Challenges and Opportunities for Maintaining Ponderosa Pine Forests in the Southwestern United States

Thomas Kolb, Aalap Dixit, and Owen Burney

Professor, School of Forestry, Northern Arizona University, Flagstaff, AZ; Graduate Research Assistant, School of Forestry, Northern Arizona University, Flagstaff, AZ; Associate Professor and Superintendent, John T. Harrington Forestry Research Center, New Mexico State University Mora, NM.

Abstract

Deforestation caused by wildfire and bark beetle attacks in southwestern ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson.) forests has increased over the past century due to climate warming. Continued warming is expected to increase deforestation. Ponderosa pine regeneration after deforestation often is inadequate in the region. Opportunities exist for active management to mitigate deforestation. First, planting can promote reforestation, but survival of planted seedlings is generally poor and highly variable among sites. The region needs more research about improving early seedling performance. Secondly, improving aridity adaptation of planted seedlings by seed source selection may improve outplanting performance. New common garden studies of seedling aridity adaptation of Arizona and New Mexico provenances suggest genetic variation in aridity adaptation among populations. Early results show genetic variation in survival under extreme drought conditions. Greenhouse experiments are investigating genetic variation in mechanisms of aridity tolerance. Promotion of forest recovery using these emerging approaches will be critical for sustaining forests in the increasingly arid Southwestern United States. This paper was presented at the Joint Annual Meeting of the Western Forest and Conservation Nursery Association and the Intermountain Container Seedling Growers Association (Coeur d'Alene, ID, October 25–26, 2018).

Introduction

Ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson.) has the largest geographic range of any pine in the United States, occurring in 14 Western States (Hardin et al. 2001). It is a large tree at maturity with valuable wood in commercial quantities throughout its range. Moreover, it dominates forests in upland watersheds that supply clean water for human consumption and agriculture. Ponderosa pine forests provide numerous ecosystem services, including wood products, wildlife habitat, carbon sequestration, clean air, and temperature amelioration. Yet these services are threatened by deforestation resulting from increases in drought, wildfire, and bark beetle attacks (Kolb et al. 2016a, Williams et al. 2010, Williams et al. 2013). The threat is particularly severe in the Southwestern United States, where ponderosa pine is the dominant tree in most upland watersheds. Forests in this arid region are scarce compared to other U.S. regions (only about 27 percent of Arizona and New Mexico are forested), and consequently are disproportionally important for ecosystem services.

Threats to Ponderosa Pine Forests

The Southwestern United States has experienced a century of warming and unusually high tree mortality. Directly measured temperatures from weather stations show warming throughout the region of 2 to 5 °F (1 to 2.5 °C) since 1901 in both maximum and minimum air temperatures (Garfin et al. 2013). A pulse of ponderosa pine mortality occurred during the latter part of the century of warming. Since the mid-1980s, between 11 and 18 percent of ponderosa pine trees died in Arizona and New Mexico from drought-associated wildfire and bark beetle attacks (Hicke et al. 2016, Williams et al. 2010). Area burned by wildfire increased during this period of warming (Westerling et al. 2006), which includes the largest forest fires in the recorded history of Arizona (Wallow Fire, 469,300 ac [190,000 ha]) and New Mexico (Whitewater-Baldy Fire, 297,635 ac [120,500 ha]) in 2011. Moreover, forest area attacked by bark beetles also increased in the Southwestern United States during this period of warming (Hicke et al. 2016, Raffa et al. 2008).

Ponderosa pine regeneration has been meager and slow after severe stand disturbance during this period of warming. This slow regeneration is due to lack of seed trees and the presence of harsh abiotic conditions (Puhlick et al. 2012) and is exacerbated by ponderosa pine's lack of fire-adapted, serotinous cones and lack of vegetative resprouting (Burns and Honkala 1990). Natural regeneration of ponderosa pine in deforested areas can occur on moister sites when seed trees are within about 500 ft (164 m) of openings (Bonnet et al. 2005, Haffey et al. 2018, Haire and McGarigal 2010, Owen et al. 2017). Many recent wildfires in the Southwestern United States, however, have produced large openings on dry sites that are significantly distant from seed trees, thereby limiting ponderosa pine regeneration (figure 1). Many recent studies report inadequate ponderosa pine regeneration after intense burning, leading to transitions from forests to grass- or shrublands (Allen and Breshears 1998, Chambers et al. 2016, Dore et al. 2012; Haffey et al. 2018, Ouzts et al. 2015, Roccaforte et al. 2012, Rother and Veblen 2016, Savage et al. 2013). Similar findings of a decrease in forest resilience to severe burning have been reported for multiple forest types in Western North America (Stevens-Rumann et al. 2017).

All of the aforementioned threats to southwestern ponderosa pine forests are expected to increase in the future with continued warming. Climate models for the Southwestern United States predict further increases in mean annual and maximum summer temperatures and more frequent severe droughts (Garfin et al. 2013, Seager et al. 2007). Future changes in precipitation are poorly understood, but winter precipitation in montane watersheds is expected to shift from snow to rain (Garfin et al. 2013). Forest area burned in the Southwest is also projected to increase in the future (Flannigan et al. 2013, Littrell et al. 2009, Xu et al. 2013). Aridity stress to forests caused by warming will be especially severe in semi-arid forests of the Southwestern United States because productivity is already strongly constrained by low precipitation (Boisvenue and Running 2006, Williams et al. 2012). Greater future aridity is projected to reduce establishment and growth and increase mortality of tree species in semi-arid forests such as in the Southwest (Adams and Kolb 2005, Bell et al. 2014, Petrie et al. 2017, Puhlick et al. 2012, Rother et al. 2015, Wu et al. 2011). Tree mortality due to bark beetle attacks in the region is expected to increase in the future as warming makes droughts more intense (Kolb et al. 2016a). Consequently, climate-change and climate-envelope models project substantial loss of ponderosa pine forests in the Southwestern United States over the next century (Rehfeldt et al. 2006, Williams et al. 2013).

