

# Soil properties affect pinyon pine – juniper response to drought

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## ABSTRACT

Since the late 1990s, drought-driven dieback has affected more than a million hectares of pinyon pine-juniper woodlands in the southwestern USA. Analysis of annual aerial surveys by the US Forest Service and soil survey data shows that most of the mortality occurred between 2003 and 2004 and that 70% was restricted to soils mapped as having available water storage capacities ( $A_c$ ) <100 mm. We conducted a more refined analysis and found that as  $A_c$  increased in increments of 50 mm up to 300 mm, the distribution of areas with observed mortality decreased exponentially from 42% to 3% ( $n=6$  classes,  $r^2=0.93$ ). We used this information in a process-based stand growth model, physiological principles predicting growth, to assess year to year variation in gross photosynthesis between 1985 and 2005 with climatic data at monthly intervals from four weather stations where pinyon-juniper woodlands were confirmed by satellite imagery. A sensitivity analysis identified sustained periods of drought and supported field observations that once canopy leaf area approaches a maximum value, the majority of mortality should be restricted to soils with  $A_c$  values <100 mm. Additional analyses indicated that differences in soil texture played a small part (<10%) in the variation of gross photosynthesis and that consecutive years of drought may have a cumulative effect on pinyon pine vulnerability to bark beetle attack. Disturbances reducing canopy leaf area index should result in less pine mortality in the future, although conversion to shrub and grassland may occur if climate conditions continue to become less favorable. Copyright © 2012 John Wiley & Sons, Ltd.

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## INTRODUCTION

Pinyon pine (*Pinus edulis*), in association with juniper (*Juniperus osteosperma* and *Juniperus scopulorum*), covers approximately 15 million acres in Utah, Colorado, New Mexico and Arizona with sporadic occurrences in Texas, Oklahoma, Wyoming, California and Mexico. Over the areas that these species occupy, elevations range between 1370 and 2440 m, and mean precipitation varies from 250 to 560 mm annually (Burns and Honkala, 1990). Studies of pollen fossils from the 13th and 14th centuries indicate that pinyon pine expanded its range in response to increases in precipitation and contracted its distribution following prolonged periods of drought on approximately decadal intervals (Gray *et al.*, 2006). The explanation for the shift in dominance from juniper to pinyon pine reflects differences in tree physiology. Pinyon pine has higher photosynthetic rates than juniper when water is more available, whereas juniper continues to photosynthesize longer with increasing water stress (Lajtha and Barnes, 1991; Schwinning *et al.*, 2002; Williams and Snyder, 2003).

More recently, between 1998 and 2010, scientists in the southwestern USA have reported extensive dieback in pinyon-juniper associated with multiple-year drought (Shaw *et al.*, 2005; Breshears *et al.*, 2009; Floyd *et al.*,

2009). Research is underway to clarify the exact cause of mortality (Gray *et al.*, 2006; McDowell *et al.*, 2008; Barger *et al.*, 2009; Allen *et al.*, 2010). Under prolonged drought, a lower photosynthetic rate may prevent pine from producing sufficient oleoresins, making trees more susceptible to bark beetles, fungi and other biotic agents (Cobb *et al.*, 1997; McDowell *et al.*, 2008). Juniper, although not attacked by bark beetles, may continue to transpire until the vascular system becomes inoperative (McDowell *et al.*, 2008).

Mature stands of pinyon pine growing with juniper normally exhibit tree mortality rates of <0.5% annually (Shaw *et al.*, 2005). Stand growth models, using a  $-3/2$  power function between tree number and stand biomass, predict similar low rates of mortality under stable climatic conditions (Landsberg and Waring, 1997). Under variable climatic conditions, mortality rates may vary considerably from the norm. Regional observations indicate that recent pinyon pine mortality, although widespread, varies considerably year to year and place to place (Shaw *et al.*, 2005). Ogle *et al.* (2000) compared growth rates of trees over a range of sites and found that those that died showed more interannual variation in ring widths during the previous decade than those that survived.

Tree physiologists refined the correlation by noting that tree susceptibility to insect attack is better related to wood production per unit of leaf area than to diameter growth alone (Larsson *et al.*, 1983; Mitchell *et al.*, 1983; Waring and Pitman, 1983). Betancourt *et al.* (1993) suggested that further insights might be gained by using process-based

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models to investigate when drought differentially affects pinyon pine and juniper. West *et al.* (2008) developed such a model, but in considering competition among species, extensive data requirements limit its application.

