

Modeling the Interactive Effects of Spruce Beetle Infestation and Climate on Subalpine Vegetation

Adrianna C. Foster, Jacquelyn K. Shuman, Herman H. Shugart, and Jose Negron

Supplementary Material

Species Parameter Table

Species Name	AGE _{max}	DBH _{max} (cm)	H _{max} (m)	s	g	ρ_w^*	l_c^\dagger	DD _{min} [‡]	DD _{opt} [‡]	DD _{max} [‡]	shade	drought	nutrient
<i>Abies lasiocarpa</i>	250	61	30	1.03	1.041	0.43	0.5	200	500	1665	1	5	3
<i>Juniperus scopulorum</i>	300	43	15	0.69	0.455	0.46	0.5	800	1900	3200	4	1	1
<i>Picea engelmannii</i>	500	95	40	1	0.689	0.45	0.5	250	600	1665	2	4	1
<i>Picea pungens</i>	600	150	38	0.52	0.55	0.45	0.5	600	1550	2300	3	3	3
<i>Pinus contorta</i>	400	46	27	0.58	1.19	0.45	0.5	450	900	2500	4	3	1
<i>Pinus edulis</i>	400	46	10.7	0.46	0.256	0.45	0.5	800	1900	3200	5	2	1
<i>Pinus ponderosa</i>	600	127	40	0.56	0.579	0.45	0.5	800	1600	2500	3	3	1
<i>Pinus flexilis</i>	900	90	15	0.33	0.157	0.46	0.5	300	1600	3000	3	3	3
<i>Populus tremuloides</i>	200	75	22	0.61	0.986	0.42	0.316	350	1500	2200	5	3	2
<i>Populus angustifolia</i>	200	76	18	0.47	0.82	0.42	0.316	600	1550	2500	5	5	2
<i>Pseudotsuga menziesii</i>	400	152	49	0.66	1.054	0.48	0.5	700	1400	2300	3	3	1

Table S1. Relevant parameter input for the eleven species used in UVAFME simulations. AGE_{max} , DBH_{max} , and H_{max} are the species-specific maximum age (yr), diameter at breast height (cm), and height (m); s and g are growth parameters; ρ_w is the wood bulk density (tonnes m⁻³); l_c is the specific leaf area ratio (tonnes C ha⁻¹); DD_{min} , DD_{opt} , and DD_{max} , are the minimum, optimum, and maximum growing degree days for the species; $shade$ is the relative shade tolerance of the species, from 1 to 5, 5 being the least tolerant; $drought$ is the relative drought tolerance of the species, from 1 to 6, 6 being the least tolerant; $nutrient$ is the relative nutrient availability tolerance of the species, from 1 to 3, 3 being the least tolerant. All parameter inputs are derived from information in Burns & Honkala (1990) unless otherwise denoted with a superscript (*: wood bulk density derived from USFS Western Core Table Reports; †: specific leaf area ratios derived from default model values; ‡: minimum, maximum, and optimum GDD values are derived from environmental lapse rates derived from climate data.

Species parameter table continued

Species Name	b_{thick}^{\S}	fire regen	stress	old	invader	seed	NDE	NDS
<i>Abies lasiocarpa</i>	0.015	6	2	1	1	1	0.6	0.6
<i>Juniperus scopulorum</i>	0.015	4	2	1	1	1	0.5	0.5
<i>Picea engelmannii</i>	0.022	5	1	1	1	1	0.8	0.8
<i>Picea pungens</i>	0.022	3	3	1	1	1	0.5	0.5
<i>Pinus contorta</i>	0.055	1	1	1	0.5	1	0.7	0.7
<i>Pinus edulis</i>	0.03	3	2	1	0.5	1	0.6	0.6
<i>Pinus ponderosa</i>	0.063	1	2	1	1	1	0.8	0.8
<i>Pinus flexilis</i>	0.03	2	1	1	0.5	1	0.56	0.5
<i>Populus tremuloides</i>	0.014	1	4	2	1	100	0.78	0.31
<i>Populus angustifolia</i>	0.014	3	3	1	1	100	0.78	0.31
<i>Pseudotsuga menziesii</i>	0.063	2	2	2	1	1	0.7	0.7

