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ASPECT REDUCES SOIL MOISTURE AND TREE COVER, BUT NOT NITROGEN MINERALIZATION OR GRASS COVER, IN SEMIARID PINYON-JUNIPER WOODLANDS OF THE SOUTHWESTERN UNITED STATES

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ABSTRACT—Global climate change is expected to increase the aridity of semiarid landscapes by increasing heat stress and decreasing soil moisture, negatively impacting plant survival, growth, and reproduction and forcing major shifts in plant community composition. To better understand potential vegetation shifts, we investigated how aspect-mediated differences in soil moisture and nitrogen influence tree-grass and tree species coexistence in pinyon-juniper woodlands in the southwestern United States (at the Sevilleta Long Term Ecological Research Station in New Mexico). We measured soil moisture, total mineralized soil nitrogen, grass cover, and woody cover and demography of the two dominant trees—two-needle pinyon pine (*Pinus edulis*) and one-seeded juniper (*Juniperus monosperma*)—along 32 transects on north-facing and south-facing slopes. Tree cover was greater on north-facing than on south-facing slopes, reflecting significantly higher soil moisture on northern aspects. Aspect did not affect soil nitrogen or grass cover. Population structure for juniper was influenced by aspect while reproductive output was influenced by aspect in both species, suggesting that differences in drought tolerance between these codominant tree species may be responsible for differences in the utilization of resources in our study area. Our results suggest that soil moisture can affect tree cover and tree-grass coexistence more than does nitrogen. Increasing aridity due to global climate change is likely to decrease woody cover in semiarid landscapes, resulting in systems codominated by grasses and woody species.

RESUMEN—Los futuros escenarios para el cambio de clima global predicen un aumento de la aridez en paisajes semiáridos a través de estrés térmico y la disminución de la humedad del suelo, reduciendo la supervivencia, crecimiento, y reproducción de plantas, y forzando cambios drásticos en la composición de comunidades vegetales. Para entender mejor estos posibles cambios en la vegetación, investigamos cómo diferencias en la humedad del suelo y niveles de nitrógeno debido a la topografía, influyen la coexistencia entre árboles y pastos, y entre árboles en un bosque tipo piñón-enebro en el suroeste de los Estados Unidos US (en Sevilleta Long Term Ecological Research Station in New Mexico)). Medimos la humedad del suelo, nitrógeno total mineralizado en el suelo, cobertura de pasto, y cobertura y demografía de las dos especies dominantes de árboles—piñón de dos agujas (*Pinus edulis*) y enebro de una semilla (*Juniperus monosperma*)—en 32 transectos, de vertiente norte y vertiente sur. La cobertura de árboles fue mayor en las vertientes orientadas al norte que en las orientadas al sur, reflejando una mayor humedad en el suelo en estas superficies topográficas. La orientación no tuvo ninguna influencia en la cantidad de nitrógeno ni en la cobertura de pasto. La estructura de la población fue influenciada por la orientación topográfica enel enebro, mientras que el rendimiento reproductivo fue influenciado por la orientación topográfica en ambas especies. Esto sugiere que debido a las diferencias en los niveles de tolerancia a la sequía en estos dos árboles co-dominantes, estas especies utilizan los recursos de maneras distintas dentro de nuestra área de estudio. Nuestros resultados sugieren que la humedad del suelo puede influir más a la cobertura de árboles y a la coexistencia entre árboles y pastos que el nitrógeno. Es probable que el aumento en aridez, debido a cambios en el clima a la escala global, reduzca la cobertura de plantas leñosas en paisajes semiáridos, resultando en sistemas co-dominados por pastos y especies leñosas.

Global climate change is expected to increase aridity and negatively impact vegetation in many semiarid landscapes (Allen and Breshears, 1998; Breshears et al., 2005). Increasing aridity is likely to affect growth, survival, and reproduction differently for plant species and functional groups that vary in their drought tolerance (Breshears and Barnes, 1999), mediating potentially major shifts in plant community composition over time

(Mueller et al., 2005; Allen et al., 2010). Large-scale, rapid, drought-induced mortality of trees can be the most dramatic vegetation response to increased aridity associated with global climate change (Breshears et al., 2005; Allen et al., 2010), and it can lead to ecosystem-scale consequences such as shrub encroachment, reduction or expansion of grasslands, altered disturbance regimes, and exotic plant invasions (Levine et al., 2003).