Figure 1. Examples of no ponderosa pine regeneration several years after severe forest burning in northern Arizona. (Photo by Thomas Kolb, 2013)

Opportunities for Reforestation by Planting

Artificial regeneration by planting has the potential to slow recent losses of ponderosa pine forests in the Southwestern United States. The backlog of understocked areas that previously supported ponderosa pine forests in the Southwest is, however, formidable. The amount of U.S. Department of Agriculture (USDA), Forest Service lands in the Southwestern Region needing active planting of tree seedlings after wildfire was estimated to be 159,418 ac (64,542 ha) in 2015 with a projected cost of approximately $79M (USDA Forest Service 2016). This amount is a conservative estimate because of the increasing occurrence of wildfire. Most of these planting needs are in ponderosa pine forests, which represent over 60 percent of the forest cover in the Southwestern Region.

Establishment of ponderosa pine seedlings by planting in the Southwestern United States is difficult due to short frost-free seasons, dry spring weather, and extreme variation in temperature and precipitation. Research about artificial regeneration of ponderosa pine in the Southwest is scant and most studies were performed decades ago (Schubert et al. 1970, Schubert 1974). Recent studies have confirmed the difficulty in establishing ponderosa pine by planting in the region. For example, survival of ponderosa pine seedlings planted recently in the Davis Mountains in West Texas ranged between 22 and 34 percent in fall plantings, and between 9 and 25 percent in late-summer plantings (Vickers et al. 2018). Physical weed control increased survival in both seasons. The most important mortality agents were pocket gophers and desiccation. A recent survey of ponderosa pine plantings in severely burned areas in Arizona and New Mexico reported average survival of 25 percent over eight sites (5 to 8 years after planting), with high variation among sites; some sites had no survival, others had survival between 10 and 40 percent, and the best site had 60 percent survival (Ouzts et al. 2015). The sites with no survival of planted seedlings also had no evidence of natural ponderosa pine regeneration and were converted from pine-dominated forests to shrublands or grasslands.

Ouzts et al. (2015) also addressed whether planting resulted in enough established seedlings to put the stand on a trajectory towards recovery of a ponderosa-dominated forest. They assumed a regeneration target of at least 49 established seedlings per ac (120 per ha) to produce a low-density ponderosa pine overstory, with the expectation that survival between the established seedling and mature tree stages would be 44 percent based on DeWald and Mahalovich (2008). The regeneration target is based on ecological restoration principles derived from the historical range of tree-density variation in southwestern ponderosa pine forests exposed to frequent, low-intensity burning (Reynolds et al. 2013). Planting seedlings produced close to this regeneration target at five of the eight sites (figure 2). This result shows that successful post-wildfire plantings of ponderosa pine can put stands on a trajectory towards forest recovery. Obviously, low survival of planted seedlings in the Southwest should be anticipated and compensated for by planting more seedlings than ultimately desired.

Opportunities exist to improve survival and performance of planted ponderosa pine seedlings in the Southwest although little contemporary research has been done. Approaches needing new research include:

- Planting season (e.g., Vickers et al. 2018)
- Stocktype (e.g., Pinto et al. 2011)
- Nursery conditioning for drought tolerance (e.g., Trickler et al. 2013)
- Physical protection of stems and roots from animals (e.g., Engemann et al. 1999)
- Irregular, cluster planting designs (e.g., North et al. 2019, Vickers et al. 2018)
- Nucleation plantings in favorable microsites (e.g., North et al. 2019)
- Facilitation by living (e.g. other plants) and non-living objects (e.g., logs, rocks) (e.g., Gómez et al. 2004; Burney et al. 2007)
- Selection of arid-adapted seed sources (e.g., Kolb et al. 2016b)

Opportunities to Improve Seedling Aridity Adaptation by Seed Source Selection

Recommendations to use strictly local seed sources in reforestation are likely outdated for the future with continued climate warming and increasing drought. Instead, reforestation projects should emphasize the planting of seedlings that are adapted to forecasted warmer and drier conditions (Williams and Dumroese 2013). Much evidence indicates that natural selection has produced populations that are preadapted for future arid sites (Alberto et al. 2013). For example, seedlings of several tree species from arid/warm locations performed better at warm sites than seedlings from wetter/cooler locations (Bingham and Simard 2013, Drake et al. 2015, Taibi et al. 2014). Past recommendations to use local seed sources in active reforestation of ponderosa pine in the Southwestern United States were based on common-garden tests of widely separated geographic sources planted many decades ago during cooler, wetter periods (DeWald and Mahalovich 2008). Such recommendations are likely no longer valid given rapid climate change. Instead, recent recommendations based on the concepts of preadaptation and assisted population migration call for use of arid-adapted genotypes in reforestation projects, especially at trailing-edge sites (e.g., low-elevation and southern range edges), to reduce adaptation lag times, and to reduce the number of generations required for evolution to produce populations attuned for warmer climates (Rehfeldt et al. 2014a, 2014b; Williams and Dumroese 2013, Taibi et al. 2014). These recommendations and supporting research have