Table S1 Continued. Relevant parameter input for the eleven species used in UVAFME simulations. b_{thick} is the bark thickness parameter (cm bark cm DBH⁻¹); *fire regen* is the relative response of regeneration to fire, from 1 to 6, 6 being the least tolerant; *stress* is the relative stress tolerance of the species, from 1 to 5, 5 being the least tolerant; *old* is the likelihood of that species surviving to its maximum age, from 1 to 3, 3 being the lowest probability; *invader* is the probability of seeds “invading” from nearby locations, with wind-dispersed seeds generally having a probability of 1; *seed* is the seed numbers from inside the plot, and is related to seed and dispersal type (i.e. cones = 1, samaras/maple keys = 10, wind-dispersed = 100); *NDE* is the coefficient for annual reduction of the seed bank, 0 to 1; and *NDS* is the coefficient for annual reduction of seedlings, 0 to 1. All parameter inputs are derived from information in Burns & Honkala (1990) unless otherwise denoted with a superscript (§: bark thickness coefficients adapted from Keane et al. (2011); ||: seed and seedling-bank reduction values adapted from genus-level parameters in Shugart et al. (1992), guided by species-level information in Burns & Honkala (1990)).

Spruce beetle submodel

Climate factors for this submodel were derived from studies on the phenology of spruce beetles and what influences their shift from a semivoltine to a univoltine life cycle (Hansen et al. 2001, Sherriff et al. 2011, Hansen et al. 2011). Based on a detailed spruce beetle phenology study by Hansen et al. (2001), calculations were included to determine whether the beetle population on each plot has a semivoltine (two-year) or univoltine (one-year) life cycle. This calculation is based on the cumulative hours above 17°C during the period of 40 to 90 days prior to the beetles' peak flight. Peak flight is set to June 10 based on Dyer (1975) and Schmid and Frye (1977). In order to calculate cumulative hours, modeled daily minimum (T_{min} , °C) and maximum (T_{max} , °C) temperatures are converted into hourly temperatures via a sinusoidal formula from Reicosky et al. (1989). This formulation is based on inputs of daily minimum and maximum temperatures as well as sunrise time. Daily temperatures are derived from input distributions of mean monthly minimum and maximum temperatures (see the UVAFME User's Manual; Foster et al. 2017 for further information). Hourly temperature (T_H , °C) is calculated as:

$$T_H = \begin{cases} T_{av} + \left(\frac{T_{max} - T_{min}}{2} \right) \cos \left(\frac{\pi H'}{10.0 + H_{rise}} \right), & 0 \leq H < H_{rise} \text{ and } 14 < H \leq 24 \\ T_{av} - \left(\frac{T_{max} - T_{min}}{2} \right) \cos \left(\frac{\pi(H - H_{rise})}{14.0 - H_{rise}} \right), & H_{rise} \leq H \leq 14 \end{cases} \quad (S1)$$

where T_{av} is average daily temperature, defined as $T_{av} = (T_{max} + T_{min})/2$, H_{rise} is the hour of sunrise, and H' is defined as $H' = H + 10$ when $H < H_{rise}$, and $H' = H + 14$ when $H > 14$ (Fig. S1). This equation is then used to accumulate the number of hours above 17°C (H_{17}) during 40 to 90 days prior to peak spruce beetle flight, defined as March 12 through May 1 in these simulations. Cumulative hours above 17°C is equal across all plots within an individual site, but may change from year to year and from site to site. The probability of any one plot having

beetles with a univoltine life cycle (p_{uv} ; Eq. S2, S3), from Hansen et al. (2001), is then calculated and is used to influence the infestation probability of each individual tree on that plot.

