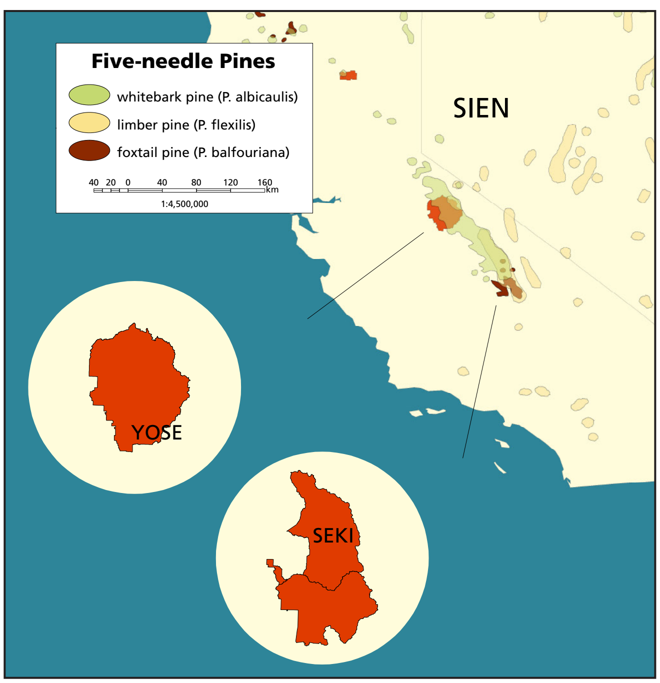
High Elevation Five-Needle Pine Forests

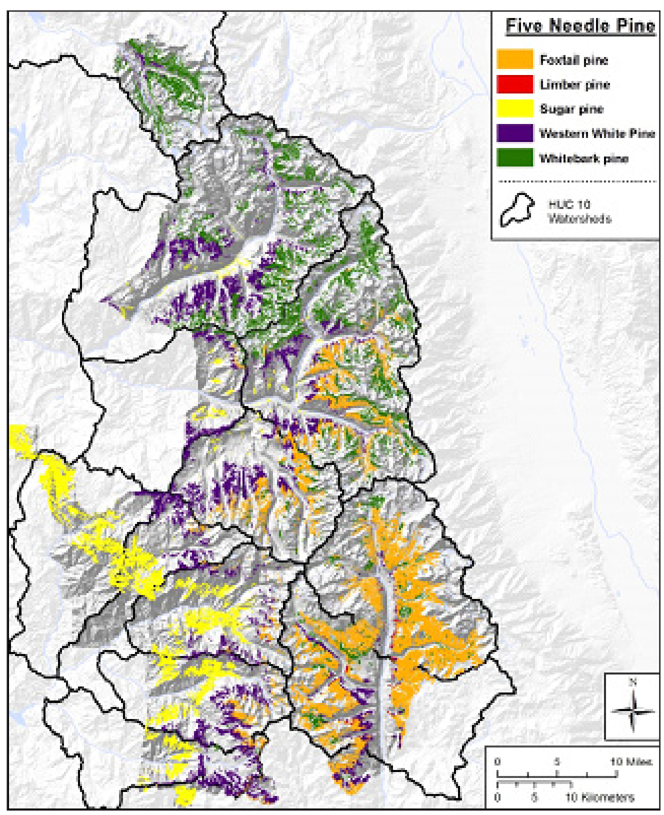
A Southern Sierra Adaptation Workshop Information Brief

DISTRIBUTION OVERVIEW

High-elevation five-needle pines are an important component of subalpine communities in the southern Sierra Nevada. These pines regulate ecosystem processes and community composition and are crucial for supporting biodiversity in these high elevation ecosystems[1,2]. For example, they contribute to soil development, reduce erosion, and serve as important food sources and physical shelter for many species[3] including Clark's nutcracker *(Nucifraga columbiana),* which is an obligate mutualist of whitebark *(Pinus albicaulis)* pine[4,5].

The high elevation white pines that are the focus on this brief are whitebark pine, foxtail pine *(Pinus balfouriana),* limber pine *(Pinus flexilis),* and western white pine *(Pinus monticola)*. Sugar pine *(Pinus lambertiana)* is discussed in the mixed conifer brief. While these pines generally are found in high elevation ecosystems, the geographic distribution of each species is distinct, reflecting their unique environmental tolerances, life histories, and origins of spread. These species occupy both regionally narrow, restricted areas (e.g. foxtail pine), and wide-ranging multi-regional distributions (e.g. whitebark pine; Figure 1). Subalpine communities in the S. Sierra Nevada are found at elevations of approximately 2,900-3,660 meters (9,500–12,000 feet)[6,10], where the understory vegetation often is fragmented with





Figures 1a and 1b: Left (1a): Range of whitebark, limber, and foxtail pine in the Sierra Nevada (Note: bright red are parks, not trees). Adapted from the Sierra Nevada Inventory and Monitoring website. Right (1b): Current distribution of high- elevation five-needle pines within SEKI. Adapted from NRCA Appendix 11.

bare rock and a mixture of dwarf shrubs and low-growing plant species[7]. The high elevation white pines are poor competitors and survive best where conditions are too harsh for other trees8. With the exception of western white pine, these species can form "climax" self-replacing stands at treeline where they are exposed to harsh conditions including strong winds, solar radiation, aridity, and nutrient-poor soils[8,9].