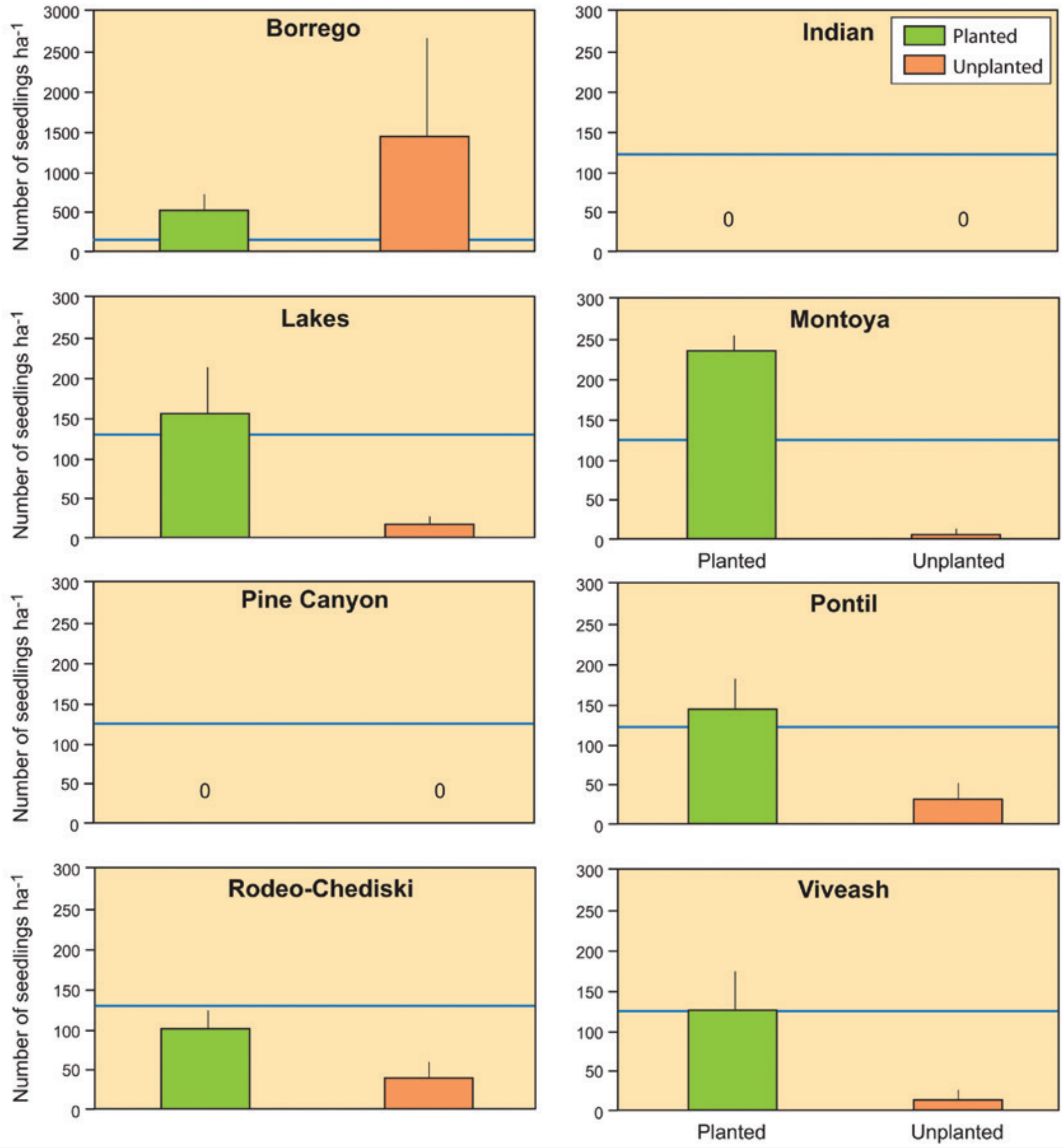

Figure 2. Ponderosa pine seedling density at eight severely burned sites in plots planted with ponderosa pine seedlings, and paired unplanted plots. Density at the Borrego site was nearly 10 times more than the other sites. The horizontal line in each panel is the minimum target seedling density (49/ac [120/ha]) projected for producing an open-structure forest of ponderosa pine in the future. Vertical lines are 1 standard error. Modified from Ouzts et al. (2015).

led to the development of decision-support tools for selecting seed sources adapted to future climates, such as the seedlot selection tool (https://seedlotselection-tool.org/sst/). Predictions of this tool, which are based on climate-matching algorithms, rarely have been tested, especially for trees in the Southwest.