$$L_{H_{17}} = -3.954 + 0.01944H_{17} \quad (S2)$$

$$p_{uv} = \frac{1.0}{1.0 + e^{-L_{H_{17}}}} \quad (S3)$$

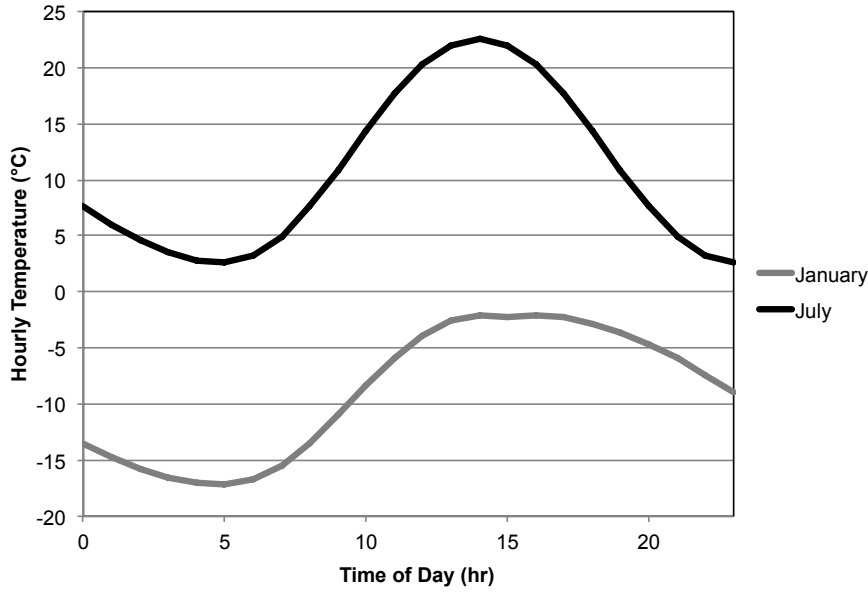


Figure S1. Example of hourly temperature calculated based on Equation S1 for a typical day in January ($T_{min} = -17.22$, $T_{max} = -2.14$) and July ($T_{min} = 2.63$, $T_{max} = 22.63$) in the southern Rocky Mountains.

Plot-level factors are calculated each year based on individual plot characteristics, and thus will vary between the simulated plots at a given site. These plot-level factors are based on spruce beetle susceptibility stand ratings from Schmid and Frye (1976). As in their stand rating system, this model uses average DBH of live spruce above 25.4 cm DBH, plot-level spruce basal area, and percent of spruce in the canopy as factors for determining plot-wide susceptibility to spruce beetle attacks. Depending on the value of each of the three factors, each plot receives three factor ratings from 1 to 3 (Table S2), and the ratings from each individual factor are added together to produce an overall stand rating (possible values being 3 to 9). The overall stand rating

is then used to calculate the probability for spruce beetle infestation in each tree due solely to plot characteristics (f_{stand} , 0 to 1; Eq. S4). This stand-level probability is utilized to calculate the individual-tree infestation probability (Eq. S7) and is the same for every tree on the same plot in a given year.

$$f_{stand} = 0.75 \ln(f_{DBH} + f_{BA} + f_{can}) - 0.8 \quad (S4)$$

This overall stand rating is then modified based on recent windthrow events to account for the high influence of blowdown on bark beetle outbreaks (Christiansen et al. 1987, Wichmann and Ravn 2001, Mezei et al. 2014). Following a windthrow event, the overall stand infestation probability is increased by 0.3 for the first three years, 0.2 from four to six

Table S2. Values of plot factors associated with each factor rating used to calculate overall plot-wide probability of spruce beetle infestation (from Schmid and Frye 1976).

