Drought Induced Tree Mortality and Ensuing Bark Beetle Outbreaks in Southwestern Pinyon-Juniper Woodlands

Michael J. Clifford[1], Monique E. Rocca[2], Robert Delph[1], Paulette L. Ford[3], and Neil S. Cobb[1]

***Abstract**—The current drought and ensuing bark beetle outbreaks during 2002 to 2004 in the Southwest have greatly increased tree mortality in pinyon-juniper woodlands. We studied causes and consequences of the drought-induced mortality. First, we tested the paradigm that high stand densities in pinyon-juniper woodlands would increase tree mortality. Stand densities did not impact mortality levels for either tree species, which does not support tree thinning to reduce susceptibility to drought-bark beetle outbreaks. Second, we monitored changes in stand structure and dead woody biomass to test whether altered fuel loads might affect potential fire behavior. Mortality can significantly affect torching index but has little effect on crowning index. Finally, we predicted that ground-dwelling arthropods would be highly responsive to habitat changes resulting from dead trees. Although we found significant responses, they were not as strong as predicted. Together, these results suggest that impacts of drought-induced tree mortality may not appear for years or decades after a major mortality event.*

Introduction

The southwestern United States has experienced drought in 9 of the past 10 years, with an extreme drought occurring in 2002 (NOAA 2002). Impacts of these drought conditions have been magnified in the semi-arid areas. Current and recent extreme drought conditions, coupled with increased regional temperatures, lead to stressed pinyon pines (*Pinus edulis*), which were then more susceptible to ips beetles (*Ips confusus*) (Breshears and others 2005). The combination of these three factors caused mortality among pinyons as high as 80 percent in many areas throughout the region (Breshears and others 2005; Shaw and others 2005; fig. 1). Drought and water-stressed host trees have been shown to lead to eruptive insect herbivore outbreaks in the past (Waring and Cobb 1992). With the relatively high susceptibility to climatic variations, pinyons have acted as "barometers of change" in Southwest ecosystems (Gitlin and others 2006; Ruel and Whitham 2002). Previous droughts in Southwest ecosystems have resulted in vegetation changes and shifts of ecotones (Allan and Breshears 1998). Outside the Southwest, climate change effects on vegetation have also been documented (Bigler and others 2006, Fensham and Holman 1999). Current global climate projections indicate further increases in temperatures and more extreme climatic events, such as drought (Easterling and others 2000; Hoerling and Kumar 2004; Intergovernmental Panel on Climate Change 2001). Likely scenarios include increased insect outbreaks (Logan and others 2003), elevational up-shifts of vegetation (Dullinger and others 2004), and increased frequency of extreme climatic events (Easterling and others 2000).

In: Gottfried, Gerald J.; Shaw, John D.; Ford, Paulette L., compilers. 2008. Ecology, management, and restoration of piñon-juniper and ponderosa pine ecosystems: combined proceedings of the 2005 St. George, Utah and 2006 Albuquerque, New Mexico workshops. Proceedings RMRS-P-51. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

[1] Merriam-Powell Center for Environmental Research and Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ.

[2] Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Fort Collins, CO.

[3] USDA Forest Service Rocky Mountain Research Station, Albuquerque, NM.

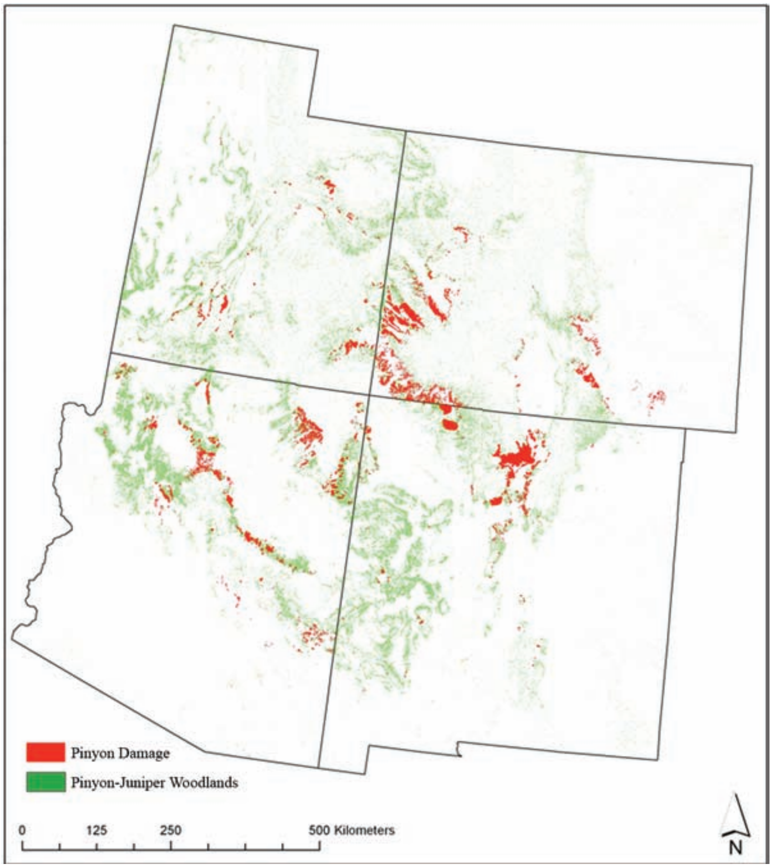

Figure 1—Forest Health Enterprise Team, USDA Forest Service aerial survey of pinyon damage in the Southwest from 2000-2005.

