Age-related Changes in Tree Growth and Physiology

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Advanced article

Article Contents

Trees pass through specific developmental phases as they age, including juvenile to adult, and vegetative to reproductive phases. The timing of these transitions is regulated genetically but is also highly influenced by the environment. Tree species have evolved different strategies and life histories that affect how they age – for example some pioneer species are fast growing and become sexually mature at younger ages but have shorter life spans. Trees do not have a strictly programmed senescence, and their life span is influenced by factors including challenges associated with increasing size, and ability to cope with environmental stress such as water availability, rot fungi, insects and disease pressure. Some long-lived tree species escape threats in exceptionally dry environments, while others use clonal reproduction through sprouts from stumps or roots to enable the same genotype to persist for thousands of years. On longer timescales, tree species migrate across landscapes to suitable environments.

Introduction

Trees undergo stages of maturation as they age, which are modified in response to environmental conditions. These stages can include differences in development and physiology that provide specific adaptive advantages at juvenile versus adult stages, such as faster growth rates of juvenile stages in some species that pioneer newly disturbed sites. Tree species have evolved various strategies to exploit different environmental niches that can drastically affect their maturation and longevity, ranging from fast growing pioneer species with short life spans to longer lived shade-tolerant species that can define some climax forest communities. The molecular mechanisms that regulate juvenile to adult transitions have only recently begun to be uncovered and include evolutionarily conserved micro-RNA (ribonucleic acid)-mediated mechanisms that influence juvenile to adult transitions and vegetative to reproductive transitions in a range of annual and perennial angiosperm species, including trees. Transition to reproduction is also influenced by conserved mechanisms in angiosperm trees, which determine when to flower by integration of information from physiological changes associated with size and carbohydrate metabolism with measurement of seasonal and environmental factors. The life span of trees may be influenced by the increasing reproductive potential over time as they become larger, in contrast to most species whose reproductive value is highest early in life and that experience natural selective pressures against old age. But trees do not have a strictly regulated age of senescence. Instead, the life span of trees is often dictated by size-related stress, abiotic stress, pathogens or rot-inducing fungi that digest their woody bodies.

eLS subject area: Plant Science

How to cite:
Groover, Andrew (June 2017) Age-related Changes in Tree Growth and Physiology. In: eLS. John Wiley & Sons, Ltd: Chichester.
DOI: 10.1002/9780470015902.a0023924

Ageing in Trees

As they grow, trees pass through phases of maturation, including juvenile to adult vegetative phase change, and vegetative to reproductive phase change. While these different types of phase change are genetically regulated, they are malleable and responsive to environmental cues.

Juvenile to adult vegetative phase transitions in trees can be associated with morphological and physiological changes, which may be striking or subtle depending on the species. Interestingly, the same tree can be composed of both juvenile and adult tissues and organs. In general, trees will display more juvenile characteristics in the inner canopy near the base of the tree and more adult characteristics towards the apical meristems and higher on the tree canopy (Wendling *et al*., 2014). Morphologically, differences in leaf shape (heteroblasty) (Critchfield, 1960), the presence of thorns or changes in bark texture are among the traits that can show distinctions between juvenile and adult forms. Juvenile trees may display larger and thinner leaves and can have architectures and leaf displays that maximise light capture and photosynthesis when shaded by larger trees. In some species, more juvenile portions of the tree may retain dead leaves after dormancy in the fall, while in more adult portions of the tree, leaves will be abscised and shed (Borchert, 1976).

Pronounced differences in physiology and phenology can also occur between juvenile and adult forms of trees (Augspurger and Bartlett, 2003). For many species, bud break is influenced by life stage and canopy position, with juvenile trees breaking bud and expanding leaves earlier in spring than adult trees. This observation may reflect a strategy for increasing photosynthesis and carbon gains by capturing light early in the growing season before canopy shading occurring after larger, adult trees leaf out. In general, adult trees tend to have lower photosynthetic rates (Bond, 2000) and may become less developmentally plastic. For example, in general, juvenile branches tend to be more amenable to development of adventitious roots than mature branches (Wendling *et al*., 2014).