Evaluations of appropriate ponderosa pine seed sources for a more arid climate in the Southwest have started. Kolb et al. (2016b) reported that ponderosa pine seedlings from low-elevation, drier seed sources in northern Arizona had a more drought-adapted architecture (lower shoot-root ratio) and longer survival of experimentally induced drought in the greenhouse than high-elevation, wetter sources. A new investigation builds on this finding by expanding investigations of seedling drought tolerance to 21 seed sources from a broad gradient of elevation, temperature, and precipitation over Arizona and New Mexico (figures 3 and 4). Seeds used in the investigation were compiled from collections made over the last three decades by John Harrington (New Mexico State University), Phillip Patterson (Northern Arizona University), and the authors. The John T. Harrington Forestry Research Center in Mora, NM, produced the seedlings, which were planted in July 2018 at the onset of monsoon rains at three common-garden experiments across an elevational gradient: (1) a cool, high-elevation site

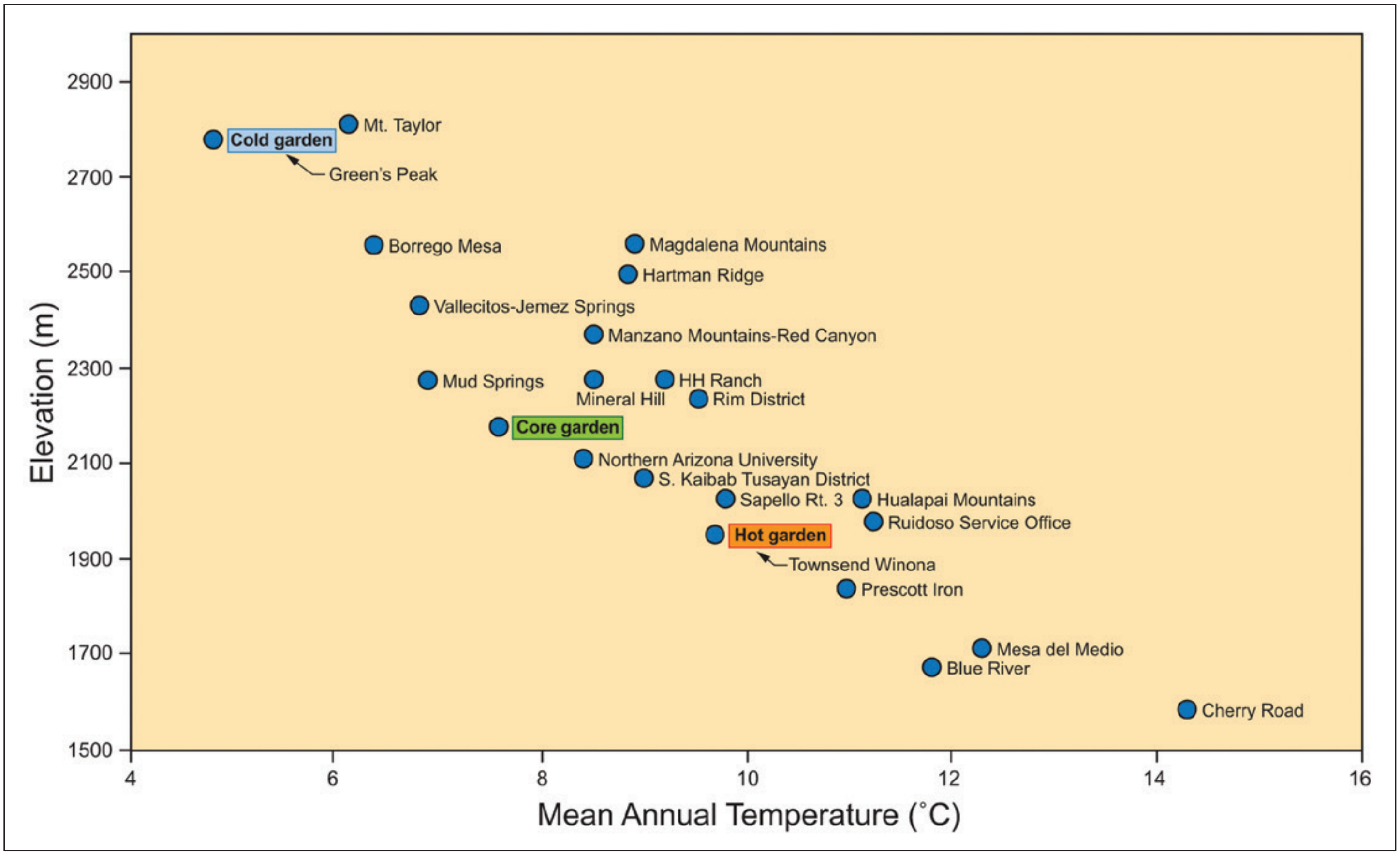

Figure 3. Elevation, mean annual air temperature (1981-2010 obtained from PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu), and site name of 21 seed sources from Arizona and New Mexico used in the new provenance experiments. The colored boxes are the three field common-garden sites where seed sources were planted in summer 2018.

currently supporting mixed conifer and aspen forests; (2) a moderate temperature, mid-elevation site currently supporting ponderosa pine; and (3) a hot, low-elevation site currently supporting pinyon-juniper woodland. A fourth common-garden experiment, located in the greenhouse at Northern Arizona University, will be used to investigate mechanisms of heat and drought tolerance (figure 5). Seedling survival has been high (greater than 95 percent) at the high- and mid-elevation sites 3 months after planting. In contrast, most seedlings died at the low-elevation site within 2 months after planting due to desiccation. Seedlings were planted at the low-elevation site in the middle of July, after the start of late-summer monsoon rains, but little rain fell for 3 weeks after planting and over 90 percent of seedlings died (figure 6). Interestingly, seedlings from

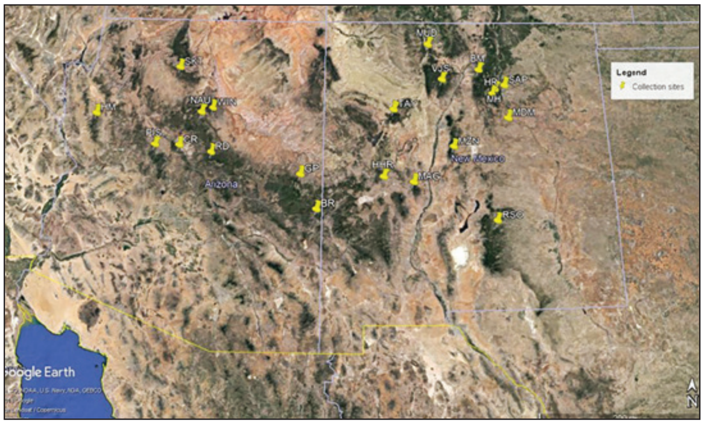

Figure 4. Location of the 21 seed sources from Arizona and New Mexico used in the new provenance experiments (Google Earth 2018).