Pinyon-juniper woodlands are the third largest vegetation type in United States and cover over 19 million ha in the Southwest (Evans 1988). These woodlands are used for livestock grazing and wood harvest, and are culturally important to many Native American tribes. Current woodlands in many areas are denser than they were prior to Euro-American settlement. High density woodlands can increase tree stress from competition between trees, thus promoting increased disease susceptibility (Negron and Wilson 2003). Several studies examining pinyon stress and insect herbivore responses show that increases in environmental stressors alter tree-herbivore dynamics (Brown and others 2001; Cobb and others 1997; Waring and Cobb 1992). Expansion of pinyon-juniper woodlands since Euro-American settlement has produced efforts to reduce or remove pinyons and juniper in order to restore woodlands back to pre-settlement conditions (Brockway and others 2002; Ffolliott and Gottfried 2002).

Pinyon-juniper woodlands in northern Arizona and north-central New Mexico were surveyed. In each area, the majority of pinyon mortality occurred from the drought of 2002 (Breshears and others 2005). In these areas, we focused on several issues associated with causes and consequences of tree die-off. First, shifts in stand structures, needle retention, and tree fall of dead pinyons were documented while testing the paradigm that increased stand density will promote tree mortality. Negron and Wilson (2003) showed a positive relationship between pinyon death and an increased stand density index at a smaller, local scale before the major ips beetle outbreak of 2002. This paradigm was examined at the landscape scale after the major drought and pinyon die-off. Second, with changes in stand structure and increased dead woody debris throughout the woodlands, we hypothesized that fire dynamics would be altered in areas of high pinyon mortality. Third, after mortality of pinyons, ground-dwelling arthropod communities were expected to respond to altered habitat at both the population and community levels. By examining these hypotheses, we expect to quantify the response of several key woodland characteristics to a major co-dominant vegetation die-off. These results will assist in evaluating alternative management scenarios and will help to understand ecosystem responses to a future climate.

Methods

Study Sites

New Mexico—Study areas were located in the Middle Rio Grande Basin (MRGB) in north-central New Mexico. We created two types of sites in New Mexico: 1) intensive uniform study sites located in the north, central, and southern areas of the MRGB, and 2) random vegetation sites located throughout the MRGB. The intensive uniform sites were located in a grid pattern and separated into high and low pinyon mortality sites for each area. High and low mortality sites were relative to the mortality throughout the area. High mortality sites were determined to have visually higher mortality than low mortality sites. Each grid within the high and low mortality sites was 100 x 200 m, which was originally designed for 32 evenly spaced ground-dwelling arthropod pitfall traps. These sites were surveyed in 2005, tree status (in other words, alive, dead, standing, downed) and fuels data were collected in a 100 m^2 area around 16 of the 32 pitfall traps at each site. The random vegetation sites were located throughout the MRGB and were surveyed in 2005 and 2006. Each site was placed >5 km from another site. A site consisted of three 100 m^2 plots placed 75 m apart forming a triangular shape.

Arizona—The Arizona study area consisted of 52 sites located in northern Arizona. These sites were 200 x 10 m and split into 100 m^2 plots. Half of the plots were randomly selected for survey and were surveyed annually from 1998 to 2004. Sites were in pinyon-juniper woodlands at varying elevations, ranging from the upper to lower ecotones, and are representative of woodlands throughout the Region (Floyd and others, submitted).

Stand Structures

At each site in New Mexico (n = 53), all trees were measured for basal trunk diameter (BTD, also called root collar diameter), crown height and width, crown base height, and tree status. The documentation of spatial extent and intensity of pinyon die-off in the MRGB was determined by the random vegetation sites. These sites were also used to determine altered stand structures and shifts in age structures of pinyons, and the projected fall of pinyon snags. To test the effect of stand density on pinyon mortality, we used data from high and low mortality areas of the uniform plots. For this comparison, a one-way ANOVA was performed in SPSS (Version 14.0, 2005).

Arizona sites were surveyed from 1998 to 2004. The status of each tree was collected and the percent of needles remaining on dead pinyons was estimated. Estimates of percent crown foliage remaining were used to determine needle retention of dead trees.

Fire Model

Dead and down woody debris (in other words, fuel load measurements) were taken on all intensive uniform sites in each region of the MRGB, New Mexico, using a transect running north to south (see Brown 1974). Estimates of dead and down woody fuel loads were made for high and low mortality stands according to the procedure outlined in Brown and others (1982). Custom fuel models were developed based on average fuel loads for the high mortality and low mortality stands. Percentile weather scenarios were generated based on weather records from the Pecos RAWS, which were analyzed using the FireFamilyPlus software package to generate local estimates for a range of percentile weather conditions. Using the fire behavior program NEXUS (Scott 1999), fire behavior was simulated at the stand scale for high and low mortality stands under a range of percentile weather scenarios.

Arthropod Sampling

To test differences in the ground-dwelling arthropod community between high and low levels of pinyon mortality, pit-fall traps were used to capture arthropods. Pitfall traps (25 mm diameter) included Brosilicate glass test tubes encased by SDR 35 material PVC pipe, complete with a PVC lid to detour rain and debris from falling in the trap. Each test tube was filled with a 1:1 dilution of water and propylene glycol. We established 100 x 200-m grids within each sample area where 32 small pitfall traps were placed on a uniform grid at 35 m intervals.

Arthropod communities were analyzed using nonparametric multi-dimensional scaling (NMDS). This ordination shows differences or similarities between community structures in high and low mortality areas of the uniform sites in New Mexico. Indicator species analysis was also used to determine whether any arthropod species or groups showed a positive association with high or low pinyon mortality areas.

Results

Spatial Patterns of Mortality

Using random vegetation sites throughout the MRGB, we mapped the spatial extent and severity of tree mortality. The current patterns of pinyon mortality in the MRGB show a latitudinal gradient of mortality (fig. 2). In the southern portion (for example, Manzano Mountains) of the study area, pinyon mortality was relatively low (1.2 percent) compared to the central and northern areas (47 percent and 62 percent, respectively). The cause of this latitudinal gradient is unknown, as stand structures throughout the MRGB were similar. Perhaps this pattern can be attributed to associated susceptibility and origin of the initial ips outbreak. If the northern and central areas had a naturally higher ips population before 2002 than the southern area, there may not have been as eruptive outbreak in this area.