Topographic aspect has a large influence on microclimate, as it affects the intensity of solar radiation and thus evapotranspiration, soil moisture, and ultimately vegetation structure and its response to climate change (Fekedulegn et al., 2003; Chesson et al., 2004; Bradley and Fleishman, 2008). The microclimatic differences between north-facing and south-facing slopes provide an excellent opportunity for quantifying how climate can affect vegetation, and especially so in semiarid, drought-sensitive landscapes. South-facing slopes are generally known to experience higher incident solar radiation, resulting in higher temperatures, higher evapotranspiration, and lower soil moisture (Jenny, 1980; Klemmedson and Wienhold, 1992; Breshears et al., 1997; Clifford et al., 2013), a less-favorable environment for trees than are north-facing slopes. Although aspect directly mediates climate (a primary abiotic factor controlling vegetation distribution), it can indirectly affect other environmental variables that influence vegetation; for example, soil properties and nutrient content (Johnson and Miller, 2006; Shukla et al., 2006).

Semiarid pinyon-juniper woodland is one of the most widespread vegetation types of the continental United States, covering approximately 20–30 million ha, and codominated by two-pinyon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*) (Miller and Wigand, 1994). The pinyon-juniper woodland has been expanding within the Great Basin at an unprecedented rate in recent decades due to factors such as climatic shifts and fire suppression (Miller and Wigand, 1994). Concurrently, Breshears et al. (2005) documented a large-scale die-off of pinyon within the Four Corners region of the southwestern United States (Utah, Colorado, Arizona, and New Mexico) and attributed their findings to persistent regional drought in the early 2000s. Consequently, it is increasingly important to more-fully understand the ecological mechanisms that control the distribution and structure of this important vegetation type in the southwestern United States under the changing climate.

The two dominant tree species in pinyon-juniper woodland respond differently to the availability of resources such as moisture and nitrogen. Juniper maintains high water use efficiency during drought and is more resistant to xylem cavitation, resulting in higher tolerance of low soil moisture compared to pinyon pine (Lajtha and Barnes, 1991; Mueller et al., 2005; Koepke and Kolb, 2013). Consequently, junipers tend to dominate in drier locations (Tausch et al., 1981; Padien and Lajtha, 1992). However, West et al. (2007) found that pinyon pines have longer taproots than some juniper species, allowing them to utilize summer precipitation pulses and deep-soil water. Access to soil nutrients, and especially nitrogen, is also affected by vertical root distributions because nutrient levels in arid environments tend to decline rapidly with increasing soil depth (Evans and Ehleringer, 1994).

A substantial increase in aridity can impact tree-grass coexistence and thus the broader physiognomy of pinyon-juniper woodlands (Callaway et al., 1996; Soliveres et al., 2010). Grasses generally tend to tolerate lower soil moisture in the upper soil horizons than do trees because most grass species have a more drought-adapted physiology (C4 vs. C3 photosynthetic pathway) and morphology (Sankaran et al., 2004). Grasses can outcompete small tree seedlings that lack a well-developed root system and are sensitive to low soil-water content, contributing to decreased tree establishment during dry periods (Scholes and Archer, 1997). Because tree drought-tolerance and the ability to compete with grasses for soil moisture increases with tree developmental stage (c.f., regeneration niche; Grubb, 1977; Padien and Lajtha, 1992), moister periods or locations on a landscape can allow periodic tree seedling establishment and their recruitment to larger, more drought-tolerant size classes and thus affect tree population structure and vegetation character (Dovčiak et al., 2005).

In this study, we aimed to increase our understanding of the links among resource availability (moisture and nitrogen), tree-grass coexistence, and coexistence of dominant tree species in semiarid pinyon-juniper woodlands, an important vegetation type of the North American Southwest. Our particular objectives were to (1) quantify how aspect can mediate changes in soil moisture and nitrogen; (2) determine how vegetation responds to aspect-induced variation in resource levels; and (3) discuss how the ongoing climatic changes in the region, especially the increasing aridity, can affect regional vegetation patterns.

