June, July, and August.

We examined the relative severity of dry or wet periods within the study area by including Palmer drought severity indices (PDSIs). The PDSI data selected for this study were reconstructed by Cook et al. (1998) for 154 grid points spaced at 2° latitude by 3° longitude locations in the continental United States from a dense network of annual tree-ring chronologies. The grid points covering the study area were 39, 40, 49, and 50, located near Price, UT, Kanab, UT, Gunnison, CO, and Denver, CO, respectively. PDSIs derived from instrumental measurements for each of the corresponding grid points were originally developed to test the validity of tree-ring estimates (Cook et al. 1998) and also were used for analysis in this study. The range of PDSI values in each data set ranged from −6 (extremely dry) to 6 (extremely wet), with 0 indicating normal precipitation. Mean annual estimates from the reconstructed PDSI data set were considered most meaningful for this analysis because historic spruce beetle outbreaks were based on yearly observations. Also, the reconstructed PDSI estimates were of particular interest because they potentially reflect physiological responses of trees to stress induced by periods of drought.

Additionally, we included the averages of all mean monthly, seasonal, and PDSI data for 2- to 5-yr periods proceeding the observed year in our data set. Finally, we lagged all climate variables for 1–5 yr proceeding the observed year. Our rationale for including these data in our analysis was that (1) spruce beetle dynamics might be associated with certain climate patterns that develop during successive years, (2) climate stressors may not cause a significant decline in host vigor unless trees have been affected for several years, (3) spruce beetles have life histories that may range from 1 to 3 yr, and depending on the life history of the local populations, the development of an outbreak may require 1–5 yr after a potential climate trigger, and (4) reports of spruce beetle outbreaks may have been delayed by factors that constrained the detection of infested trees.

Data Analysis. The range of years providing the most complete data set from all sources of climate and

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Table 1. Chronology of historic spruce beetle outbreaks within the study area

Year[a]	Outbreak	State	Source
1870s	Grand Mesa	Colorado	Knight and McCambridge 1952; Schmid and Frye 1977
1875	White River Plateau	Colorado	Hopkins 1909; Packard 1877 in McCambridge 1951
≈1884	White River NF	Colorado	Hopkins 1909
1905	Manti National Forest	Utah	Hopkins 1909
1916	Aquarius Plateau	Utah	Schmid and Frye 1977
1937	Dixie NF, Cedar City RD	Utah	Jones 1937
1940	Dixie NF, Cedar City RD	Utah	Furniss 1940
1941	White River NF	Colorado	Knight 1953; Massey and Wygant 1954
1944	Grand Mesa NF	Colorado	Knight 1953; Schmid and Frye 1977
1944	Cedar Breaks National Monument, Dixie NF, Cedar RD	Utah	Rice 1944
1950	Uncompahgre and San Juan NF	Colorado	Wygant 1956
1955	Dixie National Forest, Boulder Top	Utah	Anonymous 1960
1957	Ashley, Unita, Wasatch NF, Uinta Mountains	Utah	Washburn and Knopf 1958; Anonymous 1960
1961	Dixie NF, Abajo Peak	Utah	Knopf 1962
1962	Dixie NF, Aquarius Plateau, Griffin Springs	Utah	Knopf 1962
1967	Fishlake NF, Loa RD	Utah	Klein 1967
Early 1970s	Wolf Creek Pass	Colorado	Schmid and Frye 1972; Schmid and Frye 1977
1970	Manti-LaSal NF, Huntington Cyn.	Utah	Parker 1973
1970	Fishlake NF, Beaver RD	Utah	Klein 1971
1981	Uinta NF, Heber RD, Mill Hollow	Utah	Holland 1983
1981	Manti LaSal NF, Moab RD	Utah	Knopf 1981
1984	Manti-LaSal NF, Moab RD	Utah	Knapp 1985
1984	Manti-LaSal NF, Monticello RD	Utah	Knapp 1985
1987	Wasatch-Cache NF, Salt Lake RD	Utah	Anhold 1987
1987	Manti LaSal NF, San Pete RD	Utah	Dymerski et al. 2001
1989	Dixie NF	Utah	Munson and DeBlander 1992
1989	Fishlake NF, Loa RD	Utah	Anhold et al.1992