Stand Structures

Stand density did not significantly affect pinyon mortality across sites in New Mexico ($P = 0.281$). The high and low mortality sites did not have significantly different stand densities, but did have significantly different levels of pinyon mortality ($P < 0.0001$) (fig. 3) validating that visual observations were correct in classifying high and low mortality sites. This is evidence that increased stand densities do not predispose woodlands to tree mortality and therefore does not support the common paradigm at these scales. These results support the findings of Floyd and others (submitted),

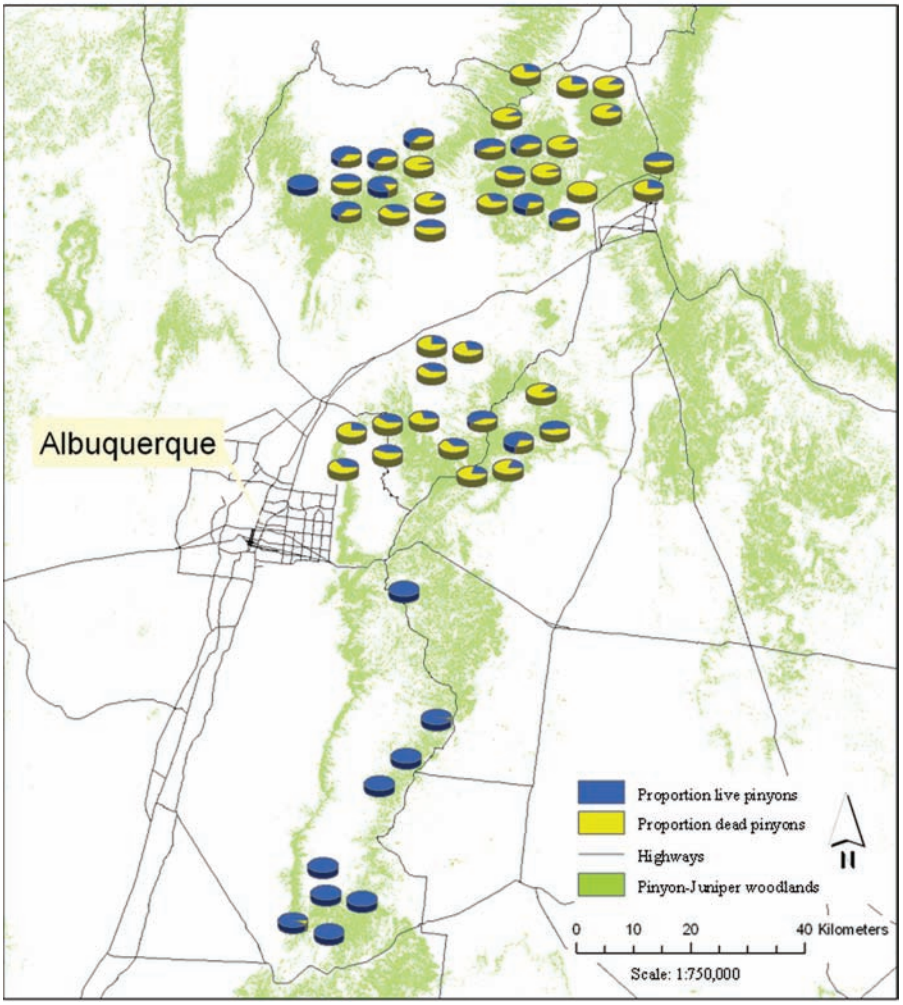

Figure 2—Pinyon mortality in the Middle Rio Grande Basin, New Mexico. The northern (62 percent) and central (47 percent) areas have much higher mortality of pinyons when compared the southern areas (1.2 percent).

which used linear regressions to explore the relationship of stand density and pinyon mortality. Perhaps, under outbreak conditions, traditional stressors (in other words, increased stand densities) are less important in tree mortality than insect population dynamics or landscape scale processes.

The stand structures of the pinyon-juniper woodlands were altered with the high mortality of pinyons. There was an overall shift toward a younger population of pinyons, as the larger, mature pinyons sustained a large loss (fig. 4A). The overall stand structures of the woodlands were altered with the reductions in basal area of pinyons. There remains a component of mature trees in these woodlands due to the retention of junipers (fig. 4B). Reductions in pinyon populations will alter future stand structures, and the current snags and dead trees will continue to alter and shape future stand structures. After 4 years, the majority of dead trees are still standing. It is expected that it will take an additional 7 years for all snags to fall (fig. 5). The effect of the falling snags will likely continue to alter fire regimes and ground-dwelling arthropod population dynamics. We also found that it takes an average of 9 months after mortality for pinyons to lose their needles (fig. 6). This confirms the observations of many others in the Southwest and indicates that for pinyon-juniper woodlands, extreme fire danger from dead retained needles occurs at approximately 9 months after tree death.