Materials and Methods—*Study Species*—Two-needle pinyon pine, *Pinus edulis*, is a slow-growing, long-lived conifer found primarily in the Southwestern United States and the Colorado Plateau at elevations between 1,400 and 2,700 meters above sea level (m a.s.l.; with greater abundance at higher elevations). Pinyon pine is a short tree (5–12 m in height) with a root system composed of a long taproot ($\leq$6 m in depth) and shallow lateral roots ($\leq$40 cm in depth) that can limit understory vegetation by competing for soil moisture (Ronco, 1990). With the exception of seedlings, pinyon pine is shade intolerant (Gottfried, 2004), and its litter has been associated with reduced biomass production in grasses (Jameson, 1966). This monoecious species requires three growing seasons to form mature cones, which start developing during the late summer months following pollination during the period from May–June (Jeffers, 1994).

One-seeded juniper, *Juniperus monosperma*, is a slow-growing, long-lived evergreen tree commonly found in desert grasslands and pinyon-juniper woodlands throughout New Mexico and parts of Arizona at elevations ranging from 1,200-1,500 m a.s.l. on mesas, plateaus, and mountain slopes (Lajtha and Getz, 1993). Juniper has a shrubby form, ordinarily ranging at maturity from 3–10.5 m in height (Phillips, 1909). It has an extensive root system adapted for growth in xeric conditions (Johnsen, 1962). Mature trees have taproots ranging from 46 cm–3.7 m in length and much-longer lateral roots, commonly 2.5–3 times longer than the height of the tree (Johnsen, 1962). Litter from Ashe juniper (*Juniperus ashei*) has been shown to decrease recruitment of grasses and understory herbs, likely due to physical limitations on water availability rather than to the presence of inhibitory chemicals (Yager and Smeins, 1999). Juniper is a dioecious species that requires one summer growing season to produce small, "berry-like" cones which reach maturity in August and persist for 1–2 y (Chambers et al., 1999).

Study Area—The study was carried out in the Los Pinos Mountains in New Mexico on four sites adjacent to the Pinyon-Juniper Core Site (Cerro Montoso) of the Sevilleta Long Term Ecological Research (Sevilleta LTER) Project in the eastern portion of the Sevilleta National Wildlife Refuge (34°21′N, 106°32′W). The Los Pinos Mountains represent the southern-most topographically offset extension of the Southern Rocky Mountains, similar in geology and physiography to the adjacent Sandia and Manzano mountains (Stark and Dapples, 1946). The highest peaks of the Los Pinos Mountains exceed 2,100 m a.s.l. in elevation with a mean elevation of 1,919 m. Geological substrate is composed of sedimentary and volcanic rocks (Manley, 1981) and soils are classified as Puertecito moist-Rock outcrop complex and Torriothents ustic-Rock outcrop complex (Johnson, 1988).

The Sevilleta LTER Site has a mean annual temperature of 13.28°C and temperatures range from 3.3°C in December to 31°C in July (Sevilleta LTER, http://sev.lternet.edu/data/sev-1). Mean annual precipitation is 362.7 mm and 60% occurs during the monsoon season (July–September). The Pinyon Juniper Core Site has a higher mean annual precipitation of 379 mm (seasonally ranging from 246–599 mm; Vanderbilt et. al, 2008) and a lower mean annual temperature of 12.7°C (with mean June and July temperatures of 22.16 and 23.27°C) (1991–2011 data from Cerro Montoso Meteorological Station, http://sev.lternet.edu/node/3565).

The prominent vegetation type is conifer woodland dominated by pinyon pine, juniper (Padien and Lajtha, 1992), and grasses that include dominant perennial species such as blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eripoda*) (Vanderbilt et al., 2008) and other species from families characteristic of arid and semiarid regions (e.g., Cactaceae, Euphorbiaceae).

Vegetation Sampling—We selected four study sites within the Los Pinos Mountains, based on their accessibility (in areas with roads, elevations <2,000 m a.s.l. and on moderate slopes), using topographic maps of the area (U.S. Geological Survey, 1952, 1979). Two sites were located in the northern and two in the southern section of the mountain range; all four sites were within 5 km of one another. For each site, we determined their location (including elevation) using a global positioning system unit (either Trimble GeoXT, Trimble Navigation Limited, Sunnyvale, California; or Garmin, Garmin Ltd., Olathe, Kansas).