Trees frequently show differences in the wood they produce in juvenile versus adult forms. Juvenile wood in general displays lower density, shorter cell lengths and higher cellulose microfibril angle in comparison to later-formed mature wood (Zobel and Sprague, 1998). Ecologically, it is possible that the more flexible juvenile wood provides flexibility allowing smaller diameter stems to tolerate wind, while more rigid mature wood is required to support the increasing weight of larger stems. In addition, wood is the water-conducting tissue of tree stems, and differences in the characteristics of water-conducting conduits in juvenile versus mature wood have a direct impact on growth and physiological processes.

Molecular Basis of Phase Changes

The biological mechanisms regulating vegetative to adult phase change in trees are only recently being uncovered, but at least one important mechanism has been described that suggests overlap between phase change in perennial trees and herbaceous angiosperms. Evolutionarily ancient microRNAs, miR156 and miR157, have been identified in both herbaceous and perennial angiosperms that target the transcripts of specific genes associated with phase change for degradation (Wang *et al*., 2011). The function of miRNA156 has been studied in detail, and the transition from juvenile to adult is associated with decrease in expression of miR156, allowing the increased accumulation of miRNA156-targeted transcripts encoding SQUAMOSA PROMOTER BINDING PROTEIN (SBP/SPL) transcription factors that promote the expression of adult traits. Interestingly, expression of miR156 is positively regulated by the same SBP/SPL transcription factors whose transcripts they degrade, and this negative feedback regulatory loop is believed to stabilise juvenile and adult phases (Wu *et al*., 2009). What initiates changes in miR156 expression? Physiological changes in carbohydrate metabolism have long been recognised as critical to juvenile to adult phase change, and sugar is thought to play a long-distance signalling role to repress expression of miR156 (Yang *et al*., 2013). Mechanistically, repression of miR156 expression is epigenetic, through increase in the histone H3 lysine 27 trimethylation (H3k27me3) chromatin mark on the miR156 promoter (Xu *et al*., 2015). (**see also**: **MicroRNAs (miRNAs) and Plant Development**)

Multiple molecular mechanisms also influence the transition to reproduction, and in at least some angiosperm species, phase change from vegetative to reproductive development is linked to juvenile to adult phase change. After transition to the adult phase, repression of miR156 expression leads to increased expression of SBP/SPL transcription factors, which in turn leads to increased expression of miRNA172. miRNA172 downregulates expression of AP2-like transcription factors that inhibit flowering (Aukerman and Sakai, 2003), thus creating permissive conditions for flowering when induced by appropriate environmental, physiological and developmental conditions.

The Varied Lifestyles and Life Histories of Trees Affect Maturation and Ageing

Forest tree species have evolved various lifestyles that have enabled them to occupy diverse ecosystems, ranging from tropical rainforests, to tundra, to desert. Tree species within a given ecosystem must cope with dynamic combinations of abiotic and biotic factors over their life spans, which can influence maturation, ageing and longevity. Within a given ecosystem, there can often be found tree species with different strategies to exploit the same habitat, and these strategies in turn also affect how a given species matures, reproduces and ultimately dies.

For example, in the western United States, juvenile quaking aspen (*Populus tremuloides*) can aggressively establish on sites after fire. The individual stems of these trees tend to be short lived (<200 years) but reach sexual maturity at relatively young age. In contrast, shade-tolerant conifer species (e.g. *Picea* and *Abies* spp.) can establish under aspens and in the absence of further fire or disturbance overtop and ultimately replace the shade-intolerant aspen (**Figure 1**). These longer lived species

Figure 1 **Forest succession can lead to mortality**. On this slope near Rabbit Ears Pass in Colorado, spruce (green trees) can be seen encroaching into an aspen stand (yellow trees). In the absence of disturbance such as fire, the longer lived shade-tolerant spruce can establish under the aspen, eventually overtopping and replacing the stand. Photo credit: Barry Lilly, US Forest Service.

Figure 2 **Extreme changes in maturation in longleaf pine**. Longleaf pine frequently establishes in sites after fire and can grow for many years in a 'grass' stage, which helps protect the apical and cambial meristems from fire (a). After establishing a root system that can support rapid growth, seedlings switch to elongative growth to achieve the mature form (b). Photo credit: John Kush, Auburn University.

also have adaptations, such as more rot-resistant wood, that allow individual trees to persist, potentially for many hundreds of years. Forest management regimes can have a major effect on aspen, with exclusion of fire and disturbance favouring eventual encroachment and replacement by conifers (Krasnow and Stephens, 2015).