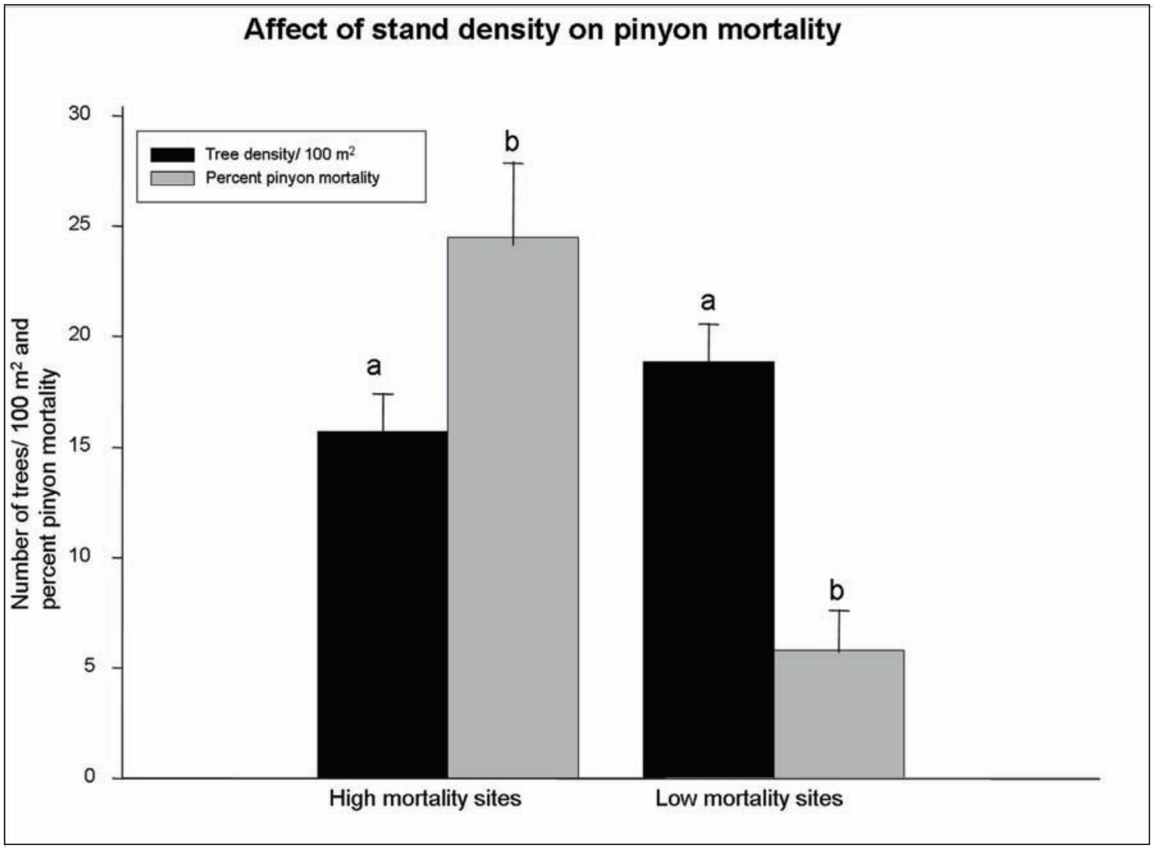

Figure 3—Stand density did not significantly affect pinyon mortality ($P = 0.281$). The high mortality area had significantly more pinyon die-off than the low mortality area ($P < 0.0001$). An "a" indicates non-significance, while a "b" is significant.

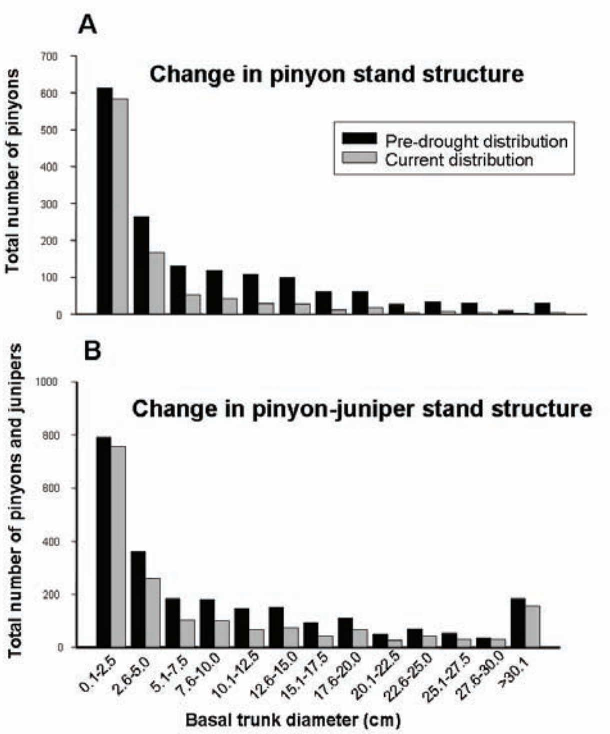

Figure 4—Pinyon stand structure, based on basal trunk diameters, showed severe reduction in larger, reproductive trees (A). When compared to total stand changes (which include junipers), there was still a large loss of larger trees in the population (B).

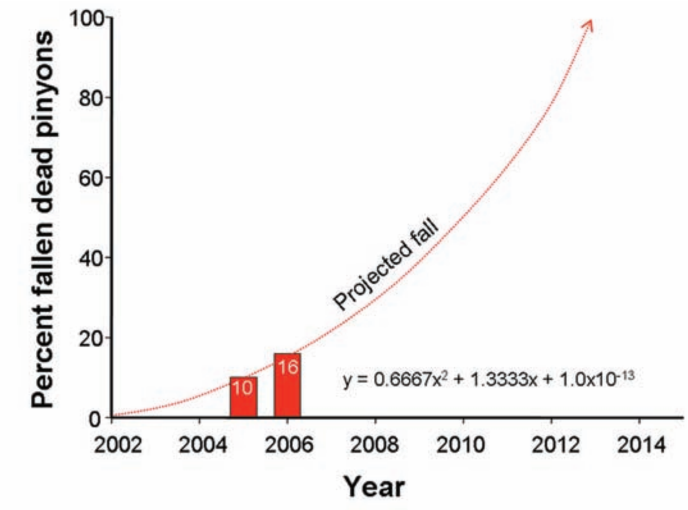

Figure 5—Projected fall of pinyon snags in the MRGB, New Mexico.