Whitebark Pine

Whitebark pine occurs across a broad geographic range in the western US and Canada, but it reaches its southern limit in the S. Sierra near Mount Whitney. It can be found at elevations from 2,220–3,660 m (7,280–12,000 ft) in California[10]. Considered a foundational and keystone species in treeline forests, whitebark pine can occur as the only tree species in environments too harsh for other species[2]. They have thicker bark, thinner crowns, and deeper roots compared to other co-occurring tree species, giving them an advantage over shade-tolerant competitors following low intensity fire[11]. After burns, seed dispersal by Clark's nutcracker helps to facilitate seed dispersal and rapidly stimulate regeneration[12,13,14].

Foxtail Pine

At Sequoia – Kings Canyon National Parks (SEKI), this species has the most extensive distribution of the five-needle pines. There are two distinct populations within California with one occurring in the S. Sierra Nevada (subsp. austrina) and the other in the Klamath Mountains (subsp. balfouriana). Within the S. Sierra, it can be found at elevations of 2,600–3,660 m (8,530–12,000 ft)[6]. They are shade intolerant and often form monocultures near timberline, especially on north-facing slopes with shallow, well-drained soils[2,15,16]. Despite the harsh environment where this species occurs, it can attain a large size upwards of 24 m in height and 2 m in diameter[6] and reach ages of up to 3,000 years[17].

Limber Pine

This species has the most restricted distribution of the five-needle pines in the S. Sierra and in SEKI is found only on canyon walls of main drainages within the Kern watershed[18]. They grow mostly in windy, droughty, and rocky sites near treeline[2,6], and are one of the few tree species that can grow in these areas. Throughout much of its range, limber pine is a pioneer after fire and its regeneration after these events is aided by the Clark's nutcracker[19,20,21,22]. Without periodic disturbance such as fire, limber pine is generally replaced by shade-tolerant conifers, except at higher elevations[23].

Western White Pine

This tree is moderately tolerant of shade and is dependent on fire and other disturbances for regeneration[2]. They are found between 1800-2300 m (5900–7550 ft) in central California[24] and between 2,774-2,976 m (9,000-9,800 ft) in SEKI[18] (Figure 1b). Throughout its range in western North America it can be found in a variety of forest types, but in SEKI is usually found at the upper montane forest – subalpine woodland boundary[18].

CURRENT STATUS AND STRESSORS

High elevation white pines are currently facing several threats across most of their range, including severe mountain pine beetle *(Dendroctonus ponderosae)* outbreaks, the introduced pathogen *Cronartium ribicola* (white pine blister rust) (Figure 2), fire suppression, and climate change[8] (Table 1). The realized and potential effect of these stressors has led to heightened concerns for the future outlook of these important forest communities. As a result, the US Fish and Wildlife Service recently determined that whitebark pine warranted listing as a threatened or endangered species under the Endangered Species Act, but that this listing was precluded by higher priority actions[25]. Whitebark pine in particular has experienced recent sharp population declines throughout much of its range due to the compounding effects of white pine blister rust and epidemic mountain pine beetle outbreaks[26,27].

Figure 2: White pine blister rust infecting a tree in SEKI. Photo: NPS-SEKI

While several high elevation white pine species are experiencing extensive population declines, populations in the S. Sierra have so far been less impacted by these stressors[28]. To date, the occurrence of white pine blister rust in the S. Sierra has been limited mainly to lower elevations where it is causing local population declines in sugar pine[29]. Whitebark pine surveys conducted in SEKI and Yosemite National Park (YOSE) indicate that less than 1% of sampled whitebark pine are infected by white pine blister rust[30,31]. The severity of mountain pine beetle outbreaks also have been considerably less in the Sierra Nevada than in other regions of western North America[28]. However, this may be changing as mountain pine beetle mortality in California's whitebark pine communities has increased from 85 ha/year during 1889-2005 to 3,100 ha/year in 2007[27,28]. Changes in temperature and drought also appear to be contributing to increased mortality of whitebark pine in the Sierra Nevada, a trend that is likely to continue given projected changes in future climate[28].

Fire suppression does not appear to be a major stressor for high elevation white pines in the S. Sierra. High elevation white pine communities within SEKI are generally within the historic fire return interval (FRI) range of 30-580 years depending on the species[32,33]. In SEKI, historic FRI's for subalpine conifers are estimated at 187 years (average FRI) and 508 years (maximum FRI), but are based on limited data[34]. Despite these trends, high elevation white pine communities are in "good" condition overall in terms of spatial area and forest health within the southern part of the Sierra Nevada protected area centered ecosystem (PACE; see Figure 4 for the boundaries of this area)[34].