At each site we established four, 50-m long and 2-m wide belt transects on north-facing and south-facing slopes (4 transects per slope, 32 total transects) at elevations between 1,940 and 1,980 m a.s.l. Our statistical analysis showed no significant effect of elevation; therefore, transects were grouped together by aspect for all reported results. We collected vegetation data during June and July, concurrent with monsoon rains. We counted the number of individual pinyon pines and junipers whose crowns were within the belt transect and measured canopy cover of the tree species as length along the belt transect. Individuals were classified based on their crown diameter as small ($\leq$100 cm), medium (101–500 cm), or large (>500 cm) to approximate demographic structure of tree species. The presence of reproductive structures (cones) was used as a crude estimate of reproductive stage of each individual. Percent grass cover was estimated using Daubenmire cover classes (Daubenmire, 1959) on 30 $\times$ 30-cm^2 plots established every 10 m along each transect (6 plots per transect or 24 plots per aspect at each site).

Soil Sampling—We quantified soil moisture under the canopies of pinyon pine and juniper, as well as under the grass cover (regardless of grass species) and on bare ground, using a gravimetric method. Soil samples (ranging from 80–150 g) were collected using hand shovels systematically at the easternmost point along each transect on each site and dried in an oven at 68°C for 72 h. All soil samples (16 per aspect at each site, one sample per category on each transect) were collected on 8 July 2009 (within a 6-h period) prior to the monsoon rains. Soil samples were collected 10 cm below the soil surface to avoid daily variability in soil moisture typical of the soil surface (Jenny, 1980). We estimated soil ammonium (NH_4^+) and nitrate (NO_3^-) using ion-exchange resin bags and combined them into total mineralized soil nitrogen (TMSN). Two resin bags constructed from nylon mesh were placed on each transect within 5 m of each other (one bag under the canopy of pinyon pine and one under the canopy of juniper), giving a total of 64 bags (16 bags per site, 4 sites). The resin bags remained in the soil for approximately 4 wk (late June–late July 2009, concurrent with start of monsoon rains) to allow for full ion exchange. Ion-exchange resin was placed inside nylon mesh bags, allowing the resin to take up and retain ions from the soil by exchanging its own lower-affinity ions (Gibson, 1986). All laboratory procedures followed Lajtha (1988).

Statistical Analyses—For each transect we calculated the percent cover of grass, tree species (total, pinyon pine, and juniper), tree-to-grass ratio (pinyon and juniper cover divided by grass cover), and juniper proportion (juniper cover divided by pinyon and juniper covers combined). The demography of each tree species was characterized by calculating the proportions of small individuals (with crowns $\leq$100 cm), large individuals (with crowns >500 cm), and reproductive individuals on each transect. We calculated mean soil moisture and soil nitrogen (nitrate, ammonium, and TMSN) for each transect.

We tested the effect of aspect on all above response variables either using nested analysis of variance (ANOVA) or Kruskal-Wallis tests. We conducted nested ANOVAs, using site and transect as random factors, and transect nested within site. We included aspect as a fixed factor to test for main effects. We graphically examined the normality of residuals to determine when ANOVA was appropriate to use, and we transformed our data to achieve normality whenever possible. Soil moisture, tree size, and the proportion of trees bearing cones were normally