In this paper, we simplify the data requirements for process modeling by combining the properties of pinyon pine and juniper into a generic woodland type. We hypothesize that once equilibrium leaf area for a site is reached, the spatial variation in recent tree mortality will be accounted for by interannual climatic variation combined with the soil water holding capacity. To test this hypothesis, we first collected maps of areas within the pinyon-juniper woodland type in Utah, Arizona, Colorado and New Mexico that have shown significant spatial and temporal variation in mortality. Next, we overlaid maps classifying differences in soil water holding capacity ( $A_c$ ) and tallied the corresponding areas with observed mortality to seek a predictive relationship. Finally, to evaluate the importance of soil water storage capacity versus soil texture in explaining the observed patterns of mortality, we utilized a simplified process-based growth model to analyse and interpret relative variations in gross photosynthesis between 1985 and 2005 at representative sites in the four southwestern states.

## METHODS

### *GIS analysis of pinyon-juniper mortality and soil characteristics*

The pinyon-juniper dieback data were developed by the Merriam-Powell Center for Environmental Research (MPCER) at Northern Arizona University from an aerial mapping project of the United States Department Forest Service (USFS), Forest Health Technology Enterprise Team (FHTET). MPCER selected individual species from the United States Forest Service original dataset, which used aerial detection surveys to map insect, disease and abiotic damage to forested areas in the USA. The USFS aerial surveys combine low-level flights (315–630 m above ground level) and United States Geological Survey paper maps (1:100,000 scale) as well as a digital sketchmap system [global positioning system (GPS) and geographic information system (GIS) database] to record disturbance on an annual basis. Because of the size of the polygons and the patchy nature of forest insect activity, some polygons may contain unaffected areas. For the sake of recording new damage, only trees with yellow, brown or red foliage or some defoliation were mapped as part of the aerial survey. Dead trees with no foliage were assumed to be recorded in a previous year's study. The MPCER dataset refined the FHTET dataset to remove the effects of past dieback and focus the data on individual species.

We aggregated the tree dieback dataset for all years (2000–2007) to create one large dieback dataset and intersected this with the Natural Resources Conservation Service Soil Geographic Database (SSURGO) for the region. SSURGO soil surveys are usually 1:20 000 to

1:24 000 in scale and reported on the county level. We used a Python script to aggregate all soil survey data available for Arizona, New Mexico, Colorado and Utah, and attached the relevant fields from the National Soil Information System database to the map units as attributes. There were some gaps in the SSURGO coverage of the region, especially in Utah, but most of these did not overlap areas where tree mortality was recorded. The total difference between the tree mortality dataset and the SSURGO soils data within the dieback polygons was only ~1%. The US General Soil Map (STATSGO2, 1:250 000) was far too coarse to improve the soils dataset by filling in the minor gaps. The intersected SSURGO soil map units with similar values were aggregated to create two new datasets representing available water storage capacity and texture. X-Tools Pro (Data East) was used in ArcMap (ESRI) to calculate the areas where mortality was extensive. The results of the GIS analysis are used in the physiological principles predicting growth (3-PG) model to learn where, why and when drought and soil available water affect pinyon-juniper woodlands.

### *Site description*

The climate throughout southwestern North America is notably dry with most of the precipitation falling from late June through September (Sheppard *et al.*, 2002). The El Niño-Southern Oscillation cycles cause extreme variation in precipitation. Weiss *et al.* (2004) documented that such variation is reflected in a consistent manner from satellite-derived estimates of greenness across six broad types of vegetation, including pinyon-juniper woodlands. Ogle *et al.* (2000) confirmed that interannual variation in precipitation is reflected in tree-ring records. Although the general climatic patterns are widespread, the effect of drought may differ depending on the density of vegetation and local climatic conditions. We downloaded monthly temperature and precipitation records from sites in Arizona, Colorado, New Mexico and Utah, available from the Western Climate Center (<http://www.wrcc.dri.edu>). The weather stations, their location and climatic summaries for the period 1985–2005 are presented in Table I. Included in the summaries is an assessment of the relative decrease in the number of subfreezing days over the years analysed, which varied from 5% to 24% over the two decades.

### *Processing of climatic data*

To understand and model how climatic conditions affect tree growth requires additional information beyond that recorded at most weather stations. The upper limits on photosynthesis are set by the amount of visible light intercepted by leaves, and further constrained by frost, the atmospheric vapor pressure deficit, and the net radiation. Fortunately, these additional variables can be derived from monthly mean temperature extremes along with knowledge of the location, calendar date, physiography and canopy leaf area.

To estimate mean monthly daytime vapor pressure deficits ( $D$ ), we assumed that the water vapor concentration

Table 1. Location and climatic summaries (1985–2005) for meteorological stations obtained from the Western Regional Climate Center.