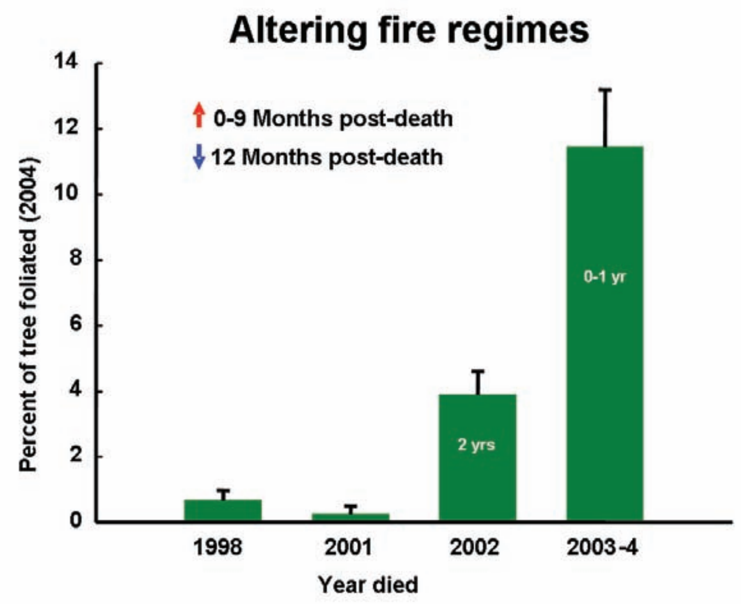

Figure 6—Time of needle retention for dead pinyons in Arizona. Needles were retained for an average of nine months.

Fire Modeling

The fire dynamics in pinyon-juniper woodlands were altered in areas of high pinyon mortality (fig. 7), supporting our hypothesis. Torching and crowning indices capture the severity of weather conditions required to initiate and propagate crown fire, respectively. The torching index is the windspeed (as measured 20 ft above the ground) that will cause the fire to be intense enough to begin to torch individual trees from below (passive crown fire). The crowning index is the windspeed that will cause the fire to spread from tree to tree (active crown fire). Moisture conditions below the 9th percentile will not carry fire (fig. 7).

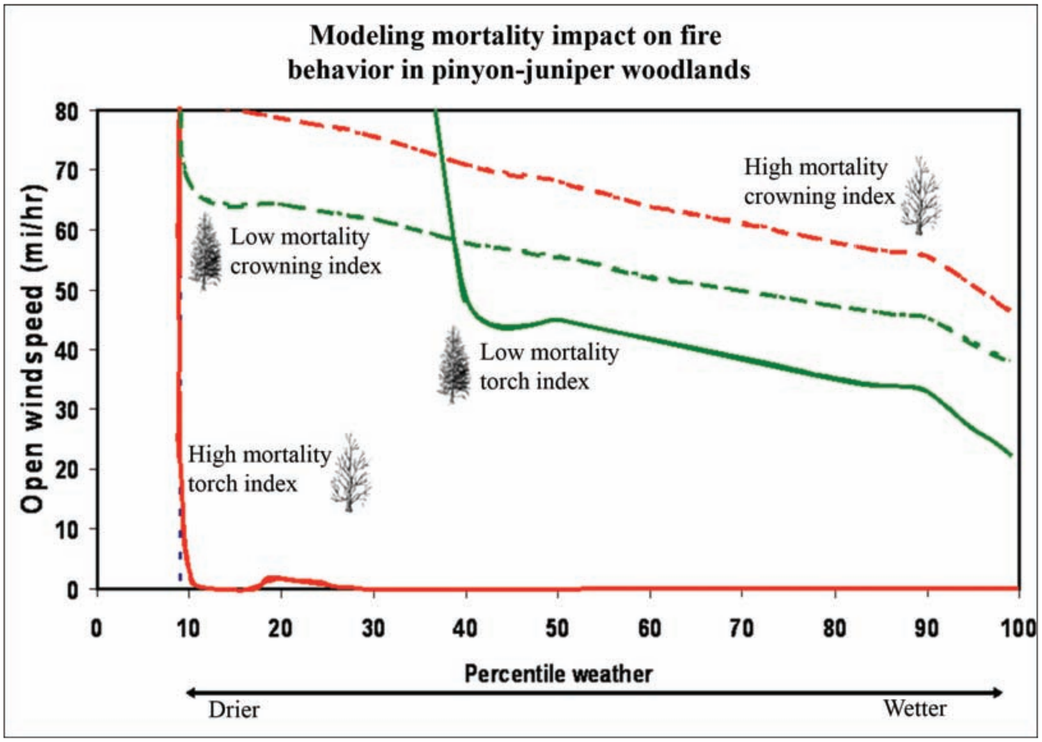

Figure 7—Model showing probability of fire start (torching index) and probability of a crown fire (crowning index) in high and low mortality sites of New Mexico.

Our models predict that fire ignitions will lead to surface fire behavior for the low tree mortality stands under most moisture conditions and for wind speeds up to 22 mph on the driest days. Higher winds will cause tree torching (passive crown fire), which will easily transition to active crown fire due to a relatively dense canopy structure. Due to higher surface fuel loads, high mortality stands cannot carry a surface fire under any weather conditions (fig. 7) without exhibiting torching fire behavior. However, the loss of much of the available canopy fuel (needles and twigs on tree canopies) has raised the crowning index.

Arthropod Indicators

It was hypothesized there would be a strong community response in areas of high pinyon mortality. Data indicate there are differences at the community level between high and low areas of pinyon mortality on the north and central sites, but not at the south site (fig. 8). The southern site had relatively low mortality, even in the “high” mortality areas, when compared to the north and central sites. This lack of high mortality, relative to other sites, may help to explain the lack of community response of ground-dwelling arthropods at this site. These community responses are not as strong as predicted, which may be due to a high number of pinyon snags that have not fallen. There were 15 indicator species (table 1), in high and low mortality areas, supporting our hypothesis. This shows there are responses at the species level and not just an overall community response to increased pinyon mortality.