[a] Only outbreak years from 1905 to 1996 were used in the data analysis.

historic spruce beetle outbreak data were from 1905 to 1996. As a consequence, spruce beetle outbreaks occurring outside of that time period were omitted from further analysis. A classification and regression tree analysis (CART) (Brieman et al. 1984, Steinberg and Colla 1997) was used to predict historic spruce beetle outbreaks from the set of climate and PDSI data within each climate division. Several CART models were constructed with spruce beetle outbreak years grouped into two response classes (0 = nonoutbreak years, 1 = outbreak years). The default setting of equal priors gave the most satisfactory analysis ". . . because it tends to treat each class as equally important for classification accuracy" (Steinberg and Colla 1997). Setting priors to other configurations such as proportional to the observed data or an average of the data proportions generally failed to produce trees. This is likely because of the noisy nature of the underlying signal, the relationship between the predictor variables, and the outbreaks or the relatively small sample size for this study.

The CART procedure considered all variables from the initial data using recursive binary splitting to produce classification trees of increasingly homogenous subsets. At each split, CART imposed a "goodness of split criterion," not unlike the method of least squares, to optimize splitting for each variable and ultimately minimize the overall probability of misclassifying the response variable. CART continued splitting until the classification tree achieved a maximum size, i.e., no further splits were possible. In the final step, CART removed variables or collapsed splits that provided no predictive power to the model or contributed minimally to reducing the measure of model error. The model growing procedure was cross-validated by partitioning the original data set into 10 subsets. Observations in each subset were estimated from the tree grown from the other nine subsets. The final classification tree was the one that minimized the overall misclassification probability. To further explore model results, Student's *t*-tests were also used to compare mean differences between nonoutbreak and outbreak years for variables comprising the final classification tree.

Results

Historic Spruce Beetle Outbreaks. The first historic accounts of spruce beetle outbreaks in the study area were from the early 1870s to 1875, where spruce beetle activity was reported near Manitou and Blackhawk on Grand Mesa and the White River Plateau in Colorado (Hopkins 1909, Packard 1877 in McCambridge 1951, Knight and McCambridge 1952). Another major spruce beetle outbreak occurred during the mid 1880s in the vicinity of Deep Lake, CO, resulting in the loss of ≈20% of mature spruce (Hopkins 1906 in McCambridge 1951). Tree-ring analyses provided evidence of spruce beetle outbreaks around 1490, 1585, 1716, 1827, the 1840s, and the 1870s in northwestern Colorado (Veblen et al. 1994, Eisenhart 1999).

From 1905 to 1996 (the period of study), spruce beetle outbreaks were reported during 17 different yr within the study area, leaving a total of 74 nonoutbreak yr. The chronology of all outbreaks occurring during these years is provided in Table 1. The first spruce beetle outbreak reported was on the Manti National Forest, UT, in 1905 (Hopkins 1906 in McCambridge

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Table 2. Cross-validation classification probability table

Actual class	Predicted class		Actual total
	0	1	
0	0.671	0.329	1.000
1	0.297	0.703	1.000

1951). Between 1916 and 1928, spruce beetles killed all but the smallest diameter trees over 115,000 acres on the Aquarius Plateau in southern Utah (Mielke 1950, Schmid and Frye 1977). From 1941 to 1952, perhaps the most extensive and widely documented outbreaks occurred on the White River, Routt, Grand Mesa, Umcompahgre, and San Juan National Forests in Colorado (McCambridge 1951, Massey and Wygant 1954, Schmid and Frye 1977). During this same time, several sizable infestations were also detected on various portions of the Cedar City Ranger District, Dixie National Forest, UT, and neighboring Cedar Breaks National Monument and forests outside of the study area including the Santa Fe National Forest in New Mexico (Appendix 1).