Station	Latitude (decimal degrees)	Longitude (decimal degrees)	Elevation (m)	Mean max monthly temp (°C)	Mean min monthly temp (°C)	Mean annual precip (mm)	Mean annual frost days	% decrease frost days – 20-yr period
Bowie, AZ	32.32647	-109.4870	1147	36.3	-0.1	313	41	5%
Socorro, NM	34.06167	-106.8994	1442	34.3	-5.4	250	98	8%
Blanding, UT	37.62333	-109.4789	1899	32.9	-5.8	353	102	20%
Cortez, CO	37.34917	-108.5792	1893	33.3	-10.0	335	154	24%

present throughout the day was equivalent to that held at the mean minimum temperature. Because humidity deficits in the summer often exceed a threshold limit (in the model) where stomata close (i.e.  $>3.0$  kPa), no adjustments were made to compensate for conditions where the humidity was less than 100% at night (Kimball *et al.*, 1997). The maximum  $D$  was calculated each month as the difference between the saturated vapor pressure at the mean maximum and minimum temperatures. Mean daytime  $D$  was calculated at half of the maximum value.

The number of days per month with subfreezing temperatures ( $\leq 2^\circ\text{C}$ ) was estimated from empirical equations with mean minimum temperature (Coops *et al.*, 1998). In modeling, we did not attempt to account for extremes in temperature that might directly kill trees, because both live pinyon and juniper exceeding 300 years in age were reported in the region (Gray *et al.*, 2006).

Monthly estimates of total incoming short-wave radiation were calculated using an approach detailed by Coops *et al.* (2000) where the potential radiation for any latitude and physiographic setting was first calculated and then reduced, on the basis of the clarity (transmissivity) of the atmosphere. Changes in the atmospheric transmissivity were mirrored in temperature extremes (Bristow and Campbell, 1984). The modeling approach, when compared with direct measurements, predicted both the direct and diffuse components of mean monthly incoming radiation with 93–99% accuracy on flat surfaces with a mean error  $< 2 \text{ MJ m}^{-2} \text{ day}^{-1}$ , conditions that we assumed generally applied for this modeling exercise. The visible portion of short-wave radiation was about half of the total (Landsberg and Waring, 1997).

#### Process-based growth model

There are a variety of physiologically based process models available, but only a few have been designed to scale projections of photosynthesis, growth and mortality across landscapes (see reviews by Mäkelä *et al.*, 2000; Landsberg, 2003; Nightingale *et al.*, 2004). Among the most widely used is 3-PG developed by Landsberg and Waring (1997). The model is based on a number of established biophysical relationships and constants and incorporates simplifications that have emerged from studies conducted over a wide range of forests (Landsberg *et al.*, 2003). 3-PG has been successful in predicting gross photosynthesis and water balances in deciduous and evergreen forests (Waring *et al.*, 1995; Law *et al.*, 2000; Soares and Almeida, 2001; Coops *et al.*, 2007).

The model simplifications include the following assumptions: (i) that monthly time-steps in climatic data are adequate to capture major trends, (ii) that knowledge of the most limiting variable constraining photosynthesis each month is sufficient, (iii) that autotrophic respiration ( $R_a$ ) and net primary production ( $P_{\text{net}}$ ) are approximately equal fractions of gross photosynthesis ( $P_g$ ), and (iv) that the proportion of photosynthate allocated to roots increases with drought and decreases with nutrient availability. The model incorporates the  $-3/2$  power function, which results, under stable climatic conditions, in generating mortality rates at canopy closure

similar to those recorded in forestry yield tables (Waring and McDowell, 2002). In addition, the model includes an age-related decrease in photosynthesis, which is associated with a progressive increase in hydrologic resistance to water movement as stems approach their maximum extension for a site (Koch *et al.*, 2004).

The 3-PG model calculates gross photosynthesis, transpiration, growth allocation and litter production at monthly intervals, and takes into account deficiencies in precipitation in previous months and years by sequentially up-dating a soil water balance. A monthly time-step excludes accurate calculation of evaporation from the canopy and soil. Similarly, the model is unable to compute an accurate snow water balance, although it may be assumed that most of the precipitation in months with average temperatures below freezing is in the form of snow. Subfreezing temperatures at night are known to halt photosynthesis the following day (Hadley, 2000); thus the number of frost days per month needs to be estimated, along with mean monthly temperature extremes, humidity deficits, solar radiation and precipitation.

In regard to biological properties, two sets of allometric equations are required; one to describe the relationship between growth and tree diameter (at breast height, 1.37 m) and the other, the relationship between tree diameter and the growth of new foliage. The annual rate of foliage turnover also must be estimated to calculate net change in canopy leaf area within and between years.