Figure 5. Ponderosa pine seedlings being grown in the Northern Arizona University Research Greenhouse for drought tolerance experiments. (Photo by Aalap Dixit 2018)

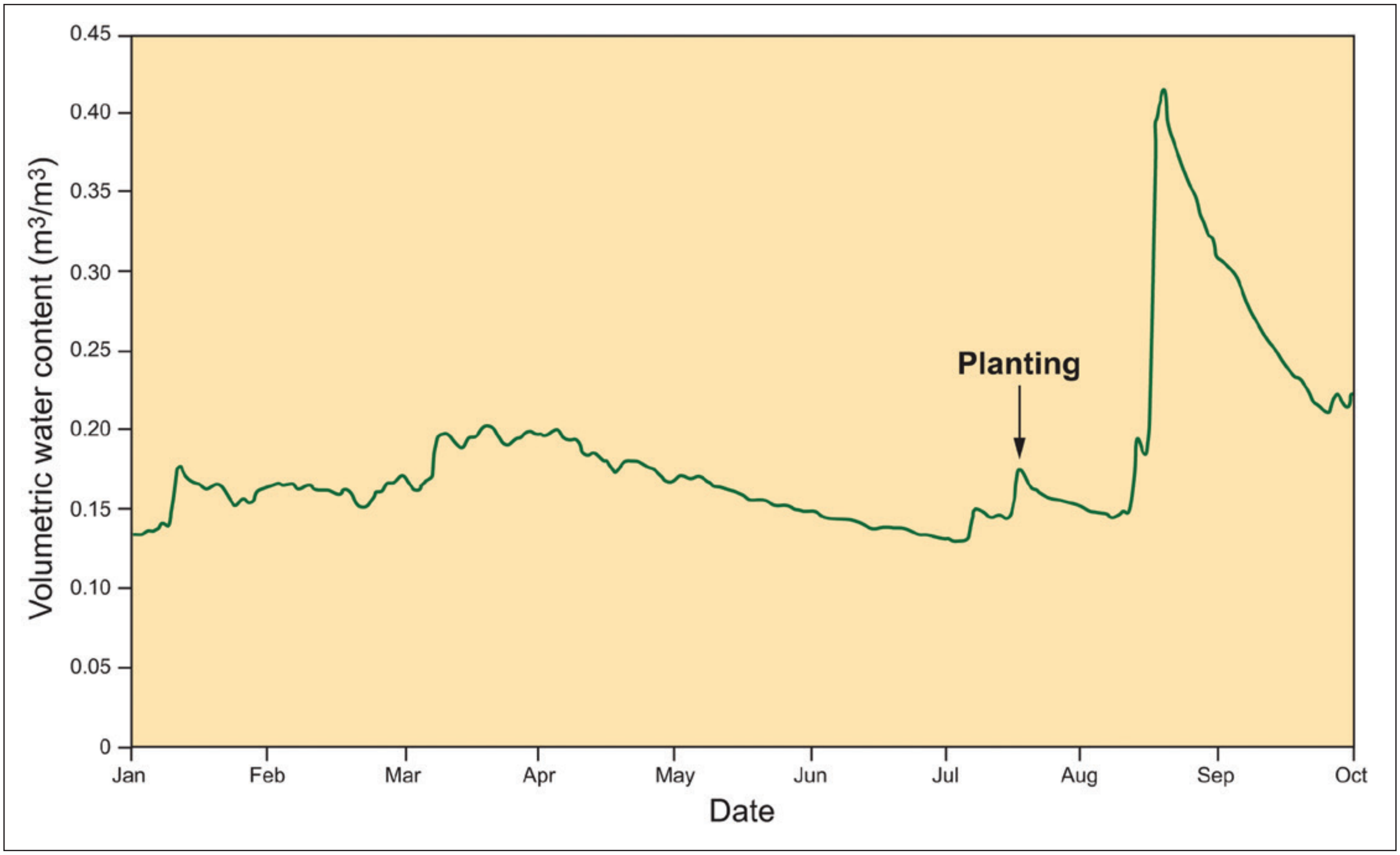

Figure 6. Soil volumetric water content (1 ft. depth) at the low-elevation test site in 2018. Seedlings were planted in mid-July when rains started, and most died in the next month when rains stopped for several weeks and soil water content dropped to about 0.15.

high-elevation (greater than 8,000 ft [2,438 m]) sources died fastest, and seedlings from low-elevation (less than 6,500 ft [1,981 m]) sources died slowest (figure 7). This result suggests greater inherent drought tolerance of low-elevation sources. Continuing measurements at the high- and mid-elevation field sites and greenhouse will provide information about trade-offs among heat-, drought-, and cold-tolerances of seed sources, as well as source by environment interactions that will inform revision of seed zones for the region.