Widespread outbreaks were also documented during the early to mid-1950s. Although outbreaks on the Uncompaghre National Forest and Dixie National Forests were the only ones to occur within the study area, high levels of spruce beetle activity were also reported in several other western states including Idaho, New Mexico, and Arizona (Appendix 1). In 1957, spruce beetles were detected in several locations along the Provo River corridor on the Wasatch National Forest in Utah. Other outbreaks erupted in neighboring spruce-fir forests on the Ashley and Uinta National Forests, UT. As these outbreaks continued, others were detected in the Abajo Mountains of southeastern Utah and on the Aquarius Plateau. New infestations were also reported in the Santa Fe National Forest (Appendix 1).

Localized spruce beetle infestations occurred within the study area from the mid-1960s through the early 1980s. In 1967, a large outbreak occurred near Mt. Hilgard on the Fishlake National Forest, UT. However, numerous other spruce beetle outbreaks were reported across western states in 1967 and 1968, reflecting the extent of activity during those years (Appendix 1). Large outbreaks on the Manti-LaSal and Dixie National Forests erupted again in 1987. More recently, spruce beetle outbreaks have killed thousand of trees in the Fishlake and Wasatch-Cache National Forests (Matthews et al. 2005).

CART. The best CART model resulting from our analysis used mean December temperature (splitting value = −5.5°C) at the first split to separate outbreak from nonoutbreak years. Mean September temperature of the year before the observed year (splitting value = 12.8°C) was used in the second split followed by the mean estimated PDSI of the 5-yr period before the observed year (splitting value = 0.328) in the third split, and mean October precipitation (splitting value = 1.33 cm) in the final split to further optimize the classification of spruce beetle outbreak and nonoutbreak years (Fig. 2).

Cross-validation classification procedures indicated that the model correctly classified nonoutbreak and outbreak years 67 and 70% of the time, respectively (Table 2). The cross-validated relative cost was 0.626, making the adjusted pseudo-R^2 value 0.374. This relatively low model correlation can be attributed to unexplained sources of variation and the complex nature of variable interactions and perhaps the relatively small sample size.

For each of the model variables, CART also provided a set of closely associated variables to use as surrogates if necessary in further analysis or explanations of potential relationships. The surrogates most closely associated with each model variable and their splitting values are given in Table 3. Associations between surrogate and model variables were fair, with cases split somewhat differently than the primary splits. The surrogates did not perform nearly as well as model variables in the correct classification of cases as indicated by the relatively low improvement values.

Mean Comparison Tests. The results of Student's *t*-tests used to compare mean differences between nonoutbreak and outbreak years for each model variable are given in Table 4. In general, mean December temperature and mean September temperatures 1 yr before outbreak years were ≈2°C warmer than nonoutbreak years. This difference was significant at the $\alpha = 0.05$ level. The 5-yr period proceeding outbreak years also had significantly lower mean estimated PDSI values than nonoutbreak years. No difference in mean October precipitation was detected between outbreak and nonoutbreak years.

Table 3. Most closely associated surrogate variables selected for each model variable and their respective splitting values

Model variable[a]	Surrogate variable	Splitting value	Association	Improvement
Mean December temperature	Mean winter temperature	−5.3°C	0.400	0.061
	Mean December temperature$^{A\ t\text{-}3}$	−6.2°C	0.377	0.044
Mean September$^{t\text{-}1}$	Mean September temperature$^{A\ t\text{-}5}$	12.3°C	0.371	0.024
	Mean August temperature$^{A\ t\text{-}3}$	16.8°C	0.306	0.026
PDSI$^{A\ t\text{-}5}$	Estimated PDSI$^{t\text{-}2}$	2.9	0.247	0.036
	Estimated PDSI$^{A\ t\text{-}3}$	1.3	0.205	0.024
Mean October precipitation	Mean October precipitation$^{A\ t\text{-}5}$	1.3 cm	0.128	0.010
	Mean October precipitation$^{A\ t\text{-}3}$	1.0 cm	0.128	0.007

[a] *t*, observed year; *t*-1, lagged 1 yr before observed year; A, average of the no. of years indicated before the observed year.