#### Parameterization of the 3-PG model

We parameterized the model using a variety of sources to encompass a range in projected leaf area index (LAI) from 0.5 to 1.5. The values for leaf longevity and turnover were established for the woodland type by simulations (Table II). Similarly, allometric relations between stem diameter and leaf mass (and area) were derived to produce stable values of LAI under stable climatic conditions. Other values reported in Table II were constrained to limit maximum transpiration rates to <30 mm/month and stand basal area to ~20 and 40 m<sup>2</sup>/ha at 100 years for the range in LAI values assessed on the basis of detailed information acquired at a field site near Los Alamos, New Mexico (Pangle *et al.*, 2012; Plaut *et al.*, 2012). To minimize structural changes in stand properties that influence tree mortality, the initial stocking was set low at 100 trees per hectare to prevent

self-thinning, and the age-related algorithm constraining photosynthesis was turned off. This allowed detailed analyses of interannual variation in relative gross photosynthesis in response to variation in environmental conditions alone. The effect of soil texture on water availability was assessed through comparisons of soils with the same water holding capacities but significantly different water release curves, which are incorporated in 3-PG (Landsberg and Waring, 1997).

#### Simulations with the 3-PG model

We began modeling with the assumption that all four sites had similar equilibrium LAI values of 1.0, although satellite imagery indicated that the Bowie, Arizona site might support a slightly lower LAI and the Cortez, Colorado site a higher LAI. By varying estimates of soil fertility, which changes the partitioning of photosynthate, we increased and decreased LAI from the default value (1.0) by  $\pm 0.5$  LAI to evaluate when differences first appear in annual  $P_g$  as  $A_c$  was allowed to vary in 50 mm intervals from 50 to 200 mm. Over the narrow range in simulated LAI values, maximum daily rates in transpiration were simulated to increase linearly from 0.35 to 1.0 mm day<sup>-1</sup>. As in previous studies, we also performed a series of sensitivity analyses to evaluate the extent that interannual variation in the number of subfreezing days and monthly variation in vapor pressure deficits influence the relative patterns in gross photosynthesis (Waring and McDowell, 2002; Waring *et al.*, 2008).

## RESULTS

#### GIS analysis

Geographic information system analysis demonstrated that 84% of the pinyon-juniper mortality recorded in 2003 and 2004 (Figure 1A) occurred on soils mapped with an available soil water capacity ( $A_c$ ) of <150 mm (Figure 1B), with 70% on soils with <100 mm (Table III). For the six classes of  $A_c$ , a negative power function described the percentage decrease in the area on which mortality was recorded between 2003 and 2004 (Figure 2). It was not possible to assess spatial variation in soil texture because that classification was incomplete, but considerable variation was noted in areas with similar values of  $A_c$ .

Table II. Parameterization of the 3-PG stand growth model for mixed stands of pinyon pine and juniper.

Variable	Value or function	Source
Quantum efficiency	0.025 mol C mol photon	This study
Soil fertility ranking (0–1 scale)	0.05–0.3	This study
Temperature: min., opt. and max.	–2, 24, 40 °C	This study
Fraction of leaf turnover annually	1/10th	Lajtha and Getz (1993), This study
Available soil water storage capacity ( $A_s$ )	Range: 50–200 mm	This study
Soil texture	Range: sand to clay	This study
Growth in foliage biomass (kg)	Foliage biomass = 0.0483(dia <sup>2.365</sup> )	This study
Growth in stemwood biomass (kg)	Stem biomass = 0.0411(dia <sup>2.4192</sup> )	Jenkins <i>et al.</i> (2003)
Maximum canopy conductance, m/s	0.008	This study