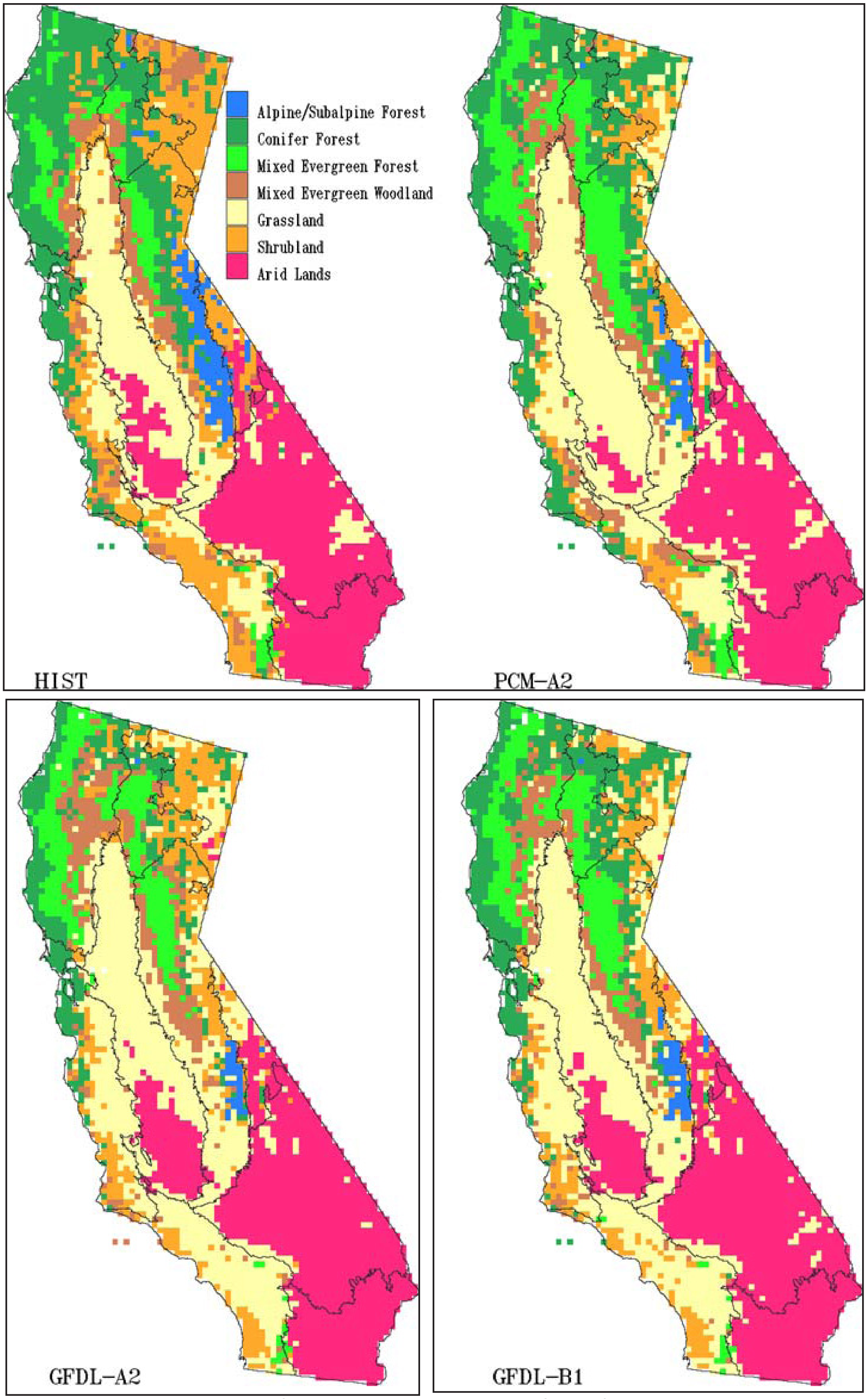


Figure 3: Vegetation class distribution for historical period (1961-1990), PCMI-A2 future (no change in precipitation and an intermediate temperature increase of less than 3 degrees C), GFDL-A2 (moderately dry with intermediate temperature increases), and GFDL-B1 (hottest and driest of the scenarios) for 2070-2099. Note the decline in alpine/subalpine forest under all scenarios. Adapted from Lenihan et al. 2008.