A dramatic example of how a tree has evolved to meet specific ecological challenges by manipulating juvenile to adult is given by longleaf pine (*Pinus palustris*). Longleaf pine is a 'pioneer' species that grows in areas of the Southeastern United States that are prone to frequent fires (Varner *et al*., 2005). Its seed requires contact with bare mineral soil to germinate, as occurs after fire. After germination, this species often grows for several years in a juvenile 'grass stage', in which there is little height growth, with a dense growth of needles protecting the fire-sensitive apical and cambial meristems (**Figure 2**). After establishing an extensive tap root that can support fast growth, the seedling can rapidly grow in height to the adult form, which is resistant to ground-level fire and can live hundreds of years (**Figure 2**). In this case, longleaf pine can play the roles of both a pioneering species and a climax species on the same site.

Adaptations that exploit a given habitat often have trade-offs. Black cottonwood (*Populus trichocarpa*) excels at pioneering new habitats after flood in its habitat in the Pacific Northwest of North America (Stetller *et al*., 1996). Cottonwood is extremely fecund, and its wind-distributed seed can be seen as 'cotton' littering the landscape in the spring. These seed can germinate on newly formed sand bars after floods and grow rapidly to out compete other species and establish new stands along streams. This species can also pioneer new sites or expand to nearby sites through rooting of branches detached in storms or through shoots emerging as 'root suckers' from established trees. These fast growing trees achieve reproduction at a relatively young age. However, their wood is not highly resistant to decay, and their moist habitat is amenable to rot-inducing fungi that often colonise and weaken their stems (**Figure 3**). Often older, massive cottonwoods will be found with broken tops or branches, as a result of wind damage to the partially decayed tree. Although they can reach a large size through fast growth, individual trees typically do not live much greater than 100 years.

How Trees Mature and Die

Trees do not have a strictly programmed time of senescence, in contrast to monocarpic species that senesce after flowering