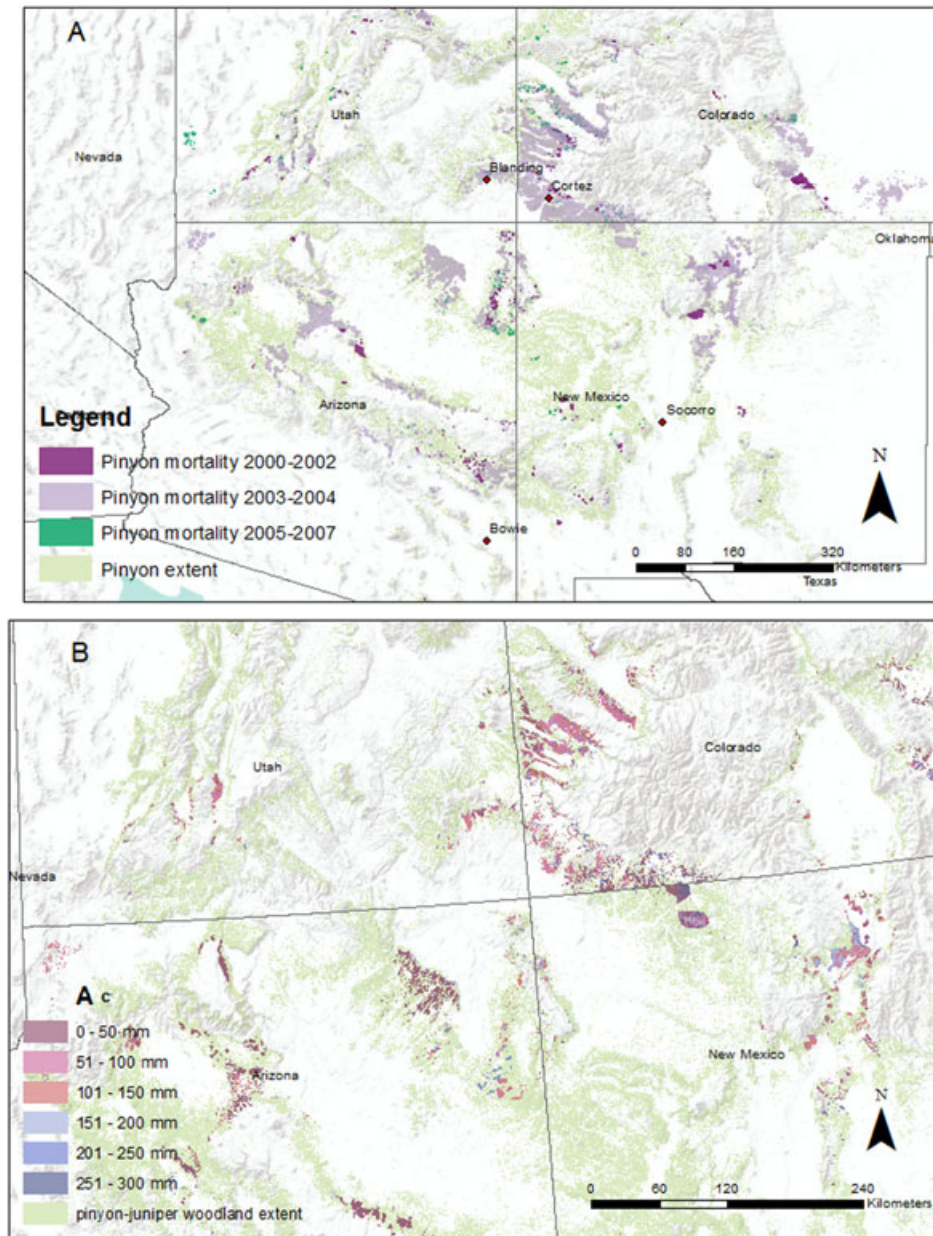


Figure 1. A. Map of the area where pinyon pine and juniper species occur together (green) indicates that mortality since the turn of the century was highest in the period 2003–2004 (US Forest Service, 2008). B. Most of the mortality recorded in 2003–2004 occurred on soils classified with available water holding capacities ( $A_c$ ) <100 mm (NRCS, SSURGO, 2011).

Table III. Area and percent of total dieback recorded from aerial surveys in 2003–2004 in reference to classification of available soil water storage capacity ( $A_c$ ) (this study, US Forest Service, 2008, NRCS SSURGO, 2011).

$A_c$	Area of mortality (ha)	% of total mortality
0–50 mm	535 877	42.4
50–100 mm	352 991	27.9
100–150 mm	167 959	13.3
150–200 mm	90 808	7.2
200–250 mm	79 739	6.3
250–300 mm	37 000	2.9
Total	1 264 374	100

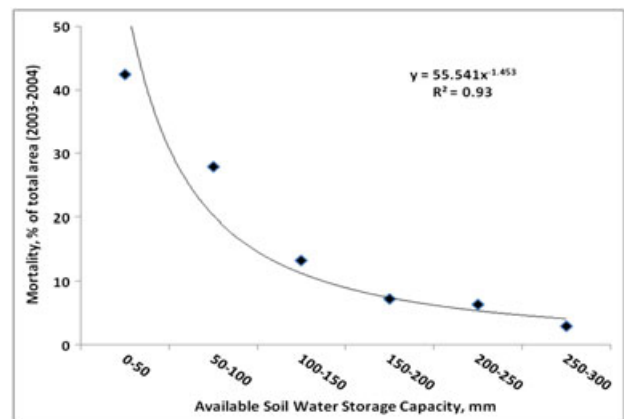


Figure 2. Graph of the relation between six mapped classes of available soil water holding capacity ( $A_c$ ) and the percentage of total area recorded with mortality in the period 2003–2004 (Table II).