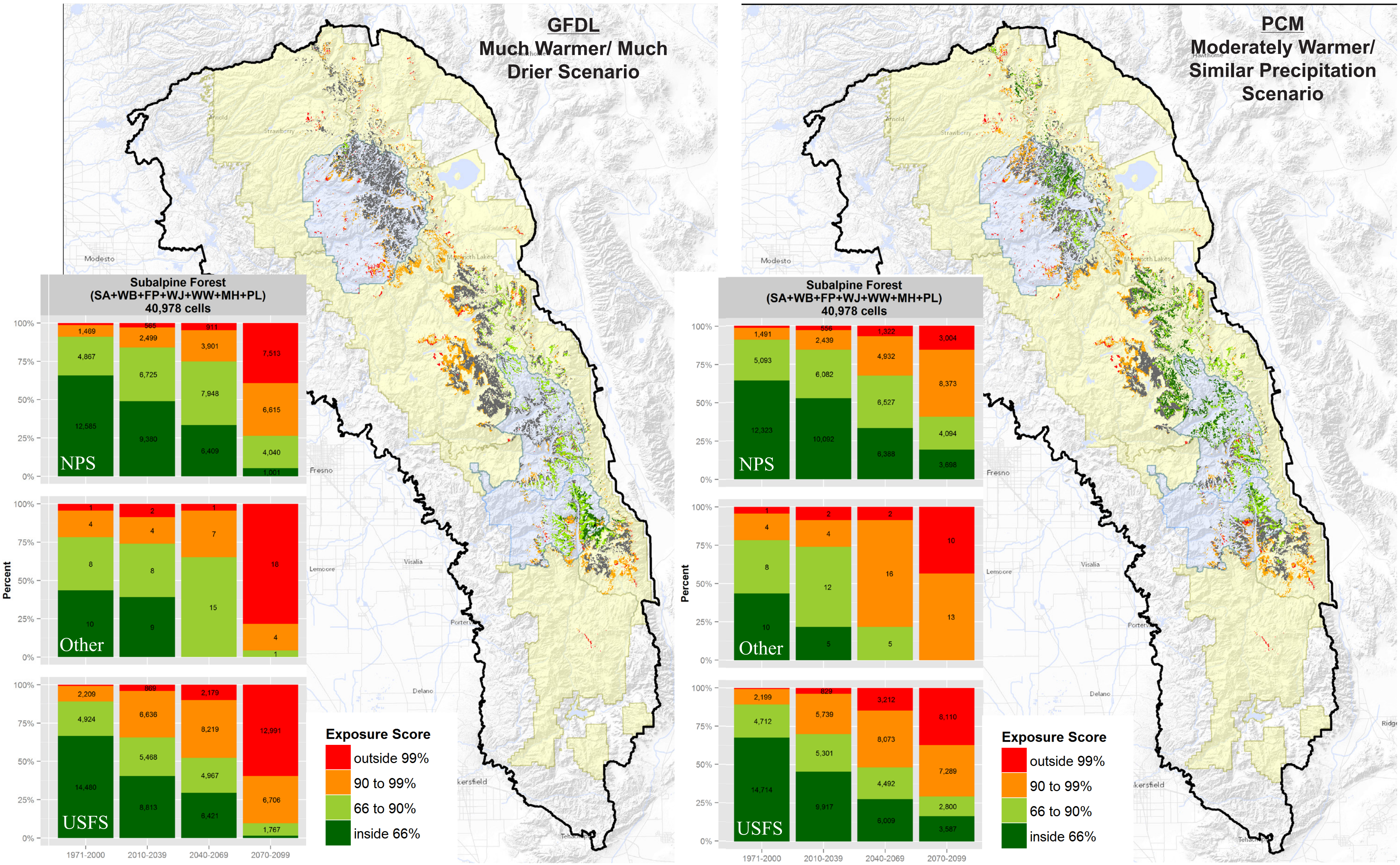


Figure 4: Two scenarios of future climate exposure for subalpine forests in the southern Sierra Nevada study area. Maps show grove area predicted to be at risk soonest (high exposure in 2010-2039) in red and orange; resilient longest (low exposure in 2070-2099) in dark and light green; and at risk later (high exposure by 2070-2099) in gray. Blue borders = NPS; yellow shading = USFS. Bar graphs show percent of study area falling within different climate exposure score categories over time (1971-2000; 2010-2039; 2040-2069; 2070-2099) for NPS, other, and USFS lands. Exposure score percentiles are based on projected future climate conditions compared to the baseline (1971-2000) climate envelope for subalpine forests, which include subalpine, whitebark pine, foxtail pine, western juniper, western white pine, limber pine, and mountain hemlock CalVeg types. These results use the IPCC A2 emissions scenario. Adapted from Schwartz et al. In Prep.

Table 1: Current stressors, potential climate change impacts, and characteristics affecting adaptive capacity for the high elevation five-needle pine ecosystem

Current Stressors	Mechanism	Potential Impact to Ecosystem
Wildfire Exclusion	Fuel buildup[65]; homogenous soils; higher proportion of dense intermediate-aged forest to young patches[66,67,68]	Severe, stand replacing crown fires, increased high-five pine mortality[45,46,47,48]; successional replacement with shade-tolerant conifers[32]
	Closed forest conditions with fewer gaps	Germination decline from loss of suitable openings49; some replacement of high-five pines with more shade-tolerant species[26,40,50,51]
Pathogens and Pests	White pine blister rust (exotic)	Mortality through cankers girdling the tree - whitebark pine most affected[52]; decreased resilience to further infections by other pathogens[53]
	Mountain pine beetle	Effects whitebark and limber pine; increased mortality; decreased resilience to other stressors
Airborne pollutants	Ozone pollution	May cause foliar damage in sensitive species[18]
	Atmospheric nitrogen (N) deposition	Reduced germination success of pine seeds from long-term reductions in litter decomposition rates and resulting thick litter layer; competitive advantage for species that can rapidly utilize extra N[54]; reductions in fine root biomass, increased nitrate in streams, increased volatilization of N from soil, decreased C:N in soil and foliage, nitrate accumulation in foliage, altered rates of letter decomposition[55,56]
Potential Climate Change Impacts	**Potential Results**	**Potential Impact to Ecosystem**
"Much Warmer/Much Drier" Scenario	Alpine/subalpine zones will receive less precipitation as snow	Longer, drier summers; colonization of higher elevation habitat by low elevation species[7]; high-five pines may experience drought stress
	Earlier snowpack melt[57,58,59]; decrease in snow pack[59,60]	
	Desired environmental parameters may disappear	Extreme range constriction or disappearance under some predictive models of both plants and animals (especially pika)[62]; disappearance from lower elevation and southern part of range[2]; lower elevation limits may be pushed above the tallest peaks and habitat could disappear[63]
	Increase in fire probability at almost all elevations except foothills and alpine areas[44,61]; increase in area burned[41]; increase in frequency in SEKI and YOSE[59]	Crown-damaging severe fires may lead to high-five pine mortality and allow shade-tolerant species to move in[32]
	Increased water deficit increase[43]	Western white pine particularly vulnerable[43]
	Change in range/distribution of mountain pine beetle	Conversion of five-needle pine stands to shade-tolerant conifers[38,39,40]
"Moderately Warmer/ Similar Precip" Scenario	Increased fire probability at almost all elevations except alpine areas[44]	Crown-damaging severe fires may lead to high-five pine mortality and allow shade-tolerant species to move in[32]
Adaptive Capacity and Vulnerabilities	**Explanation**	**Potential Impact to Ecosystem**
Limits on Dispersal and Reproduction	Long generation times	May make it difficult for high-five pines to migrate at a fast enough pace to keep up with rapid climate change[64]
Narrow Environmental Growth Range	Shade-intolerant	High-five pines could be "squeezed" out of their current ranges if lower elevation limits are pushed above the actual elevation[63]
Genetic Diversity	High genetic diversity increases stability of population	A dominant gene in sugar pine confers immunity to blister rust, but is at a low frequency in natural populations
Wind Desiccation	Whitebark pine seedlings vulnerable to desiccation in windy environments[18]	Limits whitebark pine establishment in upper elevation zones
Limited Current Range	Isolated populations for some pines/ regions	Most vulnerable to increased frequency and extent of disturbances under climate change[32]
Synergistic Effects	Already weakened high-five pines may become more vulnerable to new stressors and new combinations of stressors brought on by climate change	