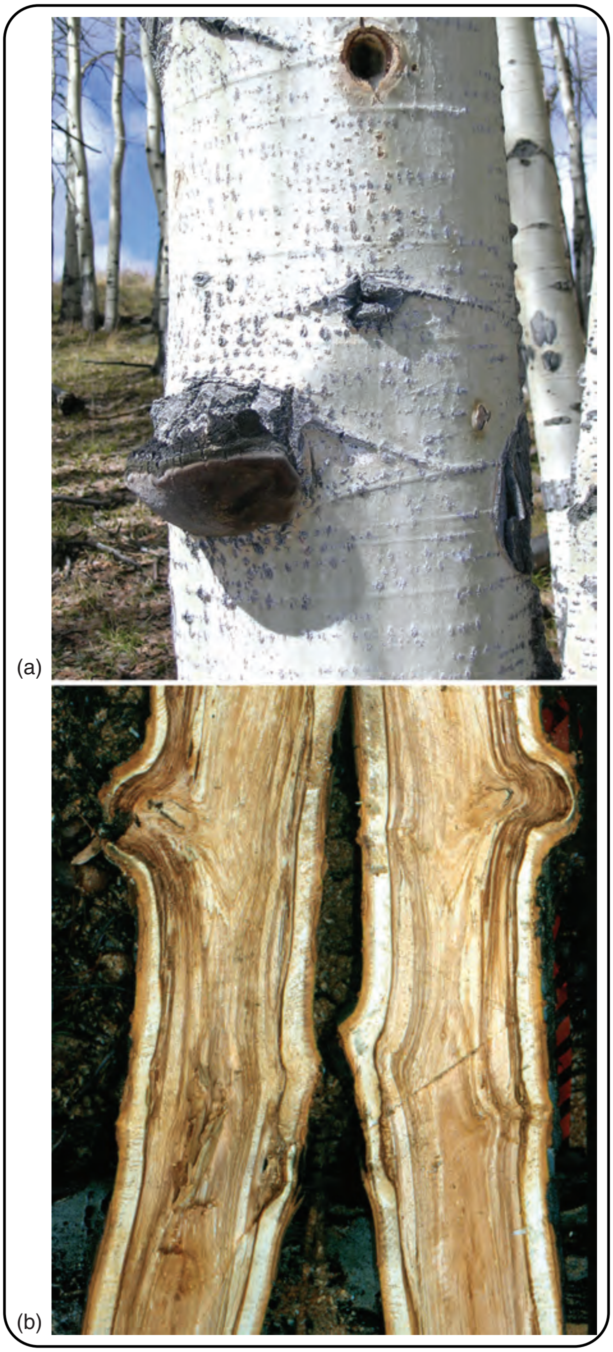

Figure 3 **Life span of individual stems in aspen is affected by fungal rots**. (a) A fruiting body of *Phellinus tremulae*, a shelf fungus and the cause of white trunk rot in aspen. (b) White trunk rot can cause death through direct damage to living sap wood and can weaken stems by decaying the heartwood, leading to susceptibility to mechanical breakage by wind or snow. An interesting ecological benefit – woodpeckers prefer making their nest cavities in aspen with decay. Photo credits: Jim Worrall, USDA Forest Service.

and producing seeds (Munné-Bosch, 2008). In fact, there has been speculation that trees may to some degree defy the forces that limit life span in most species (Ally *et al*., 2010). It has been hypothesised that senescence and limited life span may be the result of natural selection, which, in most species, is most effective during youth when reproductive capacity is greatest. In trees, however, perennial growth can result in larger bodies carrying more numerous reproductive structures and may also provide benefits to wind-based pollen or seed dispersal through greater height growth. Thus, there is potentially a large benefit to delaying senescence to enable larger growth of persistent woody bodies.

In addition to phase changes discussed previously, trees can also enter an 'old growth' period. Old age can be accompanied by decreases in rates of internode elongation, production of primary branches and height growth (Bond, 2000). Indeed, increase in overall size imposes challenges in terms of increased metabolic costs to maintain larger mass of living tissues. In addition, increased height results in challenges associated with water and mineral nutrient transport from roots to the top of the tree and transport of photoassimilate from foliage to roots. Strikingly, different tree species have predictable maximum heights, which are strongly influenced by species-specific characters associated with the anatomy and physiology of water-conducting secondary xylem (wood). It is believed that maximum tree height is limited by physical limits imposed by the cohesion–tension theory of water transport, where transpiration creates a negative pressure in the xylem which together with water adhesion and surface tension lifts water against gravity (Koch *et al*., 2004). Factors including the diameter of water-conducting tracheary elements and the types of interconnections (pits) between them contribute to differences among species in water conduction and maximum height. (**see also**: **Xylem: Differentiation, Water Transport and Ecology**)

Life span is highly influenced by how a tree interacts with abiotic and biotic environmental factors. Drought is an episodic event in most environments and a primary abiotic stress for trees and can lead to mortality directly or indirectly through 'carbon starvation' (McDowell *et al*., 2013). Stomata mediate gas exchange, including CO_2 required for photosynthesis, and also regulate loss of water through transpiration. During drought, closure of stomata can mediate water loss and also reduces the diffusion of CO_2 into the leaf, leading to deficits in photosynthesis that can lead to death over extended periods. Biotic factors that affect life span include insects and pathogens. Currently, invasive pathogens and insects are causing high mortality of numerous tree species around the world, including boreal forests that comprise the largest terrestrial biome (Sanderson *et al*., 2012). In addition, climate change drives shifts in the geographic ranges and life cycles of endemic insects and pathogens, resulting in complex interactions with potential hosts over time (Bentz *et al*., 2017). For species such as aspen (**Figure 3**), the action of wood-decaying fungi can have a major impact on life span, by digesting and weakening the primary stem and increasing risk of breakage.

Examining tree species with extreme life spans reveals two surprising strategies. The first is illustrated by species that occupy dry, harsh environments. While most *Populus* species occupy