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Table 4. Results of Student's *t*-tests comparing mean differences between non-outbreak vs outbreak years for each model variable

Model variable[a]	Nonoutbreak years	Outbreak years	*df*	*t*	*P*
Mean December temperature	−3.9°C	−2.2°C	50	4.93	<0.0001
Mean September temperature^{t-1}	14.4°C	16.1°C	45	7.37	<0.0001
PDSI$^{A\ t-5}$	0.141	−0.679	36	3.58	<0.0001
Mean October precipitation	3.4 cm	3.3 cm	52	0.34	<1.0

[a] *t*, observed year; *t*-1, lagged 1 yr before observed year; A, average of the no. of years indicated before the observed year.

Discussion

Of the climate factors we examined in this study, those related to seasonal temperatures and drought were found to be important for predicting historic spruce beetle outbreaks. These factors are consistent with existing explanations of climate/spruce beetle associations and provide further insight into spruce beetle dynamics.

The role of temperature in regulating the birth and death rates of spruce beetles and influencing their developmental processes has long been recognized (Schmid and Frye 1977). The selection of mean December temperature for classifying outbreak and nonoutbreak years in this study is perhaps most relevant with respect to brood survival during winter months. As with other bark beetle species, the survival of overwintering spruce beetles is closely related to winter temperatures with death occurring below critical thresholds (Johnson 1967, Furniss and Orr 1978, Cole 1981, Amman 1984, Safranyik 1990, Bentz et al. 1991, Bentz and Mullins 1999, Gan 2003). Although spruce beetles, particularly larval life stages, can tolerate temperatures down to −34°C, significant spruce beetle mortality has been associated with extreme cold (Massey and Wygant 1954). Wygant (1956) indicated that the White River outbreak in Colorado finally collapsed as a result of extremely low temperatures (−49°C) during the winter of 1951 that killed ≈75% of the overwintering larvae. Forty-two percent of spruce beetles were killed by record cold temperatures in Idaho and Montana during the winter of 1953–1954, and in 1971, on the Fort Apache Indian Reservation, AZ, 1 wk of low temperatures near −40°C resulted in 88% brood reduction (Frye et al. 1974).

Mild winter conditions tend to favor spruce beetle survival, particularly during years with relatively low snow covers that typically insulate more vulnerable life stages, such as hibernating adults (Massey and Wygant 1954, Knight 1961). All outbreak years had mean December temperatures ≈3°C higher than the model splitting value of −5.5°C, suggesting that relatively warm seasonal temperatures characterized these years. Approximately 70% of nonoutbreak years also had mean December temperatures that exceeded the splitting value for this variable. Mean comparison tests, however, indicated that mean December temperatures during outbreak years were significantly warmer than nonoutbreak years. Conversely, 30% of nonoutbreak years were relatively cold, with mean December temperatures less than or equal to −5.5°C. Visual examination of the climate data showed that, in some nonoutbreak years, mean December temperatures were extremely low. For example, mean winter temperatures in 1910, 1917, 1929, 1933, 1937, 1949, and 1973 throughout the study area ranged from −11 to −8.3°C. Conceivably, spruce beetle mortality resulting from extremely cold periods during these years would decrease the potential for outbreak.

Periods characterized by warm late summer and fall temperatures were also associated with outbreak years in our study. Mean September temperatures during the year before all outbreak years were higher than the model splitting value of 12.8°C. This climate factor and its surrogate variables (mean August temperatures averaged over 3 yr before outbreak years and mean September temperatures averaged over 5 yr before outbreak years) were also 2 to 3°C warmer than the mean August and September temperatures of years making up nonoutbreak periods. The significance of this result relates to temperature influences on the duration of spruce beetle development and consequently the population dynamics of the insect.