POSSIBLE FUTURE CHANGES AND ADAPTIVE CAPACITY

Although predicting future climates is extremely complex, the climate models driven by the three main IPCC emission scenarios agree that temperature in the southern Sierra Nevada will warm, with predictions between 2.6-3.9°C by 2100[35]. Less certain is the change in precipitation – of the 18 general circulation models that include California, about half predict decreases and half predict increases for the Sierra region[35]. Even with little changes in precipitation, effective drought will increase as snow melts earlier and evaporative demand increases, and could cause changes in wildfire regimes, snowmelt patterns, and more (Table 1).

Subalpine ecosystems have already experienced significant changes over the last century alone. Mean annual branch growth for whitebark pine increased by 130-400% from the first to last decade of the 20th century, accompanying a 3.7°C warming (data from composite record of three weather stations in Sacramento CA, Mina NV, and Yosemite Valley CA)[36]. Growth increased with increasing minimum temperature, but reached a plateau after which growth depending more strongly on decadal-scale climate fluctuations Pacific Decadal Oscillation (PDO; a 20-30 year climate variability shift phase causing warm or cool surface areas in Pacific Ocean) condition and precipitation. White bark and western white pine recruitment into snowfields increased between the time period 1970-1999 (40% of all trees studied established in snowfields in this period), coinciding with an accelerated warming period from 1976-2000, although this correlation was not significant[36].

In the short term, these effects seem beneficial to these high-elevation pines. However, because they are poor competitors, as warming continues high elevation areas could become more suitable for other tree species, leading to high elevation white pines being outcompeted by shade-tolerant species[37,38,39,40]. Subalpine conifer forests are predicted to decrease in extent by up to ~80% based on three climate model predictions and be replaced by a variety of different vegetation classes, including grassland, shrubland, and conifer forest (Figure 3)[41]. However, as these pines are adapted to grow in very harsh conditions, areas of refugia are likely – for example, rock outcrops with shallow soil[32]. Another way of projecting potential change is shown in Figure 4, which shows subalpine forests predicted to be at "high risk soonest" and "most resilient longest" (potential climate refugia) under two future scenarios.

The decline in large-diameter trees may accelerate as minimum temperatures increase[42,43]. Upslope migration of subalpine forests into the alpine also is predicted[41], but will be constrained by factors such as dispersal and lack of soil. Higher fire frequency also is predicted for subalpine forests (Figure 5)[44]. Fire in some areas may become more frequent than the historic fire interval, and this has unknown effects to the persistence of species adapted to longer fire intervals.

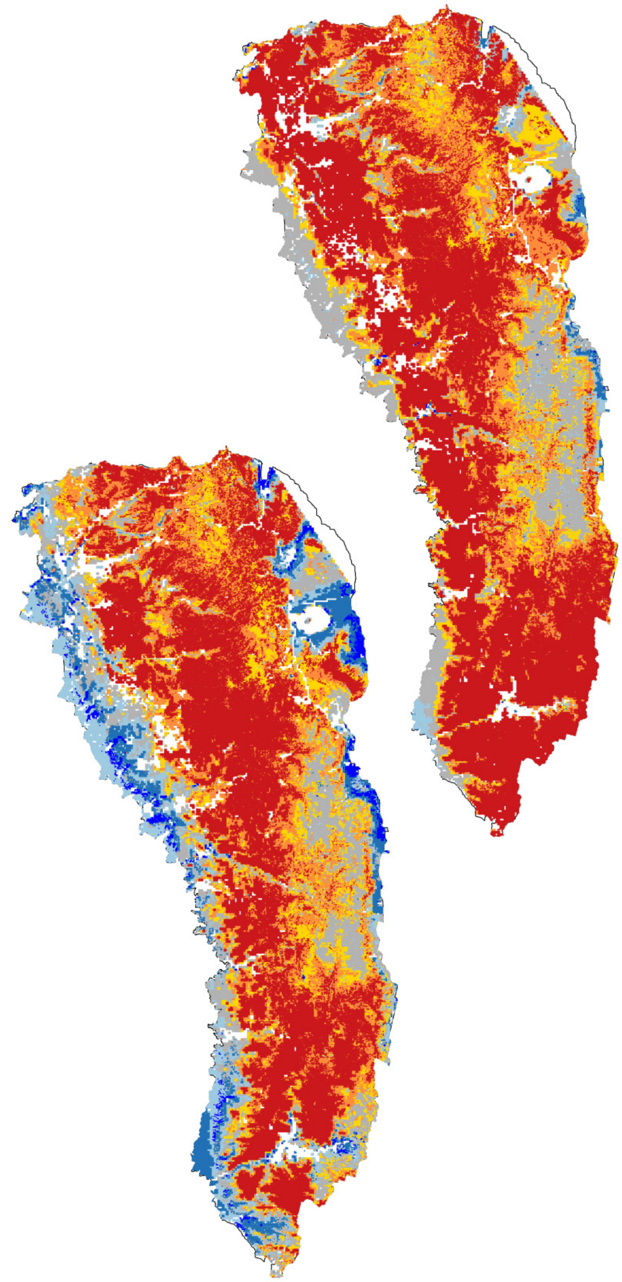


Figure 5: Projected future (2070-2099) fire probabilities in the PACE for the GFDL "much warmer-drier" (left) and PCM "moderately warmer –same precip" (right) climate scenarios. Blue colors represent decreased fire probabilities, grey is no change, and orange/red are increased probabilities. Figure adapted from Max Moritz, UC Berkeley.