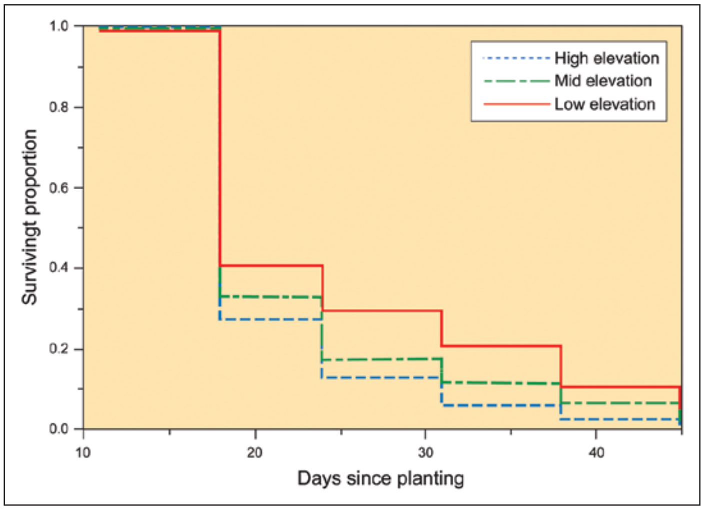

Figure 7. Surviving proportion of ponderosa pine seedlings planted in summer 2018 at the low-elevation, high-stress common-garden site from seed sources grouped by elevation (high = >8,000 ft [>2,438 m]); mid = 6,500 to 8000 ft [1,981 to 2,438 m]; low = <6,500 ft [<1,981 m]). The elevation groups differed significantly ($P < 0.05$) in survival duration.

Conclusions

We anticipate an increasing role in the Southwestern United States over the next few decades of tree-seedling production facilities, nursery cultural practices specific to semi-arid forest outplanting environments, genetic improvement of seedling drought and heat tolerances, and active reforestation by tree planting to help forests recover from severe disturbances. Such efforts are especially appropriate for publicly owned forests (e.g., Federal, State), which should be promptly regenerated after disturbance under current forest management laws. More research, such as the examples we describe here for ponderosa pine, is needed about improving the stress tolerance and performance of tree seedlings on harsh sites. We call for a renewed focus on tree regeneration by forest managers, practitioners, and scientists to sustain forests in the increasingly arid Southwestern United States.

Address correspondence to—

Thomas Kolb, Professor, School of Forestry, Northern Arizona University, Flagstaff, AZ 86001; email: tom.kolb@nau.edu

Acknowledgments

The authors thank: Diane Haase (U.S. Department of Agriculture, Forest Service) for providing helpful comments on the manuscript; the following programs for financial support: McIntire-Stennis appropriations to Northern Arizona University and New Mexico State University, and U.S. Department of Agriculture NIFA National Needs Fellowship Program Award 2011-38420-30989 to Northern Arizona University; and the following for help with establishing the greenhouse and field studies: Lorenzo Gallegos (New Mexico State University), Kevin Grady (Northern Arizona University), Karen Mock (Utah State University), Tammy Parsons (New Mexico State University), Phillip Patterson (Northern Arizona University), Carmen Rose (New Mexico State University), Ryan Zawodny (Northern Michigan University).

REFERENCES

Adams, H.D.; Kolb, T.E. 2005. Tree growth response to drought and temperature along an elevation gradient on a mountain landscape. Journal of Biogeography. 32: 1629–1640.

Alberto, F.J.; Aitken, S.N.; Alia, R.; Gonzaílez-Martinez, S.C.; Heikki, H.; Kremer, A.; Lefevre, F.; Lenormand, T.; Yeaman, S.; Whetten, R.; Savolainen, O. 2013. Potential for evolutionary responses to climate change – evidence from tree populations. Global Change Biology. 19(6): 1645–1661.

Allen, C.D.; Breshears, D.D. 1998. Drought-induced shifts of a forest-woodland ecotone: rapid landscape response to climate variation. Proceedings National Academy of Sciences. 95(25): 14839–14842.

Bell, D.M.; Bradford, J.B.; Lauenroth, W.K. 2014. Early indicators of change: divergent climate envelopes between life stages imply shifts in the western United States. Global Ecology and Biogeography. 23(2): 168–180.

Bingham, M.A.; Simard, S.W. 2013. Seedling genetics and life history outweigh mycorrhizal network potential to improve conifer regeneration under drought. Forest Ecology and Management. 287: 132–139.

Boisvenue, C.; Running, S.W. 2006. Impacts of climate change on natural forest productivity—evidence since the middle of the 20th century. Global Change Biology. 12(5): 862–882.

Bonnet, V.H.; Schoettle, A.W.; Sheppard, W.D. 2005. Postfire environmental conditions influence the spatial pattern of regeneration for Pinus ponderosa. Canadian Journal of Forest Research. 47: 37–47.

Burney, O.T.; Wing M.G.; Rose, R. 2007. Microsite influences on variability in Douglas-fir seedling development. Western Journal of Applied Forestry. 22(3): 156–162.

Burns, R.M.; Honkala, B.H., tech. coords. 1990. Silvics of North America. Vol. 1: conifers. Agriculture Handbook No. 654. Washington, DC: U.S. Department of Agriculture, Forest Service. 877 p.

Chambers, M.E.; Fornwalt, P.J.; Malone, S.L.; Battaglia, M.A. 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine-dominated forests of the Colorado Front Range. Forest Ecology and Management. 378: 57–67.