Initial studies of spruce beetle development indicated that cold temperatures generally retard larval growth (Dyer 1969). However, the majority of spruce beetle broods subject to a constant temperature regimen of 21.1°C reached pupal and teneral adult stages without interruption after an accumulation of 1,050 DD above the developmental temperature threshold of 6.1°C (Dyer and Hall 1977). Warm fall temperatures were also found to delay diapause, allowing for the development of univoltine broods (Dyer 1969).

Werner and Holsten (1985) subsequently observed a preponderance of univoltine beetles in the sun-exposed aspects of downed spruce and trees in south-facing stands on the Kenai Peninsula in Alaska. Further study indicated that direct solar heating raising phloem temperatures to a threshold of 16.5°C during the development of early-instar larvae allowed beetles to complete a 1-yr life cycle (Werner and Holsten 1985). Temperature-based voltinism models developed by Hansen et al. (2001a) suggested that cumulative air-temperature hours above 17°C, elapsed from 40 to 90 d after peak flight (roughly July through September), best estimated the proportion of univoltine versus semivoltine spruce beetle broods. The splitting value (16.8°C) of mean August temperatures averaged over 3 yr before outbreaks in this study corresponds to these critical temperature thresholds found to be important for the development of univoltine broods.

The development of univoltine populations during unusually warm summers is thought to have contributed to the intensification and expansion of spruce

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beetle populations in Alaska and western states during recent years (Werner and Holsten 1985, Reynolds and Holsten 1994, Hansen et al. 2001a, Snyder 2006). Our results suggest that univoltine populations possibly had a role in the development of the historic spruce beetle outbreaks we studied as well.

A large proportion (77%) of nonbreak years also had mean August and September temperatures exceeding the model splitting values. This result suggests that warm summer and fall temperatures are necessary, but not sufficient, for outbreak occurrence. However, 23% of the nonoutbreak years had relatively cool mean September temperatures and generally low fall temperatures. The slower rates of spruce beetle development under these conditions would initiate prepupal diapause, limiting the opportunity for rapid population growth and the initiation of outbreaks.

The CART analysis also indicated that drought may have served as a predisposing factor to historic spruce beetle outbreaks. Hopkins (1909) generally dismissed the importance of drought for western bark beetle species, concluding that dry conditions were unfavorable for infestation by the insects. Subsequent studies, however, indicated that environmental stresses on trees, such as drought, have an important role in the dynamics of bark beetle outbreaks (Blackman 1924, Craighead 1925, Beal 1927, Hopping and Mathers 1950, Hall 1958, Mattson and Haack 1987, Lorio et al. 1995, Paine et al. 1997, Gan 2003, Breshears et al. 2005, Shaw et al. 2005). Bark beetles are attracted to weakened trees and can overcome compromised host defense mechanisms with mass attacks (Paine et al. 1997).

Ninety-five percent of outbreak years in the third split had mean estimated PDSI values that averaged $\leq$0.328 during the 5 yr before outbreak, suggesting that trees had been subject to a prolonged period of below normal precipitation. The 5-yr average of mean estimated PDSI values for 39% of the remaining nonoutbreak years in this split were also $\leq$0.328. In general, however, the mean estimated PDSI values during the 5 yr before outbreaks were on average significantly lower than those of nonbreak years.

Visual examination of mean precipitation and temperature data also showed that generally warm fall and winter temperatures, climate factors associated with outbreak years, occurred in conjunction with dry fall and winter conditions. Conversely, above average winter precipitation occurred during 70% of nonoutbreak years that were characterized by cooler winter temperatures. These observations are consistent with winter climate patterns observed in the intermountain region where precipitation is typically associated with below average temperatures (Jensen et al. 1990).

Warm winter temperatures associated with dry conditions can cause excessive transpiration from tree foliage. Because water remains frozen in the soil, the tree receives no compensation for water loss from the ground, resulting in the desiccation of tree tissues and water stress (Miller 1970, Grier 1988). The rate of desiccation increases with drying winds and insufficient snow cover to insulate the ground (Miller 1970, Grier 1988). In Montana, Gibson (1992) observed large numbers of Douglas-firs and white pines (*Pinus monticola* Doug. Ex D. Don) attacked by mountain pine beetles, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), after severe drought during the winter of 1991–1992.