3-PG model simulations

The extent that variation in the available soil water holding capacity affected the interannual patterns in  $P_g$  depended on the site, the equilibrium LAI and monthly variation in precipitation. In general, when the equilibrium LAI was set at 0.5, variation in  $A_c$  had little effect. At Cortez, the site with the highest equilibrium LAI, simulations of stand development showed that the sequentially repeated 20-year climatic patterns have little impact on  $P_g$ , even when  $A_c$  was set at 50 mm, until LAI approached 80% of the maximum value (Figure 3).

When the equilibrium LAI was set at 1.0 (or 1.5 at Cortez), the patterns in  $P_g$  showed considerable sensitivity at  $A_c \leq 100$  mm. Figure 4 indicates that under climatic conditions at Socorro, New Mexico, proportionally more interannual variation in gross photosynthesis occurred over

the 20-year period as  $A_c$  decreased from 150 to 50 mm. These results are representative of soils with a texture of clay loam. Sandy soils, as shown in Figure 5, release water to roots far more easily than do clay soils. This difference in water release appears to become important only during sustained periods of drought on soils with  $A_c < 100$  mm. Under such condition, clay soils reduced modeled gross photosynthesis by 4% more than sandy soils when  $A_c = 100$  mm, and by 10% when  $A_c = 50$  mm (simulations not shown).

The impact of subfreezing conditions differed among the four sites in proportion to the number of days recorded below freezing, which range, on average, from 41 days annually at Bowie, Arizona to 154 days at Cortez, Colorado (Table I). The rate that a rise in minimum temperatures reduced subfreezing days over the period varied in parallel, from 5% at Bowie to 24% at Cortez, which has implications of bark beetle population build up (discussed in the next section).

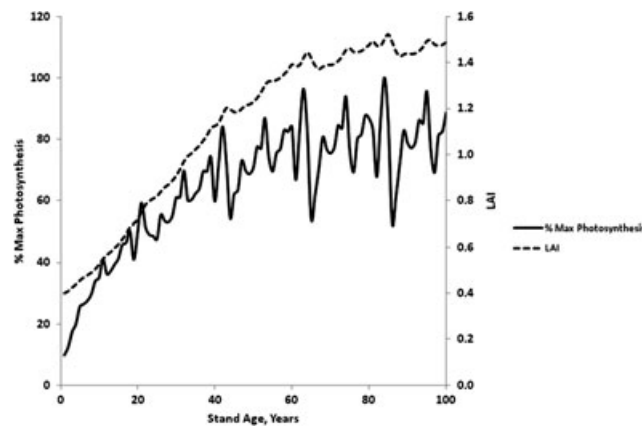


Figure 3. Simulations with repeated climatic sequence (1985–2005) show leaf area index (LAI) increasing with stand age to peak at 1.5 at Cortez, Colorado with available soil water storage set at 50 mm. Interannual variation in gross photosynthesis, here expressed as a percent of maximum, showed minimum variation until LAI > 1.2.