Susceptibility Rating	Plot Factor Value		
	Basal area of stand ($\text{m}^2 \text{ ha}^{-1}$)	Mean DBH of live Engelmann spruce over 24.5 cm DBH (cm)	Percent Engelmann spruce in canopy (%)
Low (1)	< 22.95	< 30.48	< 50.0
Medium (2)	22.95 to 34.43	30.48 to 40.64	50.0 to 65.0
High (3)	≥ 34.43	≥ 40.64	≥ 65.0

years, and 0.1 from five to nine years. Because spruce beetle populations can utilize downed spruce trees (from windthrow or other mortality factors) for reproduction at low levels (Schmid and Frye 1977), plot-wide susceptibility is also influenced based on the amount of coarse woody debris on the plot available for spruce beetle colonization. Spruce trees larger than 25.4 cm DBH that die from either windthrow, age, or low growth are added to a pool of coarse woody debris (CWD_{spruce} , tonnes C ha^{-1}). A plot-wide woody debris factor (f_{CWD} , 0 to 1) is then calculated, which increases linearly with increasing spruce woody debris:

$$f_{CWD} = \min\left(\left(\frac{CWD_{spruce}}{CWD_{base}}\right), 1.0\right) \quad (S5)$$

where CWD_{base} is set to 300 tonnes C ha⁻¹, corresponding to the potential coarse woody debris that may occur from a very severe windthrow event, as in Temperli et al. (2013).

Tree-level factors that affect the probability of spruce beetle infestation include individual tree size (f_{tDBH}), stress level (f_{stress}), and scorch volume of recent fires (f_{scorch}). Under normal conditions, trees that are smaller than 30 cm DBH are not susceptible to spruce beetle attack (DeRose and Long 2012). Under epidemic conditions (i.e. greater than 10 m² ha⁻¹ of basal area killed per year) trees as small as 10 cm DBH may be killed by spruce beetles (Peet 1981, Veblen et al. 1994, DeRose and Long 2012). Otherwise, based on information from relevant literature on bark beetle infestations (Furniss et al. 1979, Negron 1998, Hood and Bentz 2007, Zolubas et al. 2009, Mezei et al. 2014) and inventory data from the US Forest Service, infestation probability due to tree size (f_{tDBH} , 0 to 1) increases linearly with increasing tree diameter (Eq. S6).

$$f_{tDBH} = \min(0.011DBH_{tree}, 1.0) \quad (S6)$$

Many studies have shown that prolonged stress and associated low tree vigor, due to drought, age, or other factors, increases a tree's susceptibility to bark beetle attacks (Kalkstein 1976; Waring and Pitman 1980; Larsson et al. 1983; Christiansen et al. 1987; Mattson and Haack 1987; Malmstrom and Raffa 2000; McKenzie et al. 2009; Hart et al. 2014a). In this model, tree stress is quantified as prolonged low diameter increment growth (i.e. less than 0.03 cm per year). Probability of spruce beetle infestation due to stress level (f_{stress} , 0 to 1) increases by 0.1 each year the tree in question has diameter growth below 0.03 cm, and is reset to 0 if the tree has higher than 0.03 cm growth in any given year. Damage due to fire has also been cited as a potential precursor to bark beetle attack (Geiszler et al. 1984, Christiansen et al. 1987, Rasmussen et al. 1996, Hood and Bentz 2007). UVAFME calculates fire damage by percent

crown volume scorched (CK , %) based on fire dynamics equations from Keane et al. (2011) and Van Wagner (1973). In this spruce beetle model, susceptibility to beetle infestation based on fire damage (f_{scorch} , 0 to 1) is equal to the percent crown volume scorched from fires. While most fires in the southern Rocky Mountains subalpine zone are stand-replacing, and thus would not leave any surviving trees (Shoennagel et al. 2004), if a low severity fire did occur, in this region or another region of application, we would be able to capture the increased susceptibility to beetle attack. This increased beetle susceptibility follow fire scorching allows for more complete fire-insect-vegetation interactions within the model, both under the current subalpine fire regime (i.e. mostly stand-replacing, with possibility of lower-severity fires), as well as in the face of potential changes to fire frequency and intensity. Future studies which use this spruce beetle model could force or predict climate-induced fire regime shifts, and in turn the response of beetle infestations and tree mortality.