DeWald, L.E.; Mahalovich, M.F. 2008. Historical and contemporary lessons from ponderosa pine genetic studies at the Fort Valley Experiment Forest, Arizona. In: Olberding, S.D.; Moore, M.M., tech. coords. Fort Valley Experimental Forest—a century of research 1908–2008. Proceedings RMRS-P-55. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 204–313.

Dore, S.; Montes-Helu, M.; Hart, S.C.; Hungate, B.A.; Koch, G.W.; Moon, J.B.; Finkral, A.J.; Kolb, T.E. 2012. Recovery of southwestern ponderosa pine ecosystem carbon and water fluxes from thinning and stand-replacing fire. Global Change Biology. 18(10): 3171–3185.

Drake, J.E.; Aspinwall, M.J.; Pfautsch, S.; Rymer, P.D.; Reich, P.B.; Smith, R.A.; Crous, K.Y.; Tissue, D.T.; Ghannoum, O.; Tjoelker, M.G. 2015. The capacity to cope with climate warming declines from temperate to tropical latitudes in two widely distributed eucalyptus species. Global Change Biology. 21(1): 459–472.

Engemann, R.M.; Anthony, R.M.; Barnes Jr., V.G.; Krupa, H.W.; Evans, J. 1999. Evaluations of plastic mesh tubes for protecting conifer seedlings from pocket gophers in three western States. Western Journal Applied Forestry. 14(2): 86–90.

Flannigan, M.; Cantin, A.S.; de Groot, W.J.; Wotton, M.; Newberry, A., Gowman, I.M. 2013. Global wildland fire season severity in the 21st century: the mega-fire reality. Forest Ecology and Management. 294: 54–61.

Garfin, A.; Jardine, R.; Merideth, M. Black; LeRoy, S. 2013. Assessment of climate change in the southwest United States: a report prepared for the National Climate Assessment. Washington, DC: Island Press. 531 p.

Gómez, L.; Zamora, R.; Gómez, J.M.; Hódar, J.A.; Castro, J.; Baraza, E. 2004. Applying

plant facilitation to forest restoration in Mediterranean ecosystems: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications. 14(4): 1128–1138.

Haffey, C.; Sisk, T.D.; Allen, C.D.; Thode, A.E.; Margolis, E.Q. 2018. Limits to ponderosa pine regeneration following large high-severity fires in the United States Southwest. Fire Ecology. 14(1): 143–163.

Haire, S.L.; McGarigal, K. 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (Pinus ponderosa) in New Mexico and Arizona, USA. Landscape Ecology. 25(7): 1055–1069.

Hardin, J.E., Leopold, D.J., White, F.M. 2001. Textbook of dendrology. Boston, MA: McGraw-Hill. 501 p.

Hicke, J.A.; Meddens, A.J.H.; Kolden, C.A. 2016. Recent tree mortality in the western United States from bark beetles and forest fires. Forest Science. 62(2): 141–153.

Kolb, T.E.; Fettig, C.J.; Ayers, M.P.; Bentz, B.B.; Hicke, J.A.; Mathiasen, R.; Stewart, J.E.; Weed, A.S. 2016a. Observed and anticipated impacts of drought on forest insects and diseases in the United States. Forest Ecology and Management. 380: 321–334.

Kolb, T.E.; Grady, K.C.; McEttrick, M.P.; Herrero, A. 2016b. Local-scale drought adaptation of ponderosa pine seedlings at habitat ecotones. Forest Science. 62(6): 641–651.

Littrell, J.S.; McKenzie, D.; Peterson, D.L.; Westerling, A.L. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecological Applications. 19: 1003–1021.

North, M.P.; Stevens, J.T.; Green, D.F.; Coppoletta, M.; Knapp, E.E.; Latimer, A.M.; Restaino, C.M.; Tompkins, R.E.; Welch, K.R.; York, R.A.; Young, D.J.N.; Axelson, J.N.; Buckley, T.N.; Estes, B.L.; Hager, R.N.; Long, J.W.; Meyer, M.D.; Ostoja, S.M.; Safford, H.D.; Shive, K.L.; Tubbesing, C.L.; Vice, H.; Walsh, D.; Werner, C.M.; Wyrsch, P. 2019. Tamm Review: Reforestation for resilience in dry western U.S. forests. Forest Ecology and Management. 432: 209–224.

Ouzts, J.; Kolb, T.; Huffman, D.; Sanchez-Meador, A. 2015. Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. Forest Ecology and Management. 354: 281–290.

Owen, S.M.; Sieg, C.H.; Sanchez Meador, A.J.; Fule, P.Z.; Iniguez, J.M.; Baggett. L.S.; Fornwalt, P.J.; Battaglia, M.A. 2017. Spatial patterns of ponderosa pine regeneration in high-severity burn patches. Forest Ecology and Management. 405: 134–149.

Petrie, M.D.; Bradford, J.B.; Hubbard, R.M.; Lauenroth, W.K.; Andrews, C.D.; Schlaepfer, D.R. 2017. Climate change may restrict dryland forest regeneration in the 21st century. Ecology. 98(6): 1548–1559.

Pinto, J.R.; Dumroese K.R.; Davis, A.S.; Landis, T.D. 2011. Conducting seedling stocktype trials: a new approach to an old question. Journal of Forestry. 10(5): 293–299.

Puhlick, J.J.; Laughlin, D.C; Moore, M.M. 2012. Factors influencing ponderosa pine regeneration in the southwestern USA. Forest Ecology and Management. 264: 10–19.