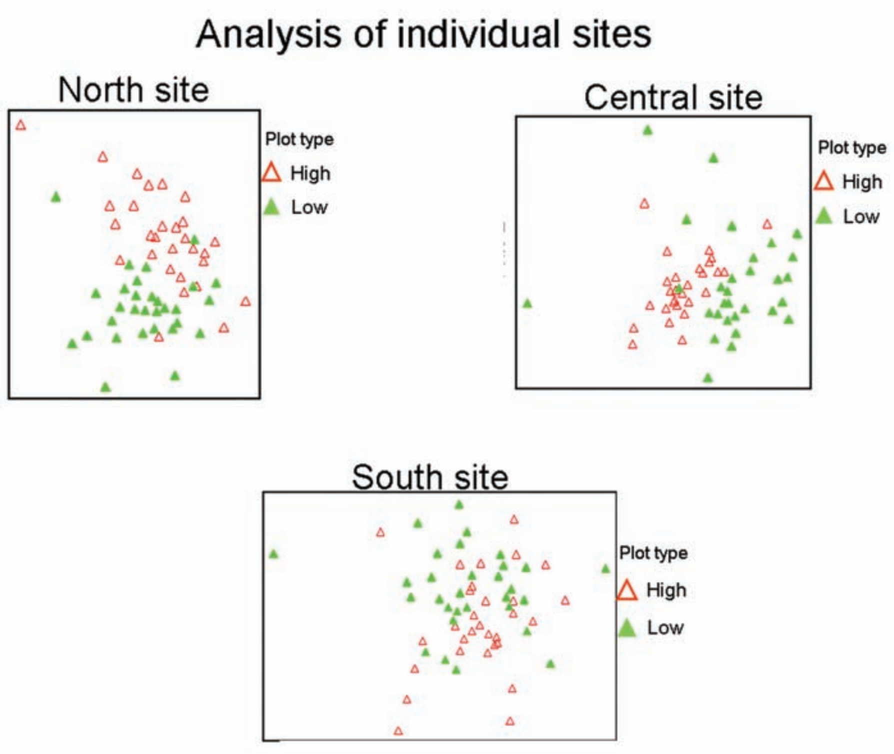

Figure 8—The scatter plots represent patterns of similarities in community structure. The affects of high and low tree mortality are the environmental variables influencing the community structure based on arthropod species abundance. Both north and central sites show strong grouping, more similar within groups than between groups of arthropod communities specific for high or low pinyon mortality areas. The south site did not show any groupings favorable for high or low pinyon mortality areas.

Table 1—List of arthropod indicator species for high and low areas of pinyon morality. Six taxa favored high pinyon mortality areas while 9 taxa favored low pinyon mortality areas. A “1” indicates presence.

			Central		North		South		Significance (α = 0.05)	
Order	**Family**	**Species**	**High**	**Low**	**High**	**Low**	**High**	**Low**	**High**	**Low**
Collembola	Hypogastruridae	COLE HYPO 001	1	1		1	1	1		0.002
Collembola	Entomobryidae	COLE ENTO 001	1	1	1	1	1	1	0.009	
Orthoptera	Gryllidae	*Gryllus* sp.		1	1	1	1	1		0.001
Coleoptera	Carabidae	*Pasimachus obsoletus*		1		1				0.001
Coleoptera	Tenebrionidae	*Eleodes obscurus*						1		0.007
Hymenoptera	Sphecidae	*Ammophila* sp.	1	1	1	1	1	1		0.042
Hymenoptera	Mutillidae	*Dasymutilla vestita*	1	1	1	1	1	1	0.001	
Hymenoptera	Formicidae	*Crematogaster depilis*	1	1	1	1	1	1	0.031	
Hymenoptera	Formicidae	*Monomorium cyaneum*	1	1	1	1	1	1	0.018	
Hymenoptera	Formicidae	*Solenopsis molesta*	1	1			1	1		0.003
Hymenoptera	Formicidae	*Liometopum apiculatum*	1				1	1	0.002	
Hymenoptera	Formicidae	*Camponotus acutirostris*	1	1	1	1	1			0.001
Aranea	Lycosidae	*Paradosa orophila*	1	1	1	1	1	1	0.025	
Acari	Erythraeidae	ACAR ERYT 001	1			1	1	1		0.047
Acari	Erythraeidae	ACAR ERYT 002	1	1	1	1	1	1		0.001

Discussion

Several aspects of pinyon mortality were documented, from potential causes of mortality to effects of mortality. First, stand densities did not influence pinyon mortality. Second, changes in stand structure altered fire dynamics and ground-dwelling arthropod communities. The die-off of a co-dominant woodland species throughout the Southwest has and will continue to alter and affect many ecological processes (in other words, fire cycle, carbon cycle, etc). Stand structures throughout the pinyon-juniper woodlands have become denser since European settlement (Ffolliott and Gottfried 2002). After 2002, these woodlands have become less dense with respect to living trees. This ips beetle-induced thinning of pinyon-juniper woodlands may indicate climatic changes or extreme events, serving as a natural thinner in a natural oscillation of woodland structures and vegetation dynamics (Allen and Breshears 1998).

Stand Structure

Regional die-off of pinyons has affected stand structure and age structure of pinyons, shifting the population toward younger, non-reproductive trees (fig. 5). The loss of many reproducing trees and reduced pinyon nut crops will likely affect granivores such as pinyon jays (*Gymnorhinus cyanocephalus*), pinyon mice (*Peromyscus truei*), and other fauna associated with pinyon-juniper woodlands. There will also be general changes in woodland ecosystem dynamics with upwards of 80 percent tree mortality. These include responses of understory plant species to the loss of canopy cover and shading with increased solar radiation and altered spatial distributions of soil moisture (Breshears and others 1997; Breshears 2006).