As with the individual plot-level factors, these tree-level factors are combined, along with the overall plot-wide factors, to produce an overall tree-level susceptibility to spruce beetles (f_{tree} , 0 to 1; Eq. S7).

$$f_{tree} = \min((0.3f_{stand} + 0.25f_{tDBH} + 0.2f_{stress} + 0.1f_{scorch} + 0.4f_{CWD}), 1.0) \quad (S7)$$

Coefficients associated with each susceptibility factor are based on susceptibility ratings from relevant literature (Schmid and Frye 1976; Seidl et al. 2007; Hart et al. 2014b). This susceptibility is used to calculate the final tree-level probability for spruce beetle infestation (Eq. S8, Fig. S2):

$$p_{beetle} = 1.0 - e^{(-2.0f_{tree}^{1.3})^{gen}} \quad (S8)$$

where gen is equal to 1.8 if the plot in question has univoltine beetles (based on uniform random draws with the probability for univoltinism (p_{uv}); Eq. S3) and 0.5 if it does not. Equation S8 was adapted from a bark beetle modeling study by Seidl et al. (2007) on the European spruce bark beetle in Norway spruce forests.

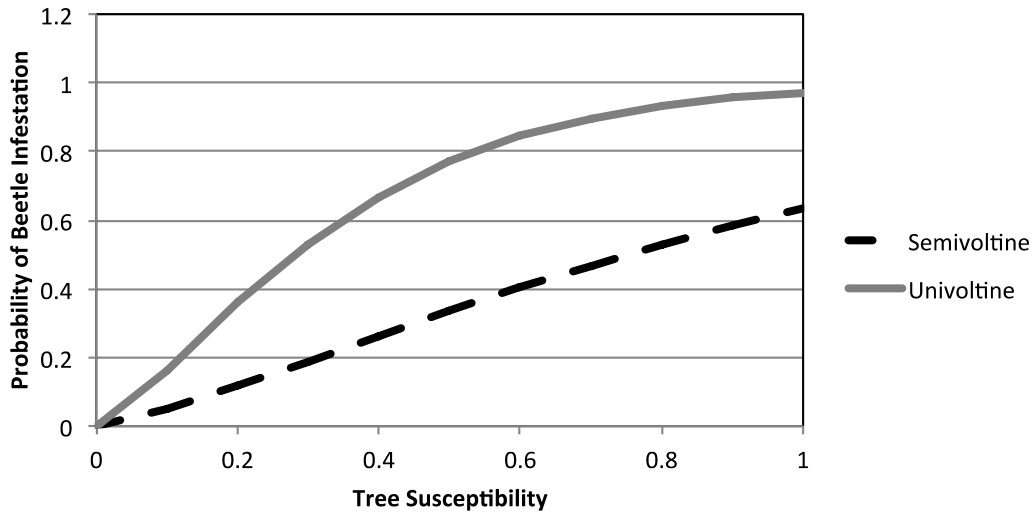


Figure S2. Probability of beetle infestation (p_{beetle}) increases with increasing tree susceptibility (f_{tree}) and with the presence of univoltine beetles (Eq. S8).

Once a tree becomes infested in this spruce beetle submodel, it ceases growth (Frank et al. 2014), and loses its needles after two years (Schmid and Frye 1977). Finally, after five years of being infested, the tree is marked as dead and is added to the soil layers for decomposition. A study by Hart et al. (2014b) found that proximity to infested spruce trees was an important factor in determining infestation probability. Thus, within this spruce beetle submodel, during the time when a tree is infested and still on a plot it increases the infestation probability of directly (by 0.3) and diagonally (by 0.1) adjacent spruce trees on the same plot. The addition of this proximity effect required the tracking of the x and y location of each simulated tree. The x/y locations of trees on each plot were set up as a 30x30 grid in order to maintain a similar number of maximum allowable trees per plot as in the non-gridded version of UVAFME. Upon

establishment, a tree is randomly assigned an x and y location not currently occupied by another tree. Thus, we currently maintain the assumption of horizontal homogeneity in resource availability and seed dispersal within a plot.