In the final split, three quarters of the remaining nonoutbreak years and all remaining outbreak years had mean October precipitation $>$1.33 cm. Differences in mean October precipitation between outbreak and nonoutbreak years were not significant. The lack of moisture during this month, however, was associated with 26% of the remaining nonoutbreak years. Precipitation during these years was on average 2 cm less than the mean October precipitation (3.3 cm). The majority of remaining nonoutbreak years (74%) with October precipitation $\leq$1.33 cm were also characterized by above average October temperatures, with some years having mean temperatures $>$3°C above normal.

While bark beetles may preferentially attack drought-stressed trees, excessively dry conditions may accelerate the deterioration of host material limiting brood success. Cole (1975) found that excessive drying of infested lodgepole pine was an important factor causing mountain pine beetle populations to return to endemic levels. Dry phloem deprived larvae of necessary moisture causing them to cease feeding, shrivel, and die (Cole 1975). Amman (1977) observed that these effects were usually more pronounced in small diameter trees. These observations indicate that, whereas drought may generally contribute to outbreaks, unusually dry fall conditions may serve to inhibit them.

Other sources of variation not integrated in the CART analysis likely prohibited obtaining higher classification probabilities and greater model correlations. In addition to the climate factors identified above, factors including stand attributes, such as structure, composition, and age have a strong influence on spruce beetle epidemiology (Lister et al. 1976, Schmid and Frye 1976, Werner et al. 1977, Schmid 1981, Jenkins et al. 1998, Holsten et al. 1999, Doak 2004, Hebertson and Jenkins 2007). Local weather patterns can either enhance or inhibit population growth affecting spruce beetle risk or the probability of infestation (Samman and Logan 2000). At high elevations, colder, wet conditions contribute to greater bark beetle mortality during dispersal and lower rates of bark beetle colonization than at low elevation sites (Johnson 1967). Predation and parasitism of all life stages can also limit population growth, decreasing spruce beetle risk (Schmid and Frye 1977).

Furthermore, the majority of historic reports did not provide reliable dates when major spruce beetle outbreaks were first initiated. The 19th century spruce beetle outbreaks, for example, were not detected until extensive bark beetle surveys were conducted in the early 1900s (Hopkins 1909). The few historic records of early spruce beetle outbreaks prevented the development of a long-term outbreak chronology. The number of documented outbreaks seemed to increase during the 1940s with the use of aerial detection sur-

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veys. Interestingly, this observation was supported by an alternate CART model, which selected the year of 1949 as a highly significant explanatory variable. An incomplete chronology might have resulted in an unrealistically disproportionate number of nonoutbreak years versus outbreak years, making meaningful associations difficult to detect. Finally, spruce beetle outbreaks occurring near the turn of the last century also were not included in this analysis because of the lack of corresponding climate data for those years. A greater number of cases could have improved estimates of spruce beetle outbreak probabilities.

Our results substantiate present understanding of climate and spruce beetle associations and provide further insight into those climate factors related to historic spruce beetle outbreaks. Additionally, these findings may have greater relevance considering predicted climate change. Increased winter survival and spruce beetle development rates, resulting from warmer temperatures, may in turn increase spruce beetle risk and the potential for outbreak. Recent models of bark beetle population dynamics under predicted climate change scenarios support this assertion (Logan and Powell 2001, Williams and Liebold 2002, Carroll et al. 2003, Gan 2003, Breshears et al. 2005).

A shift in the distribution of plant species toward higher latitudes and higher elevations might also occur with predicted temperature increases (Williams and Liebold 2002, Logan et al. 2003, Littell and Peterson 2005). Even small shifts in climate may have profound consequences on the structure and function of subalpine forests, given the complex interactions between vegetation and energy flow, water availability, temperature regimens, and disturbances that are controlled in part by climate (Covington et al. 1994, Zolbrod and Peterson 1999). One consequence of concern is the extirpation of Engelmann spruce over broad regions with losses exacerbated by prolonged drought and increased risk of spruce beetle infestations (Berg 1999, Rehfeldt 2004).