In both high and low mortality areas, stand density did not affect pinyon mortality. These results contradict the current paradigm that suggests higher density stands are more stressed and are therefore predisposed to increased mortality (Negron and Wilson 2003). The temporal context of this study differed from that of previous studies, which were conducted before the majority of pinyon die-off. The large spatial extent of our study may also explain our failure to detect a density effect on mortality. The paradigm of Negron and Wilson (2003), who's study focused on scales <10 km^2, could account for local patterns, but may not explain regional patterns of tree mortality. The severity, longevity, and increased temperatures of the current southwestern drought may have stressed trees to the point where nearly any susceptible tree, specifically pinyon, was attacked by ips beetles.

Fire Modeling

With shifts in stand structures and increases in dead woody fuel load, potential fire dynamics have changed 2 years post mortality. Less severe wind and moisture conditions are needed for crown fire initiation in high mortality areas whereas, in low mortality areas, active crown fire occurs at a lower windspeed (fig. 3). In low mortality areas, the live tree canopy has greater density of available fuel as compared to the high mortality areas. In other words, 2 years after pinyon mortality, the high mortality stands have been effectively thinned.

Associated with this "canopy thinning" are 1) a re-distribution of canopy fuels to the forest floor, and 2) a lowering of the average canopy base height of remaining live trees. A lower canopy base height is most likely an artifact of the increased relative abundance of junipers compared to pinyons after the beetle-kill event. Both factors will lower the torching index within the model framework. Yet the lower canopy base height is not "real" in the sense that the smaller surviving trees have not changed their canopy structure as individuals even though the average canopy base height has lowered. The increased surface fuel loads, however, would be expected to cause a more intense surface fire that will make torching behavior more likely for any canopy base height.

Pinyon mortality has altered potential fire dynamics in the Southwest, but the probability of a catastrophic fire due to high levels of dead trees is unlikely. For a crown fire to occur under the driest conditions (100 percentile), it would take an open wind speed of 50 mph in an area of high mortality for crown fire to be sustained.

There have been mixed results of bark beetle affects on fire regimes in many areas (Kulakowski and others 2003; Bigler and others 2005), but the mortality of pinyons was as high as 80 percent in some areas (Breshears and others 2005). The fire dynamics in pinyon-juniper woodlands have changed with the loss of canopy overstory and the addition of dead woody material on the woodland floor. Four years after the majority of the mortality event, most dead pinyons are still standing, creating a partial overstory of dead material. These new and changing characteristics have altered the probability that a fire is started and the way it will be carried in pinyon-juniper woodlands.

Arthropod Indicators

Many arthropod species (n = 15) showed either a positive or negative response to pinyon mortality (table 1). As indicator species, these arthropods will show a shift at the species level in areas of high and low pinyon mortality. Arthropod population dynamics are important for many ecosystem processes, and in current areas with high mortality there have already been responses. These responses were weaker than the predicted response, but can possibly be explained by the high amount of dead pinyons that remain standing (approximately 84 percent) (fig. 5). If these trees do not fall, then potential habitat for ground-dwelling arthropods will not be created. At the community level, we begin to show a shift in arthropod communities between differing areas of mortality (fig. 8). This community difference should increase as dead trees fall to the ground; however, the duration of this event may take another 6 years to complete (fig. 5).

Management Implications

Mortality of dominant species in major vegetation types has occurred throughout the world and continues to occur in many regions (Breshears 2006; Bigler and others 2006; Gitlin and others 2006; Logan and others 2003; Shaw and others 2005). Mortality of regionally dominant species, such as pinyon pine, suggests that climate change through increasing temperatures and frequent drought events, coupled with increased insect herbivore populations, will increase the probability of future mortality events (Breshears and others 2005). These continuing climatic conditions may alter regional vegetation and promote ecotone shifts (Allen and Breshears 1998; Risser 1995). With changes in dominant vegetation, many ecosystem processes are altered (in other words, biogeochemical processes, fire regime, ecohydrology) from local to regional scales (Breshears 2006), but the extent and intensity of these climatic driven events is still poorly understood.

In the pinyon-juniper woodlands of the Southwest, the full extent and impacts of this ongoing drought have yet to be quantified, but the effects are expected to last for decades or centuries. With the changes in stand structures and ips-induced thinning of Southwestern pinyon-juniper woodlands, mechanical treatment of woodlands considered “unhealthy” because of high tree densities will likely not be necessary. Bark beetles have shown spatially explicit patterns at the stand level and landscape level (Negron and others 2001), suggesting different spatial scales should be used to assess bark beetle induced tree mortality. The rearrangement of fuel loads may warrant management consideration, but the rapid rearrangement of canopy fuels to the forest floor appears more likely to reduce the likelihood of rapidly moving, wind-driven canopy fire rather than exacerbating it.

For management purposes, the frequency and severity of drought are more important than long-term average climate conditions. Too often land managers plan for average climate conditions rather than the climatic extremes that can be expected (Potter and Ford 2004). The future management of pinyon-juniper woodlands must take into consideration predicted extreme climatic events. Southwestern ecosystems, especially the semi-arid woodlands, are susceptible to these extreme events (Allen and Breshears 1998; Breshears and others 1997; Breshears and others 2005; Ruel and Whitham 2002; Swetnam and Betancourt 1998) and may act a barometer for climatic change.

Acknowledgments

We thank J. Vespi, J. Johnson, G. Lung, K. Mulchay, A. Horner, and J. Higgins for field assistance, arthropod sorting, and identification. Thanks to Jeanine Paschke for providing aerial survey data. This research was supported by USDA Forest Service Rocky Mountain Research Station, Middle Rio Grande Ecosystem Management Unit and National Science Foundation RCN program (RCN0443526) for the Drought Impacts on Regional Ecosystems Network (DIREnet).

References

Allen, C.D. and D.D. Breshears. 1998. Drought induced shifts of a forest-woodland ecotone: Rapid landscape response to climate variation. Proceedings National Academy of Science USA 95: 14839-14842.

Bigler, C., D. Kulakowski, and T.T. Veblen. 2005. Multiple disturbance interactions and drought influence fire severity in rocky mountain subalpine forests. Ecology 86: 3018-3029.