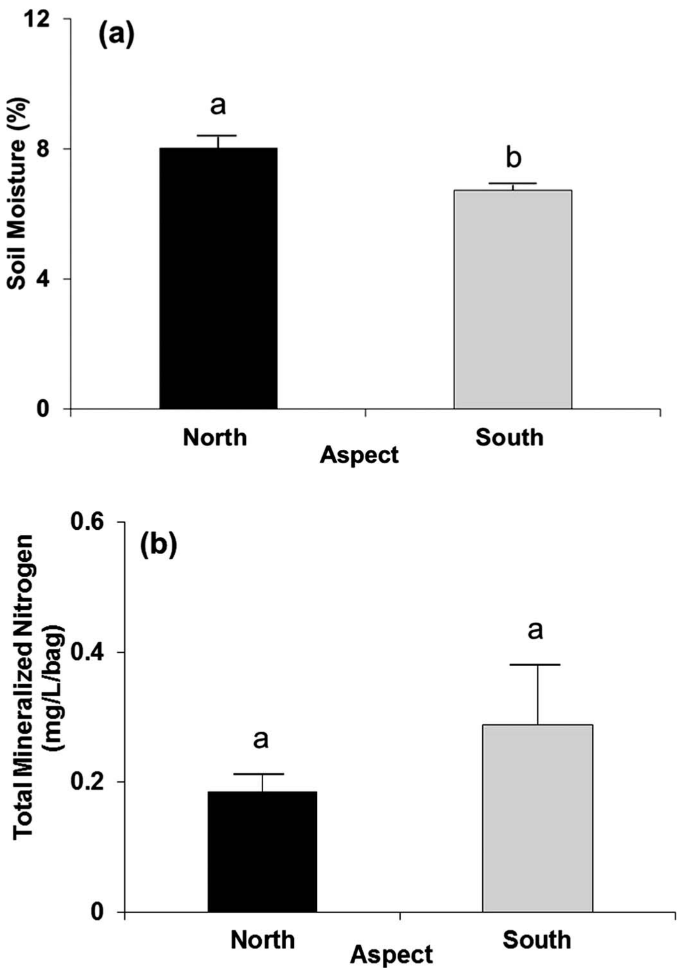

FIG. 1—Effects of aspect on the abiotic environment in Los Pinos Mountains, Sevilletta National Wildlife Refuge, New Mexico. (a) Percent soil moisture at the end of dry season. (b) Total mineralized soil nitrogen (TMSN). Values are means ± 1 *SE*. Different letters indicate statistically significant differences based on Tukey HSD test in (a) and nonparametric Steel-Dwass test in (b). Soil moisture was determined using a gravimetric method on samples taken at a depth of 10 cm, and TMSN was determined using ion exchange resin bags that remained in the soil from mid-June to mid-July (see Soil Sampling).

distributed and required no transformations. Soil nitrate and tree-to-grass ratios were successfully log transformed while percent cover data (trees and grass) were successfully arc-sine transformed, and all transformed variables were analyzed using nested ANOVA. Soil ammonium, TMSN, the proportion of large individuals, and the ratio of individual tree species' cover to total tree cover were analyzed using a nonparametric Kruskal-Wallis test. Steel-Dwass tests (a nonparametric equivalent of Tukey honest significant difference [HSD] tests) were conducted post hoc to test if the differences among multiple means were statistically significant for soil ammonium, TMSN, the proportion of large individuals, and the ratio of tree cover to total cover. Tukey HSD tests were performed on all remaining variables analyzed using ANOVA. All statistical analyses were implemented using the statistical software R (version 2.11.1, R Development Core Team, Vienna, Austria).

RESULTS—*Soil Environment*—Soil moisture was significantly higher on north-facing than on south-facing slopes when we pooled samples from underneath trees, grass, and bare areas ($P = 0.001$). Soil moisture did not differ under the two tree species (pinyon pine and juniper $P = 0.53$; Fig. 1a). Mean soil moisture in both bare ground and under grass cover was significantly lower than soil moisture under the tree canopy ($P = 0.0002$ and $P = 0.0007$, respectively), although moisture levels in the grass and bare space were not significantly different from each other ($P = 0.33$; not shown). Unlike soil moisture, soil nitrogen (TMSN, NH_4^+, and nitrate) was variable but not significantly affected by aspect (Fig. 1b) or microsite ($P > 0.05$; not shown). Soil nitrogen did not differ among grass cover, bare areas, and under tree canopies ($P > 0.05$; not shown).

Vegetation Cover—Tree cover was approximately two times greater on north-facing than on south-facing aspects ($P = 0.002$; Fig. 2a), but grass cover was not significantly affected by aspect ($P = 0.51$; Fig. 2b). The proportion of tree-to-grass cover appeared higher on north-facing than on south-facing slopes (Fig. 2c), but this was only marginally significant ($P = 0.05$). Tree cover was approximately equally partitioned between juniper and pinyon pine on both aspects ($P = 0.29$; Fig. 3a). The decline in tree cover on south-facing slopes relative to the north-facing slopes (Fig. 3a) is consistent with lower soil moisture on south aspects (Fig. 1a). The ratio of both juniper and pinyon cover with respect to total tree cover was not significantly influenced by aspect ($P = 0.33$ for both species; Fig. 3b).