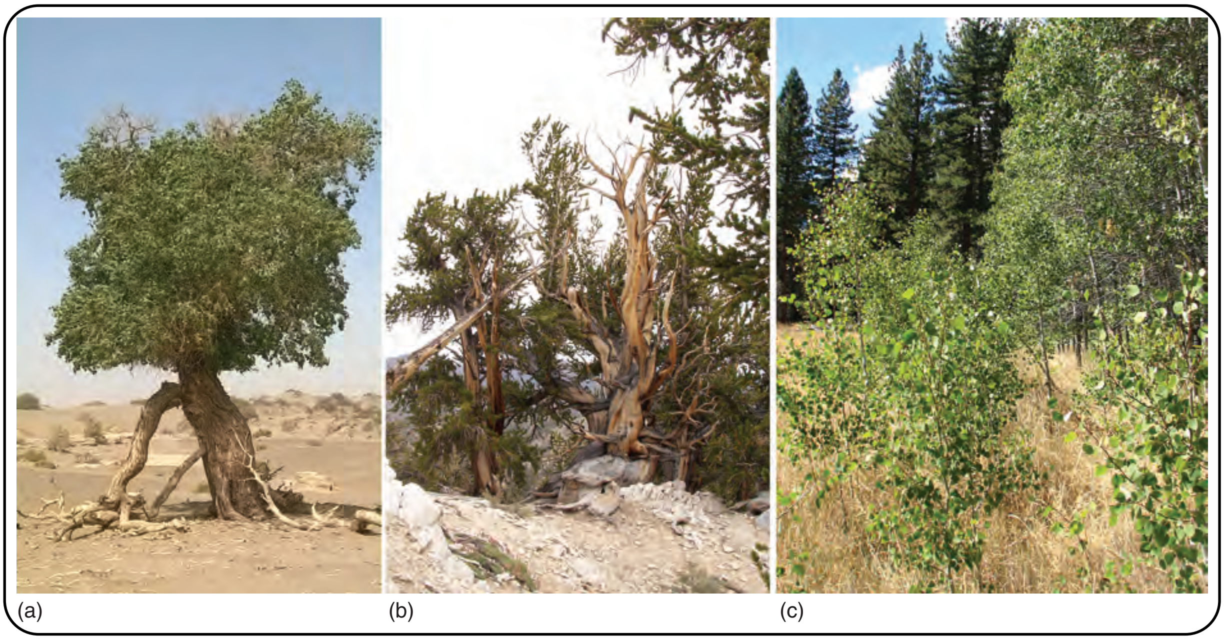

Figure 4 **Survival strategies for long-lived tree species**. (a) *Populus euphratica* growing in Inner Mongolia, China. In contrast to most trees within the genus *Populus*, individual stems of *P. euphratica* can persist for several hundred years and live in an extremely dry environment. While presenting obvious challenges, the dry environment may be the key in reducing the danger of parasitic and rot-causing fungi that can limit life span. (b) *Pinus longaeva* growing in the white mountains of California. (a,b) Photo credit: Suzanne Gerttula, US Forest Service. (c) *Populus tremuloides* clone near Lake Tahoe, California. Aspen (*P. tremuloides*) can propagate by 'root suckering', where new shoots arise from roots of established trees. The young trees in the foreground are clonal shoots extending into a meadow from the roots of older trees. In this way, aspen can incrementally pioneer new sites or else re-establish quickly after disturbances including fire. Large aspen clones can occupy dozens of hectares and live for thousands of years. (c) Photo credit: Andrew Groover, US Forest Service.

relatively moist sites, Euphrates poplar (*Populus euphratica*) is endemic to desert regions of Asia. Individual Euphrates poplar trees can achieve ages unusual for this genus – up to several hundred years (**Figure 4**). Presumably longevity in this species is enabled by low competition from other plant species, lower disease pressure from moisture-dependent pathogenic fungi and conditions antagonistic to wood-decaying fungi. The latter point is further illustrated by the observation that wood can remain standing for long periods after death of a Euphrates poplar tree. In the White Mountains of California, another tree species, bristlecone pine (*Pinus longaeva*), survives for thousands of years in dry, high elevation sites. In addition to factors enabling longevity mentioned earlier for Euphrates poplar, bristlecones likely escape fires that frequent more hospitable sites by being among the only species that can survive in its extreme habitat. In addition, bristlecone shows another feature of some long-lived species, compartmentalisation of tissues allowing strips of living stem to support a limited canopy even after the death of other stem tissues (**Figure 4**) (Lanner, 2002). Another strategy utilised by even longer lived species is clonal propagation. For example, *P. tremuloides* in the western United States can survive and propagate vegetatively through root suckers to create large clones of stems from the same genotype (**Figure 4**) (Mock *et al.*, 2008; DeWoody *et al.*, 2008). Some of these clones are believed to be tens of thousands of years old.