Bigler, C, O.U. Braker, H. Bugmann, M. Dobbertin, and A. Rigling. 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9: 330-343.

Breshears, D.D. 2006. The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? Frontiers in Ecology and the Environment 4: 96-104.

Breshears, D.D., P.M. Rich, F.J. Barnes, and K. Campbell. 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecological Applications 7: 1201-1215.

Breshears, D.D., N.S. Cobb, P.M. Rich, K.P. Price, C.D. Allen, R.G. Balice, W.H. Romme, J.H. Kastens, M.L. Floyd, J. Belnap, J.J. Anderson, O.B. Myers, and C.W. Meyer. 2005. Regional vegetation die-off in response to global-change type drought. Proceedings National Academy of Science USA 102: 15144-15148.

Brockway, D.G., R.G. Gatewood, and R.B. Paris. 2002. Restoring grassland savannas from degraded pinyon-juniper woodlands: Effects of mechanical overstory reduction and slash treatment alternatives. Journal of Environmental Management 64:179-197.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA Forest Service Gen. Tech. Rep. GTR-INT-16.

Brown, J.K., R.D. Oberheu, and C.M. Johnston. 1982. Handbook for inventorying surface fuels and biomass in the interior west. USDA Forest Service Intermountain Research Station Gen. Tech. Rep. GTR-INT-129.

Brown, J.H., T.G. Whitham, K.M. Ernest, and C.A. Gehring. 2001. Complex species interactions and the dynamics of ecological systems: Long-term experiments. Science 293: 643-650.

Cobb, N.S., S. Mopper, C.A. Gehring, M. Caouette, K.M. Christensen, and T.G. Whitham. 1997. Increased moth herbivory associated with environmental stress of pinyon pine at local and regional levels. Oecologia 109: 389-397.

Dullinger, S., T. Dirnbock, and G. Grabherr. 2004. Modelling climate change-driven treeline shifts: Relative effects of temperature increase, dispersal and invisibility. Journal of Ecology 92: 241-252.

Easterling, D.R., G.A. Meehl, C. Parmesan, S.A. Changnon, T.R. Karl, and L.O. Mearns. 2000. Climate extremes: Observations, modeling, and impacts. Science 289: 2068-2074.

Evans, R.A. 1988. Management of pinyon-juniper woodlands. Gen. Tech. Rep. INT-249, USDA Forest Service, Intermountain Research Station, Ogden, UT.

Fensham, R.J. and J.E. Holman. 1999. Temporal and spatial patterns in drought-related tree dieback in Australian savanna. Journal of Applied Ecology 36: 1035-1050.

Ffolliott, P.F. and G.J.Gottfried. 2002. Dynamics of a pinyon-juniper stand in northern Arizona: A half century of history. Gen. Tech. Rep. RMRS-RP-35. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Floyd, M.L., N. Cobb, D. Hanna, R. Delph, M. Clifford, and P. Ford. Mortality patterns in piñon-juniper woodlands in Colorado, New Mexico and Arizona: Does increasing stand density increase tree mortality? Western Journal of Applied Forestry (submitted).

Gitlin, A.R., C.M. Sthultz, M.A. Bowker, S. Stumpf, K. Ecton, K. Kennedy, A. Munoz, J.K. Bailey, and T.G. Whitham. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. Conservation Biology 20: 1477-1486.

Hoerling, M. and A. Kumar. 2004. The perfect ocean for drought. Science 299: 691-694.

Intergovernmental Panel on Climate Change. 2001. Climate Change 2001: Synthesis Report, A Contribution of Working Groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change, eds. Watson, R.T. and Corte Writing Team (Cambridge University Press, New York).

Kulakowski, D., T.T. Veblen, and P. Bebi. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. Journal of Biogeography 30: 1445-1456.

Logan, J.A., J. Regniere, and J.A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment 1: 130-137.

Negron, J.F., J.A. Anhold, and S. Munson. 2001. Within-stand spatial distribution of tree mortality caused by the Douglass-fir beetle (Coloeptera: scolytidae). Environmental Entomology 30: 215-224.

Negron, J.F. and J.L. Wilson. 2003. Attributes associated with probability of infestation by the piñon ips, *Ips confusus* (Coleoptera: scolytidae), in the piñon pine, *Pinus edulis*. Western North American Naturalist 63: 440-451.

NOAA (National Oceanic and Atmospheric Administration). 2002. U.S. Drought Monitor: http://www.drought.unl.edu/dm/index.html

Potter, D.U. and P.L. Ford. 2004. Chapter 7. Grassland sustainability. Pp. 130-141. In: D. M Finch, Editor. 2004. Assessment of grassland ecosystem conditions in the Southwestern United States. Volume 1. Gen. Tech. Rep. RMRS-GTR-135-vol. 1. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 167 p.

Risser, P.G. 1995. The status of the Science of examining ecotones. BioScience 45: 318-325.

Ruel, J. and T.G. Whitham. 2002. Fast growing juvenile pinyons suffer greater herbivory when mature. Ecology 83: 2691-2699.

Scott, J.H. 1999. NEXUS: a system for assessing crown fire hazard. Fire Management Notes 59: 20-24.

Shaw, J.D., B.E. Steed, and L.T. DeBlander. 2005. Forest Inventory and Analysis (FIA) annual inventory answers the question: What is happening to pinyon-juniper woodlands? Journal of Forestry 106: 280-285.

SPSS for Windows. 2005. Version 14.0. Chicago, Illinois. SPSS, Incorporated.

Swetnam, T.W. and J.L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. Journal of Climate 11: 3128-3147.

Waring, G.L. and N.S. Cobb. 1992. The impact of plant stress on herbivore population dynamics. Pages 167-226, volume 4 *in* E.A. Bernays, editor. Plant-Insect Interactions. CRC Press, Boca Raton Florida.