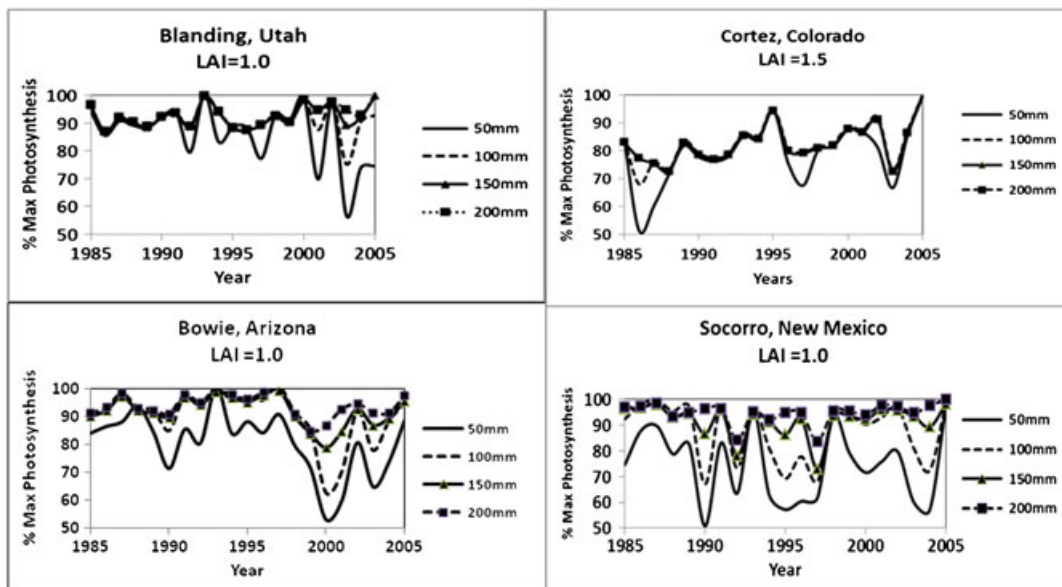


Figure 4. Simulations with the 3-PG model for mature stands of pinyon pine and juniper over the period from 1985 to 2005 indicate that gross photosynthesis decreases as the soil water storage capacity drops below 100 mm in years with consistently below average precipitation at assumed equilibrium leaf area index. Cortez, the coldest of the four sites, recorded its greatest decrease in photosynthesis between 1985 and 1990, whereas the period since 2000 was more stressful at the other sites. The Cortez site, during non-drought years, also recorded much more variation in photosynthesis, which we attribute mainly to interannual variation in the growing season vapor pressure deficit (See text).

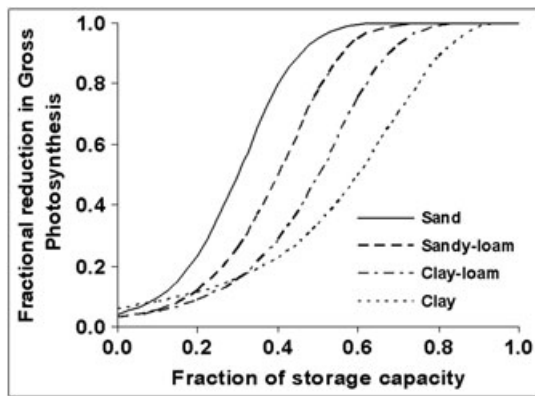


Figure 5. Coarse-textured soils hold water in a more readily available form than finer textured soils. As a result, the latter impose progressively more constraints on photosynthesis and transpiration as water is withdrawn from the soil profile (Landsberg and Waring, 1997).

During the winter, temperatures were suboptimal and solar radiation less than half that in the summer months; as a result, the maximum reduction in annual  $P_g$  at Cortez, the coldest site, averaged only 17% less with frost, at equilibrium LAI and  $A_c = 200$  mm, than without. In contrast, at Bowie, the difference was only 10%. A comparative analysis showed that interannual patterns in  $P_g$  with and without frost restrictions, were highly correlated ( $r^2 > 0.9$ , results not shown).

Although temperatures during drought years tended to average somewhat higher than in more normal years, with a maximum temperature set at 40 °C for the model, little response to variation in monthly mean temperatures was observed. This is in part because, at very high temperatures, the humidity deficit often exceeded 2.5 kPa during the day, which limited stomata conductance to very low values.

In sensitivity tests where average monthly vapor pressure deficits for the 20-year period were substituted for recorded values at all sites, annual  $P_g$  peaked near 100% of maximum at  $A_c > 150$  mm. From these analyses, we attributed the large interannual variation in  $P_g$  simulated at the Cortez site to seasonal variation in vapor pressure deficit ( $D$ ) during the growing season that matched or exceeded periodic constraints from limitations in soil storage capacity.

## DISCUSSION

### *Drought duration, frequency and of intensity*

Breshears *et al.* (2009) demonstrated that pinyon pine is able to survive short periods of drought that are sufficient to cause complete stomatal closure and thereby halt all photosynthesis. When such conditions are extended beyond 8 months, however, trees become highly susceptible to bark beetle (*Ips confusus*) attack. Similar observations have been made following experiments that artificially reduced precipitation by 50% on sites where the equilibrium LAI was estimated at 1.0 (Monica Lisa Gaylord, Northern Arizona University and Nate McDowell, Los Alamos National Laboratory, personal communications). These observations

may explain why a simulated drop to 50% of maximum  $P_g$  at Socorro in 1990 did not result in widespread mortality, whereas less extreme, multiple-year drought recorded around the turn of the century did (Figure 4).