Authorship Note

This information brief was created by Katy Cummings (NPS) and Koren Nydick (NPS), with review and contributions from Jonny Nesmith (NPS). Additional thanks to Erika Williams for graphic design guidance.

POTENTIAL MANAGEMENT STRATEGIES (WORK IN PROGRESS)

- To manage for persistence (resist change and build resilience):
  - Plant and irrigate seedlings
  - Remove blister rust cankers from trees
  - Apply insecticides during mountain pine beetle outbreaks
  - Install fire lines around rust-resistant whitebark pine to improve survival chances following fire
  - Reinstate prescribed burning in subalpine forests
  - Protect white pine blister rust resistant trees to promote genetic resistance in future progeny
  - Breed blister rust-resistant trees and out-plant these

- To manage for change (facilitate transformation):
  - Plant groves with drought resistant species and genotypes
  - Collect seed and transplant high elevation white pines upslope to promote establishment before shade-tolerant trees move into this area
  - Collect seeds and screen for white pine blister rust resistance to identify which trees in the landscape are resistant for future collections and transplanting

- Delay deciding (monitor and research):
  - Monitor moisture stress
  - Research moisture requirements
  - Monitor sequoia regeneration
  - Monitor for pathogen outbreaks

References

[1] Ellison, A.M, M.S. Bank, B.D. Clinton, et al. 2005. Loss of Foundation Species: Consequences for the Structure and Dynamics of Forested Ecosystems Frontiers in Ecology and the Environment, 3(9): 479-486.

[2] Tomback, D.F., and P. Achuff. 2010. Blister rust and western forest biodiversity: ecology, values, and outlook for white pines. Forest Pathology 40:186-225.

[3] Mattson, D. J., Kendall, K. C., Reinhart, D. P. 2001. Whitebark pine, grizzly bears, and red squirrels. Pages 121-136 In: Tomback, D. F., Arno, S. F., Keane, R. E. (eds.). 2001. Whitebark pine communities: ecology and restoration. Island Press, Washington.

[4] Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. Journal of Animal Ecology 51:451-467.

[5] Tomback, D.F., Linhart, Y. B. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology 4:185-219.

[6] Fites-Kaufman, J., P. Rundel, N. Stephenson, and D.A.Weixelman. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. In: Barbour, M., Keeler- Wolf, T., Schoenherr, A.A. (Eds.), Terrestrial Vegetation of California. University of California Press, Berkeley, pp. 456–501.

[7] Southern Sierra Partnership. 2010. Framework for Cooperative Conservation and Climate Adaptation for the southern Sierra Nevada and Tehachapi Mountains, California, USA.

[8] Tomback, D. F., Achuff, P., Schoettle, A. W., Schwandt, J. W., Mastriguiseppe, R. J. 2011. The magnificent high-elevation five-needle white pines: Ecological roles and future outlook. Pages 2-28 In: Keane, R. E.; Tomback, D. F.; Murray, M.l P.; and Smith, C. M., (eds.). 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p.

[9] Weaver, T. 2001. Whitebark pine and its environment. Pages 41-73 In: Tomback, D. F., Arno, S. F., Keane, R. E. (eds.). 2001. Whitebark pine communities: ecology and restoration. Island Press, Washington.

[10] Sawyer, J. O., Keeler-Wolf, T., Evens, J. M. 2009. A manual of California vegetation. Second Edition. California native Plant Society Press. Sacramento, California.

[11] Morgan P., Bunting, S. C., Keane, R. E., Arno, S. F. 1994. Fire Ecology of Whitebark Pine Forests of the Northern Rocky Mountains, USA. In: Proceedings of the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge. USDA Technical Repot INT-GTR-309. Ogden, UT, USA pp 136-140.

[12] Tomback, D.F., L.A. Hoffmann, S.K. Sund. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—Symposium on whitebark pine ecosystems; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 118-129.

[13] Tomback, D.F.; S.K Sund, L.A. Hoffmann. 1993. Post-fire regeneration of Pinus albicaulis: height-age relationships, age structure, and microsite characteristics. Canadian Journal of Forest Research. 23: 113-119;

[14] Tomback, D. F. 2001. Clark's nutcracker: Agent of regeneration. Pages 89-104 in Tomback, D. F., Arno, S. F., Keane, R. E. (eds.). 2001. Whitebark pine communities: ecology and restoration. Island Press, Washington.

[15] Ryerson, Diane 1983. Population structure of Pinus balfouriana Grev. & Balf. Along the margins of its distribution area in the Sierran and Klamath regions of California. Sacramento, CA: Sacramento State University. 198 p. Thesis.

[16] Eckert, Andrew J.; Sawyer, J. O. 2002. Foxtail pine importance and conifer diversity in the Klamath Mountains and southern Sierra Nevada, California. Madroño. 49: 33-45.

[17] Mastrogiuseppe, R. J.; Mastrogiuseppe, J. D. 1980. A study of Pinus balfouriana Grev. & Balf. (Pinaceae). Systematic Botany. 5(1): 86-104.

[18] Eschtruth, A.K., J.J. Battles, D. Saah. 2012. Five Needle Pine. Appendix 11, in: National Park Service. 2012. Natural Resource Condition Assessment for Sequoia and Kings Canyon National Parks. Natural Resource Report NPS/SEKI/NRR-2012/XXX. Eds. Panek, J.A. and C.A. Sydoriak. National Park Service, Fort Collins, CO.