References

- Burns, R. M., and B. H. Honkala. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. Agricultural Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC. vol. 2 877 p.
- Christiansen, E., Waring, R.H., and Berryman, A.A. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *For. Ecol. Manag.* **22**: 89–106.
- DeRose, R.J., and Long, J.N. 2012. Factors Influencing the Spatial and Temporal Dynamics of Engelmann Spruce Mortality during a Spruce Beetle Outbreak on the Markagunt Plateau, Utah. *For. Sci.* **58**(1): 1–14. doi:10.5849/forsci.10-079.
- Dyer, E.D.A. 1975. Frontalin attractant in stands infested by the spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Scolytidae). *Can. Entomol.* **107**(9): 979–988.
- Frank, J.M., Massman, W.J., Ewers, B.E., Huckaby, L.S., and Negrón, J.F. 2014. Ecosystem CO₂/H₂O fluxes are explained by hydraulically limited gas exchange during tree mortality from spruce bark beetles: CO₂/H₂O FLUX EXPLAINED FROM DISTURBANCE. *J. Geophys. Res. Biogeosciences* **119**(6): 1195–1215. doi:10.1002/2013JG002597.
- Furniss, M.M., McGregor, M.D., Foiles, M.W., and Partridge, A.D. 1979. Chronology and characteristics of a Douglas-fir beetle outbreak in northern Idaho. USDA Forest Service General Technical Report INT-59. Intermt. For. Range Exp. Stn. Ogden UT: 19.
- Geiszler, D.R., Gara, D.R., and Littke, W.R. 1984. Bark beetle infestations of lodgepole pine following a fire in south central Oregon. *Zitschrift Angew. Entomol.* **98**(1–5): 389–394.
- Hansen, E.M., Bentz, B.J., Powell, J.A., Gray, D.R., and Vandygriff, J.C. 2011. Prepupal diapause and instar IV developmental rates of the spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). *J. Insect Physiol.* **57**(10): 1347–1357. doi:10.1016/j.jinsphys.2011.06.011.
- Hansen, E.M., Bentz, B.J., and Turner, D.L. 2001. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *Can. Entomol.* **133**(6): 827–841.
- Hart, S.J., Veblen, T.T., Eisenhart, K.S., Jarvis, D., and Kulakowski, D. 2014a. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* **95**: 930–939.
- Hart, S.J., Veblen, T.T., and Kulakowski, D. 2014b. Do tree and stand-level attributes determine susceptibility of spruce-fir forests to spruce beetle outbreak in the early 21st century? *For. Ecol. Manag.* **318**: 44–53.
- Hood, S., and Bentz, B. 2007. Predicting postfire Douglas-fir beetle attacks and tree mortality in the northern Rocky Mountains. *Can. J. For. Res.* **37**: 1058–1069.
- Kalkstein, L.S. 1976. Effects of climatic stress upon outbreaks of the southern pine beetle. *Environ. Entomol.* **5**: 653–658.
- Keane, R.E., Loehman, R.A., and Holsinger, L.M. 2011. The FireBGCv2 Landscape Fire Succession Model: A research simulation platform for exploring fire and vegetation dynamics. USDA For. Serv. Gen. Tech. Rep. **RMRS-GTR-55**: 145.
- Larsson, S., Oren, R., Waring, R.H., and Barrett, J.W. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *For. Sci.* **29**(2): 395–402.
- Malmstrom, C.M., and Raffa, K.F. 2000. Biotic disturbance agents in the boreal forest: considerations for vegetation change models. *Glob. Change Biol.* **6**: 35–48.
- Mattson, W.J., and Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects.