Species Survival and Extinctions

The evolution of traits influencing age-related changes in individual trees is linked to larger scale processes, including the migration and survival of populations and species over long timescales. Although individual trees are of course sessile, over the course of thousands of years tree populations can move across landscapes through dispersal of seed, followed by natural selection determining if seedlings can survive and reproduce in newly pioneered environments. As climate and local environmental conditions change over time, progressive establishment and reproduction in new environments can lead to migration. This process is illustrated by single-leaf piñon pine, which has been progressively migrating northward from southern refugia after the past glacial maximum (**Figure 5**). Early historic Native Americans likely played a role in the relatively rapid migration of single-leaf piñon (Grayson, 2011), an interesting accidental experiment that presages current debates concerning the 'assisted migration' of species (Aitken and Bemmels, 2016). Indeed, species that become geographically restricted and genetically depauperate are especially vulnerable to extinction. The pace of ongoing climate change raises major questions about the genetic and physiological resilience of tree species, and their ability to effectively migrate to new and potentially distant favourable environments (Ledig *et al.*, 2010).

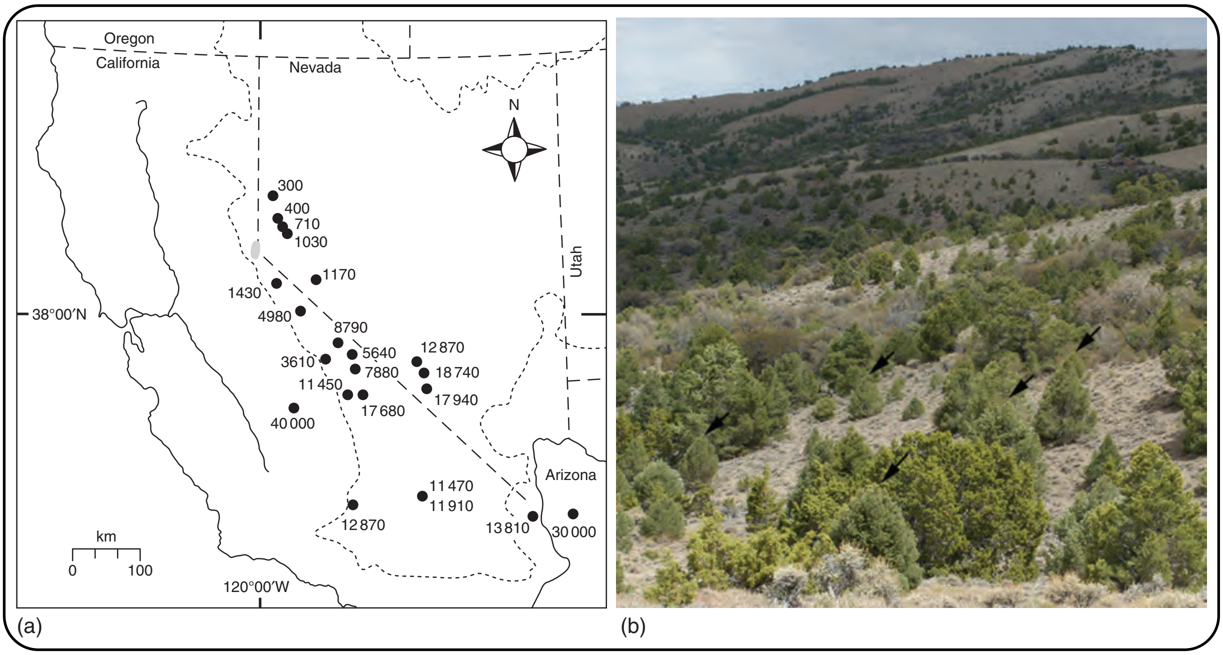

Figure 5 **Tree populations and species migrate over time in response to changes in climate**. (a) The migration of single-leaf piñon pine (*Pinus monophylla*) in the Pacific Southwest of the United States since the Last Glacial Maximum, moving from refugial regions in the current Mojave and Sonoran Desert. Data points correspond to the locations of and approximate dates of arrival (years before present) of expansion northward to its current distribution limit north of Reno, Nevada. Modified from Grayson (2011) © University of California Press. (b) Topography, water availability and other local factors influence migration patterns over the landscape. In this location in the Toquima Range of central Nevada, single-leaf piñon (arrows indicate individual piñon trees) is moving downslope to take advantage of higher water availability, as well as upslope as warming temperatures open ecological windows at higher elevations. Photo credit: Connie Millar, US Forest Service.

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