[19] Lanner, Ronald M.; Vander Wall, Stephen B. 1980. Dispersal of limber pine seed by Clark's Nutcracker. Journal of Forestry. 78 (October): 637-639.

[20] Rebertus, A.J.; Burns, B.R. and Veblen, T.T. 1991. Stand dynamics of Pinus flexilis-dominated subalpine forests in the Colorado Front Range. Journal of Vegetation Science. 2: 445-458.

[21] Donnegan, J.A. and A.J. Rebertus. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. Ecology. 80: 1370-1384.

[22] Coop, J.D. and A.W. Schoettle. 2009. Regeneration of Rocky Mountain bristlecone pine (Pinus aristata) and limber pine (Pinus flexilis) three decades after stand-replacing fires. Forest Ecology and Management. 257: 893-903.

[23] Thorne, R. F., A. Schornherr, C.D. Clements, and J.A. Young. 2007. Transomntane coniferous vegetation. Pages 574-586 in Barbour, M., Keeler-Wolf, T., Schoenherr, A.A. (eds.), Terrestrial Vegetation of California. University of California Press, Berkeley, pp. 456–501.

[24] MacDonald, G. M., Cwynar, L. C., Whitlock, C. 1998. The late Quaternary dynamics of pines in northern North America. Pages 122-152 in Richardon, D. M. (ed.). Ecology and Biogeography of Pinus. Cambridge University Press. New York, NY.

[25] Federal Register 76, no.138 [July 19, 2011]: 42631-42654

[26] Kendall, K. C., Keane, R. E. 2001. Whitebark pine decline: Infection mortality, and population trends. Pages 221-242 in Tomback, D. F., Arno, S. F., Keane, R. E. (eds.). 2001. Whitebark pine communities: ecology and restoration. Island Press, Washington.

[27] Gibson, K., S. Kjerstin, S. Kegley, C. Jorgensen, S. Smith, and J. Witcosky. 2008. Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges. U.S. For. Serv. For. Health Prot. R1-08-020. Gen. Tech. Rep. PNW-GTR-530.

[28] Millar, C.I., Westfall, R.D., Delany, D.L., Bokach, M.J., Flint, A L., Flint, L.E. 2012. Forest mortality in high-elevation whitebark pine (Pinus albicaulis) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming. Can. J. For. Res. 42:749-765.

[29] van Mantgem, P.J., N.L. Stephenson, M. Keifer, and J. Keeley. 2004. Effects of an introduced pathogen and fire exclusion on the demography of sugar pine. Ecological Applications 14:1590–1602.

[30] Duriscoe, D. M., and C. S. Duriscoe. 2002. Survey and monitoring of white pine blister rust in Sequoia and Kings Canyon National Parks: Final report on 1995-1999 survey and monitoring plot network. Science and Natural Resources Management Division Sequoia and Kings Canyon National Parks, Three Rivers, California. Unpublished.

[31] Maloney, P., J. Dunlap, D. Burton, D. Davis, D. Duriscoe, J. Pickett, R. Smith, and J. Kliejunas. 2008. White Pine Blister Rust in the High Elevation White Pines of California: A Forest Health Assessment for Long-Term Monitoring. USDA Forest Service, Forest Health Protection. Internal Draft Report. Pages 64.

[32] Campbell, E.M., R.E. Keane, E.R. Larson, M.P. Murray, A.W. Schoettle, and C. Wong. 2011. Distrubance Ecology of High-Elevation Five-needle Pine Ecosystems in Western North America. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p.

[33] Caprio, A.C. and P. Lineback. 2002. Pre-Twentieth Century Fire History of Sequoia and Kings Canyon National Parks: A Review and Evaluation of Our Knowledge. In: Proceedings of the Conference on Fire in California Ecosystems: Integrating Ecology, Prevention, and Management. Nov. 17-20, 1997, San Diego, CA. AFE Misc. Publ. No. 1.

[34] Southern Sierra Partnership. 2010. Appendix A: South Sierra Conservation Action Plan (CAP). In: Framework for Cooperative Conservation and Climate Adaptation for the southern Sierra Nevada and Tehachapi Mountains, California, USA.

[35] Gonzalez, P. 2012. Climate change trends and vulnerability to biome shifts in the Southern Sierra Nevada. Draft Report for Climate Change Response Program, August 29 2012. National Park Service: Washington, D.C.

[36] Millar, C.I., R.D. Westfall, D.L. Delany, J.C. King and L.J.Graumlich. 2004. Response of Subalpine Conifers in the Sierra Nevada, California, U.S.A., to 20th-CenturyWarming and Decadal Climate Variability. 2004. Arctic, Antarctic, and Alpine Research, Vol. 36(2):181-200.

[37] Jackson, S.; Campbell, E. 2008. Assessing the threat of mountain pine beetle to whitebark pine in British Columbia. Project Report, FIA-FSP Project #M07-5048. BC Ministry of Forests and Range.

[38] Keane, R. E. 2001. Successional dynamics: modeling an anthropogenic threat. Pages 159-192. in Whitebark pine communities: ecology and restoration. Washington: Island Press.

[39] Kipfmueller, K.F.; Kupfer, J.A. 2005. Complexity of successional pathways in subalpine forests of the Selway-Bitterroot Wilderness Area. Annuals of the Association of American Geographers. 95: 495-510.

[40] Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p.

[41] Lenihan, J.M., D. Bachelet, R.P. Neilson, R. Drapek. 2008. Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. Climatic Change 87 (Suppl 1):S215-S230.