- Bioscience **37**: 110–118.
- McKenzie, D., Peterson, D.L., and Littell, J.J. 2009. Chapter 15 Global Warming and Stress Complexes in Forests of Western North America. *In* Developments in Environmental Science. Elsevier. pp. 319–337. Available from <http://linkinghub.elsevier.com/retrieve/pii/S1474817708000156> [accessed 22 October 2015].
- Mezei, P., Grodzki, W., Blazenec, M., Skvarenina, J., Brandysova, V., and Jakus, R. 2014. Host and site factors affecting tree mortality caused by the spruce bark beetle (*Ips typographus*) in mountainous conditions. *For. Ecol. Manag.* **331**: 196–207.
- Negron, J. 1998. Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. *For. Ecol. Manag.* **107**: 71–85.
- Peet, R.K. 1981. Forest vegetation of the Colorado front range. *Vegetatio* **45**(1): 3–75.
- Rasmussen, L.A., Amman, G.D., Vandygriff, J.C., Oakes, R.D., Munson, A.S., and Gibson, K.E. 1996. Bark beetle and wood borer infestation in the greater Yellowstone area during four postfire years. USDA For. Serv. Res. Pap. INT-RP-487 Intermt. Res. Stn. Ogden UT.
- Reicosky, D.C., Winkelman, L.J., Baker, J.M., and Baker, D.G. 1989. Accuracy of hourly air temperatures calculated from daily minima and maxima. *Agric. For. Meteorol.* **46**: 193–209.
- Schmid, J.M., and Frye, R.H. 1976. Stand ratings for spruce beetles. US Dept. of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. Available from http://books.google.com/books?hl=en&lr=&id=pddZMOAdeW0C&oi=fnd&dq=%22where+subalpine+fir+is+a+stand%22+%22of+trees+before+action+was+initiated.%22+%22ago,+it+is+unsatisfactory+today.+The+nation%22+%22Forester,+San+Juan+National+Forest,+Pagosa%22+&ots=183r56z_Ug&sig=EER5jRHMfNU2EEC360azYP6XzLo [accessed 23 October 2015].
- Schmid, J.M., and Frye, R.H. 1977. Spruce beetle in the Rockies. Available from <http://digitalcommons.usu.edu/barkbeetles/86/> [accessed 20 October 2015].
- Seidl, R., Baier, P., Rammer, W., Schopf, A., and Lexer, M.J. 2007. Modelling tree mortality by bark beetle infestation in Norway spruce forests. *Ecol. Model.* **206**(3–4): 383–399.
- Sherriff, R.L., Berg, E.E., and Miller, A.E. 2011. Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. *Ecology* **92**(7): 1459–1470.
- Shoennagel, T., Veblen, T.T., and Romme, W.H. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience* **54**(7): 661–676.
- Shugart, H. H., R. Leemans, and G. B. Bonan. 1992. A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, UK.
- Temperli, C., H. Bugmann, and C. Elkin. 2013. Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach. *Ecological Monographs* **83**:383–402.
- Van Wagner, C.E. 1973. Height of crown scorch in forest fires. *Can. J. For. Res.* **3**: 373–378.
- Veblen, T.T., Hadley, K.S., Nel, E.M., Kitzberger, T., Reid, M., and Villalba, R. 1994. Disturbance Regime and Disturbance Interactions in a Rocky Mountain Subalpine Forest. *J. Ecol.* **82**(1): 125. doi:10.2307/2261392.
- Waring, R.H., and Pitman, G.B. 1980. A simple model of host resistance to bark beetles. Oregon State University, School of Forestry, Corvallis, OR.
- Wichmann, L., and Ravn, H.P. 2001. The spread of *Ips typographus* (L.)(Coleoptera, Scolytidae)

attacks following heavy windthrow in Denmark, analysed using GIS. *For. Ecol. Manag.* **148**(1): 31–39.

Zolubas, P., Negron, J., and Munson, A.S. 2009. Modelling spruce bark beetle infestation probability. *Balt. For.* **15**(1): 23–27.