In summary, our results are unique in relating specific climate factors to historic spruce beetle outbreaks in portions of Utah and Colorado. Classification and regression tree analysis indicated that historic outbreak years in the intermountain region were related to generally warm fall and winter temperatures and drought. This finding is consistent with climate factors known to influence spruce beetle brood success, development, life cycle duration, population dynamics, and host relationships. Unexplained variability in the data likely prohibited obtaining higher model correlations. The inclusion of finer scale historic climate data (i.e., mean daily and minimum/maximum values for temperature and precipitation, monthly PDSI values), the development of longer, more reliable historic spruce beetle outbreak chronologies, and information to characterize site and historic stand attributes would help improve the reliability of model estimates.

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Appendix 1. Chronology of historic spruce beetle outbreaks in other western states

Year	Outbreak	State	Source
≈1860s	White Mountains, Lincoln NF	New Mexico	Schmid and Frye 1977
≈1890s	Lincoln NF, Sierra Blanca	New Mexico	Lessard 1976
1904	White Mountains	New Mexico	Lessard 1976
1925–1930	Lincoln NF, Sacramento RD	New Mexico	Lessard 1976
Mid-1930s	Santa Fe NF, Pecos and Las Vegas RD	New Mexico	Lessard 1976
1946	Carson NF	New Mexico	Lessard 1976
1946	Santa Fe NF, Pecos RD	New Mexico	Lessard 1976
1948	White Mountains	New Mexico	Bennett 1954; Lessard 1976
Early 1950s	Carson NF, Tres Piedras RD	New Mexico	Lessard 1976
Early 1950s	Coronado NF, Mt. Graham, Safford RD	Arizona	Lessard 1976
1952	Northern Idaho, Western MT	Idaho, MT	Terrell 1952; Anonymous 1956
1953	Coconino NF, San Fran Peaks	Arizona	Lessard 1976
1960	Santa Fe NF, Pecos Wilderness	New Mexico	Lessard 1976
1962	Santa Fe NF, Pecos and Las Vegas RD, Elk Mt	New Mexico	Lessard 1976
1963	Cibola NF, Mt. Taylor	New Mexico	Lessard 1976
1966	Coconino NF, Agassiz Peak	Arizona	Lessard 1976
1966	Santa Fe NF, Pecos Wilderness, Lake Johnson	New Mexico	Lessard 1976
1967	Apache- Sitgreaves NF, Escudilla Mountain, Alpine RD	Arizona	Germain 1972 Lessard 1976
1967	Flathead NF, Glacier View RD	Montana	McGregor and Honing 1970
1968	Coconino NF, Agassiz Peak	Arizona	Lessard 1976
1968	Santa Fe NF	New Mexico	Lessard 1976; Schmid and Frye 1976
1968	Santa Fe NF, Rito drainage, Cuba RD	New Mexico	Lessard 1976
1968	Coronado NF, Webb Peak Lookout	Arizona	Lessard 1976
1969	Lincoln NF, Sierra Blanca	New Mexico	Lessard 1976
1971	Santa Fe NF, Cuba RD, Jemez Mts. Wilderness, Lake Johnson	New Mexico	Lessard 1976; Acciavatti 1977
Early 1970s	Encampment	Wyoming	Schmid and Frye 1977
1973	Coconino NF, Dunham Canyon, Inner Basin	Arizona	Lessard 1976
1974	Coconino NF, Snow Bowl	Arizona	Lessard 1976
1975	Santa Fe NF, Cuba RD, Jemez Mts.	New Mexico	Acciavatti 1975
1981	Panhandle NF, Bonners Ferry RD	Montana	Gibson and Oakes 1981
1981	Fort Apache IR	Arizona	Linnane 1985
1981	Glacier NP	Montana	Eglitis et al. 1982

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