[42] Hayhoe, K., Cayan, D., Field, C., Frumhoff, P., Maurer, E. et al.: 2004, 'Emissions pathways, climate change, and impacts on California', PNAS 101, 12422–12427.

[43] Lutz, J.A., J.W. van Wagtendonk, and J.F. Franklin. 2009. Twentieth-century decline of large-diameter trees in Yosemite National Park, California, USA. Forest Ecology and Management 257: 2296-2307.

[44] Moritz, M. 2012. Moritz Lab, University of California at Berkeley. Personal communication.

[45] Lasko, R. J. 1990. Fire behavior characteristics and management implications in whitebark pine ecosystems. Pages 319-324 in W. C. Schmidt and K. J. McDonald, compilers. Proceedings- Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. USDA Forest Service, Intermountain Research Station, General Technical Report INT- 270, Ogden, Utah.

[46] Steele, R.W. 1960. The role of forest fire in the Bob Marshall Wilderness Area. Montana Forest and Conservation Experiment Station, School of Forestry, University of Montana Report #1, Missoula.

[47] Loope, L. L. and G. E. Gruell. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. Quaternary Research 3:425-443.

[48] Arno, S. F., E. Reinhardt and J. Scott. 1993. Forest structure and landscape patterns in the subalpine lodgepole pine type: A procedure for quantifying past and present conditions. USDA Forest Service, Intermountain Research Station, General Technical Report INT-270, Ogden Utah.

[49] Keane, R. E. and P. Morgan 1994. Decline of whitebark pine in the Bob Marshall Wilderness Complex of Montana, USA. Pages 245-253 in W. C. Schmidt and F. K. Holtmeier, compilers. Proceedings of the International workshop on subalpine stone pines and their environment: The status of our knowledge. USDA Forest Service. Inter-mountain Research Station, General Technical Report INT-GTR-309, Ogden, Utah.

[50] Arno, S. F., 2001: Community types and natural disturbance processes. In: Whitebark pine communities: Ecology and restoration. Ed. By Tomback, D. F.; Arno, S. F.; Keane, R. E. Washington, DC: Island Press, pp. 74–88.

[51] Murray, M.P., S. C. Bunting, and P. Morgan. 2000. Landscape trends (1753-1993) of whitebark pine (Pinus albicaulis) forests in the West Big Hole Range of Idaho/Montana, U.S.A. Arctic, Antarctic, and Alpine Research 32, 412-418.

[52] Sniezko, R.A., A. Kegley, R. Danchok, J. Hamlin, J. Hill and D. Conklin. Rust Resistance in Seedling Families of Pinus albicaulis and Pinus strobiformis and implications for Restoration. n: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p.

[53] Geils, B. W., K.E. Hummer, Hunt, R.S., 2010: White pines, Ribes, and blister rust: a review and synthesis. Forest Pathology 40, 147–185.

[54] Chapin, F. S., III. 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst. 11:233-260

[55] Fenn, M.E., J.S. Baron, E.B. Allen, et al. 2003. Ecological effects of nitrogen deposition in the western United States. BioScience. 53(4):404-420

[56] Temple, P.J., A. Bytnerowicz, M. E. Fenn, and Mark A. Poth. 2005. Air Pollution Impacts in the Mixed Conifer Forests of Southern California. USDA Forest Service Gen. Tech. Rep. PSWGTR-195.

[57] Null, S.E., J.H. Viers, and J.F. Mount. 2010. Hydrologic response and watershed sensitivity to climate warming in California's Sierra Nevada. PLoS One 5: e9932.

[58] Young, C.A., M.I. Escobar-Arias, M. Fernandes, et al. 2009. Modeling the hydrology of climate change in California's Sierra Nevada for subwatershed scale adaptation. Journal of the American Water Resources Association 45: 1409-1423.

[59] Gonzalez, P., R.P. Neilson, J.M. Lenihan, and R.J. Drapek. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. Global Ecology and Biogeography 19: 755-768.

[60] Cayan, D., E. Maurer, M. Dettinger, M. Tyree, and K. Hayhoe. 2008. Climate change scenarios for the California region. Climatic Change 87(S1): 21–42.

[61] Westerling, A.L. and B. P. Bryant. 2008. Climate change and wildfire in California. Climatic Change 87: 231-249.

[62] Holtcamp, W. 2010. Silence of the pikas. Bioscience 60:8-12.

[63] Warwell, M. V.; Rehfeldt, G.; Crookston, N. 2007. Modeling contemporary climate profiles of whitebark pine (Pinus albicaulis) and predicting responses to global warming. Pages 139-142 in Proceedings of the conference whitebark pine: a Pacific Coast perspective. Ashland, OR. Ashland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region.

[64] Aitken, S.N., S. Yeaman, J.A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications. 1: 95-111.

[65] Gebauer, S.B. 1992. Changes in soil properties along a post-fire chronosequence in a sequoia-mixed conifer forest in Sequoia National Park, California. M.S. Thesis, Duke University, Durham, North Carolina.

[66] Bonnicksen, T.M. and E.C. Stone. 1978. An analysis of vegetation management to restore the structure and function of presettlement giant sequoia-mixed-conifer forest mosaics. National Park Service.

[67] Bonnicksen, T.M. and E.C. Stone. 1982. Reconstruction of a presettlement giant sequoia-mixed conifer forest community using the aggregation approach. Ecology 63(4): 1134-1148.

[68] Stephenson, N.L. 1987. Use of tree aggregations in forest ecology and management. Environmental Management 11:1-5.