From experiments conducted on other species, Christiansen *et al.* (1987) showed that the tree's ability to stop the spread of blue-stain fungus introduced by bark beetles is associated with a shift from wood to resin production at the sites of infection. In mature stands of pinyon pine, a relative reduction in maximum gross photosynthesis represents a proportional reduction in wood production per unit of leaf area. If trees were much older than a century, we would expect them to be more vulnerable to drought than younger trees because, as trees approach maximum height on a given site, hydraulic restrictions to water transport increase and further limit photosynthesis (Koch *et al.*, 2004). Pathogens also can weaken trees, causing them to be more susceptible to beetle attack during a drought (Negrón and Wilson, 2003).

Some of the observed mortality on soils classified with  $A_c$  values  $> 200$  mm (Figure 1B) may indicate the presence of older age classes of pine, or shallower soils interspersed among deeper soils (Greenwood and Weisberg, 2008). Similarly, the absence of mortality on some soils classified with less than 100 mm of water storage capacities may reflect recently disturbed woodlands where young trees face less competition for water because canopy leaf area has yet to reach its maximum (Figure 3). In the future, if climatic conditions continue to be less favorable for pinyon-juniper, conversion to other plant types may occur (Floyd *et al.*, 2009).

### *Variation in vapor pressure deficits and reduction in frost-free period*

Although frequent and sustained periods of drought create favorable conditions for bark beetle attack on pinyon pine and xylem failure in the more resistant juniper, other factors can also play a role. We believe that Cortez, Colorado, the coldest site among the four analysed (Table I), differs in three important ways: (i) the simulations indicated a major decrease in  $P_g$  between 1985 and 1990 not evident at the other sites, (ii) the effects of variation in growing season  $D$  on  $P_g$  were much more pronounced than at the other sites, and (iii) the reduction in subfreezing days on  $P_g$  between 1985 and 2005 was larger than at the other sites.

The greater sensitivity to variation in  $D$  during growing season at Cortez caused variation in  $P_g$  similar to that attributed to drought. Combined with the rapid warming trend recorded at Cortez over the 20-year period, conditions have also become more favorable for bark beetle reproduction (Safranyik *et al.*, 2010). It is this latter point that may explain why dieback of pinyon pine has mainly been observed locally in 2003–2004 (Personal Communication with R. Carter, Stone Free Farm, Cortez, Colorado).

### *Value of modeling climatic variation preceding observations of mortality*

The empirical relation between  $A_c$  and tree mortality shown in Figure 2 only applies widely if pinyon-juniper woodlands are

known to have reached equilibrium LAI, as demonstrated through modeling. Process-based modeling also provide an interpretation of the extent that variation in other variables, such as how a reduction in subfreezing conditions and growing season vapor pressure deficits affect tree vigor. Coops and Waring (2011) developed a general approach to assess the effects of recent climatic variation across the Pacific Northwest but lacked adequate information on soil properties to include in their analyses. Evidence that soil properties account for differential mortality of pinyon pine makes the development of methods to improve soil classifications a high priority.

#### *Increasing role of remote sensing*

In this paper, we took advantage of multi-year remote-sensing imagery from the US Forest Service to document when and where tree mortality has occurred between 2000 and 2007 in the southwestern USA. We also utilized Google Earth imagery to confirm the presence of pinyon pine-juniper woodlands near four representative weather stations. Kennedy *et al.* (2007) and Huang *et al.* (2010) have analysed historical patterns of disturbance more broadly using Landsat imagery acquired since the 1970s. These analyses include automated protocols to distinguish different types of disturbances (Kennedy *et al.*, 2007). Although differences in the background soil colors in desert environments create special challenges in estimating LAI by remote sensing, laser altimetry offers considerable promise to improve this situation (White *et al.*, 2000).

### CONCLUSIONS

We developed an empirical model that predicted tree mortality associated with soil properties that accounted for 93% of the observed variation recorded on aerial photographs in the period 2003–2004 (Figure 2). Simulations with a process-based model provided an explanation for the observed patterns and identified in which years the empirical model could be applied. The modeling also provided an assessment of the critically important equilibrium LAI. On soils with  $A_c$  values < 100 mm, at equilibrium LAI, a notable decrease in gross photosynthesis was predicted at four woodland sites around the turn of the century that presumably reduces mean tree vigor (indexed as wood production per unit of leaf area) below a threshold where bark beetles could successfully attack and kill pinyon pine. Differences in soil texture played only a minor role. Death caused by drought alone would likely be limited to very shallow soils where photosynthesis would approach zero for an entire year. The simulations also indicated that interannual variation in vapor pressure deficits and a warming trend in minimum temperatures can reduce tree vigor, creating conditions more favorable for beetle outbreaks at higher elevation sites, possibly without extreme soil drought. If climatic conditions were to continue to become less favorable for pinyon-juniper, we would expect a reduction in equilibrium LAI and conversion to other types of vegetation.

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