Raffa, K.F.; Aukema, B.H.; Bentz, B.J.; Carroll, A.L.; Hicke, J.A.; Turner, M.G.; Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: dynamics of biome-wide bark beetle eruptions. Bioscience. 58: 501–518.

Rehfeldt, G.E.; Crookston, N.L.; Warwell, M.V.; Evans, J.S. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Science. 167(6): 1123–1150.

Rehfeldt, G.E.; Janquish, B.C.; Lopez-Upton, J.; Saenz-Romero, C.; St Clair, J.B.; Leites, L.P.; Joyce, D.G. 2014a. Comparative genetic responses to climate for the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: realized climate niches. Forest Ecology and Management. 324: 126–137.

Rehfeldt, G.E.; Jaquish, B.C; Saenz-Romero, C.; Joyce, D.G.; Leites, L.P.; St Clair, J.B.; Lopez-Upton, J. 2014b. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: reforestation. Forest Ecology and Management. 324: 147–157.

Reynolds, R.T.; Sánchez Meador, A.S.; Youtz, J.A.; Nicolet, T., Matonis, M.S.; Jackson, P.L.; DeLorenzo, D.G.; Graves, A.D. 2013. Restoring composition and structure in southwestern frequent-fire forests: A science-based framework for improving ecosystem resiliency. Gen. Tech. Rep. RMRS-GTR-310. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 76 p.

Roccaforte, J.P.; Fule, P.Z.; Chancellor, W.W.; Laughlin, D.C. 2012. Woody debris and tree regeneration dynamics following severe wildfires in Arizona ponderosa pine forests. Canadian Journal of Forest Research. 42: 593–604.

Rother, M.T.; Veblen, T.T.; Furman, L.G. 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. Canadian Journal of Forest Research. 45: 1607–1616.

Rother, M.T.; Veblen, T.T. 2016. Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. Ecosphere. 7(12): Article e01594.

Savage, M.; Mast, J.N.; Feddema, J.J. 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. Canadian Journal of Forest Research. 43: 570–583.

Schubert, G.H. 1974. Silviculture of southwestern ponderosa pine: the status-of-our knowledge. Research Paper RM-123. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Forest and Range Experiment Station. 71 p.

Schubert, G.H.; Heidmann, L.J.; Larson, M.M. 1970. Artificial reforestation practices for the Southwest. Agriculture Handbook 370. Washington, DC: U.S. Department of Agriculture, Forest Service. 25 p.

Seager, R.; Ting, M.; Held, I.; Kushnir, Y.; Lu, J.; Vecchi, G.; Huang, H.; Leetmaa, A.; Lau, N.; Li, C.; Velez, J.; Naik, N. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science. 316: 1181–1184.

Stevens-Rumann, C.S.; Kemp, K.B.; Higuera, P.E.; Harvey, B.J.; Rother, M.T.; Donato, D.C.; Morgan, P.; Veblen, T.T. 2017. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters. 21(2). https://doi.org/10.1111/ele.12889.

Taibi, K.; del Campo, A.D.; Mulet, J.M.; Flors, J.; Aguado, A. 2014. Testing Aleppo pine seed sources response to climate change by using trial sites reflecting future conditions. New Forests. 45(5): 603–624.

Trickler, P.J.; Rodríguez, C.M.; Hadley, L.P.; Wagstaff, C.; Wilkinson, M.J. 2013. Pre-conditioning the epigenetic response to high vapor pressure deficit increases the drought tolerance of *Arabidopsis thaliana.* Plant Signaling and Behavior. 8:10, DOI: 10.4161/psb.25974.

USDA Forest Service. 2016. Reforestation strategy – USDA Forest Service Southwestern Region. Internal Report by James Youtz, Regional Silviculturist.

Vickers, L.A.; Houser, J.; Rooni, J.; Guldin, J.M. 2018. Restoring ponderosa pine in the Davis Mountains of West Texas: impacts of planting practices on seedling survival. In: Kirschman, J.E., comp. Proceedings of the 19th biennial southern silvicultural research conference. e-Gen. Tech. Rep. SRS- 234. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 82–88.

Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. 2006. Warming and earlier spring increases western U.S. forest wildfire activity. Science. 313: 940–943.

Williams, A.P.; Allen, C.D.; Macalady, A.K.; Griffin, D.; Woodhouse, C.A.; Meko, D.M.; Swetnam, T.W.; Rauscher, S.A.; Seager, R.; Grissino-Mayer, H.D.; Dean, J.S. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change. 3(3): 292–297.

Williams, A.P.: Allen, C.D.; Millar, C.I.: Swetnam, T.W.; Michaelsen, J.; Christopher, C.J.; Leavitt, S. 2010. Forest responses to increasing aridity and warmth in the southwestern United States. Proceedings National Academy of Sciences. 107(50): 21289–21294. www.pnas.org/cgi/doi/10.1073/pnas.0914211107

Williams, M.I.; Dumroese, R.K. 2013. Preparing for climate change: forestry and assisted migration. Journal of Forestry. 111(4): 287–297.

Wu, Z.; Dijklstra, P.; Koch, G.W.; Peñuelas, J.; Hungate, B.A. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biology. 17(2): 927–942.

Xu, Y.; Mickley, L.J.; Logan, J.A.; Kaplan, J.O. 2013. Ensemble projections of wildfire activity and carbonaceous aerosol concentrations over the western United States in the mid-21st century. Atmospheric Environment. 77: 767–780.