Population Structure of Woody Dominants—Mean tree crown size did not differ significantly between the two aspects ($P = 0.66$) but was significantly influenced by species ($P = 0.002$), where juniper crowns were an average of 72 cm larger than pinyon crowns. The proportion of large individuals was not influenced by species ($P = 0.24$) and was approximately four times greater on north-facing slopes when species were pooled ($P = 0.002$; Fig. 4b). Post hoc tests indicated that the difference in the proportion of large individuals on north-facing aspects was only significant for juniper. The proportion of small individuals was significantly influenced by species when the effect of aspect was ignored ($P = 0.04$), where pinyon had more than double the proportion of small individuals compared to juniper. The proportion of small individuals was significantly greater on north-facing slopes when species were pooled by approximately twofold ($P = 0.01$). However, our post hoc test indicated that there were no statistical differences in the proportion of small individuals by aspect or species. There was also no significant species-by-aspect interaction on the proportion of large or small individuals ($P = 0.42$ and $P = 0.33$, respectively). The proportion of reproductive individuals differed significantly by aspect ($P = 0.004$) but not by species ($P = 0.32$; Fig. 4c). The proportion of cone bearing trees was approximately 1.7 times greater on

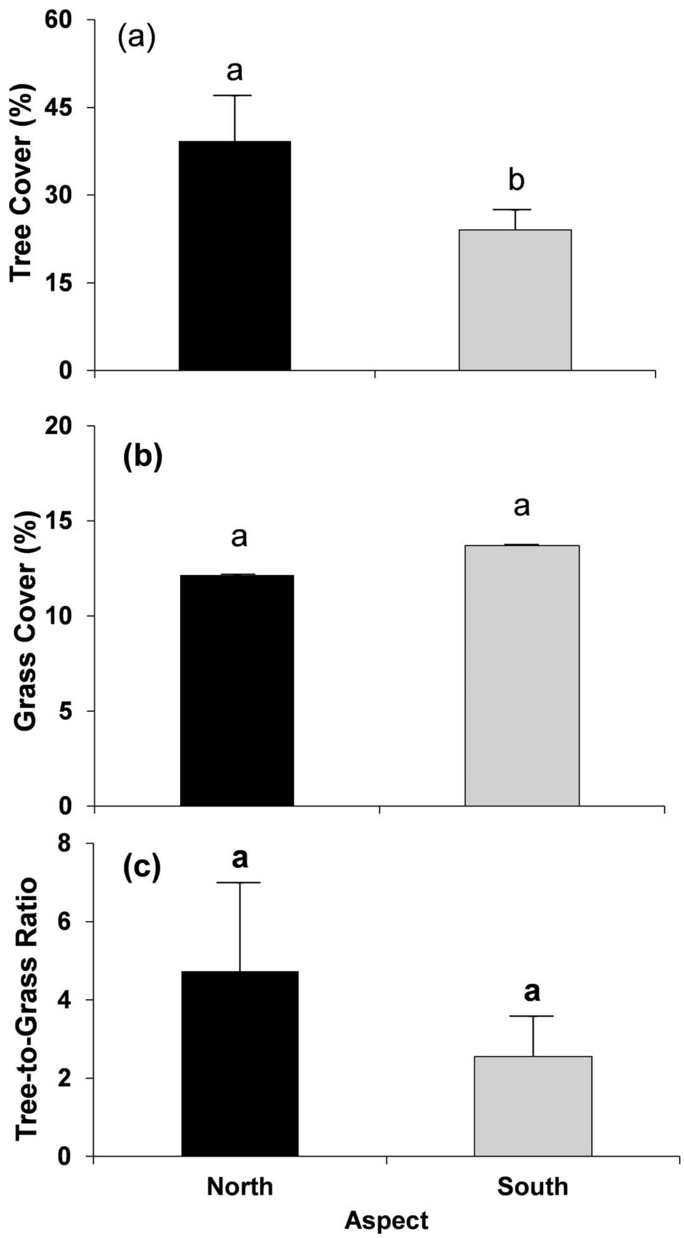

Fig. 2—Effects of aspect on plant community physiognomy in Los Pinos Mountains, Sevilletta National Wildlife Refuge, New Mexico. (a) Tree cover. (b) Grass cover. (c) Tree-to-grass ratio calculated by dividing woody plant cover by grass cover. Values are means ± 1 *SE*. Different letters indicate statistically significant differences based on Tukey HSD tests in (a) and (b) and nonparametric Steel-Dwass test in (c). Woody species were pinyon pine and juniper; most grass species were from genus *Bouteloua*.

north-facing than on south-facing slopes when species were pooled.

Discussion—*Aspect Effects on Soil Environment*—Resource pulses (especially moisture levels) have been shown to influence species interactions (Sthultz et al., 2007) and maintain plant diversity in arid and semiarid ecosystems (Chesson et al., 2004). Our results corroborate the effects

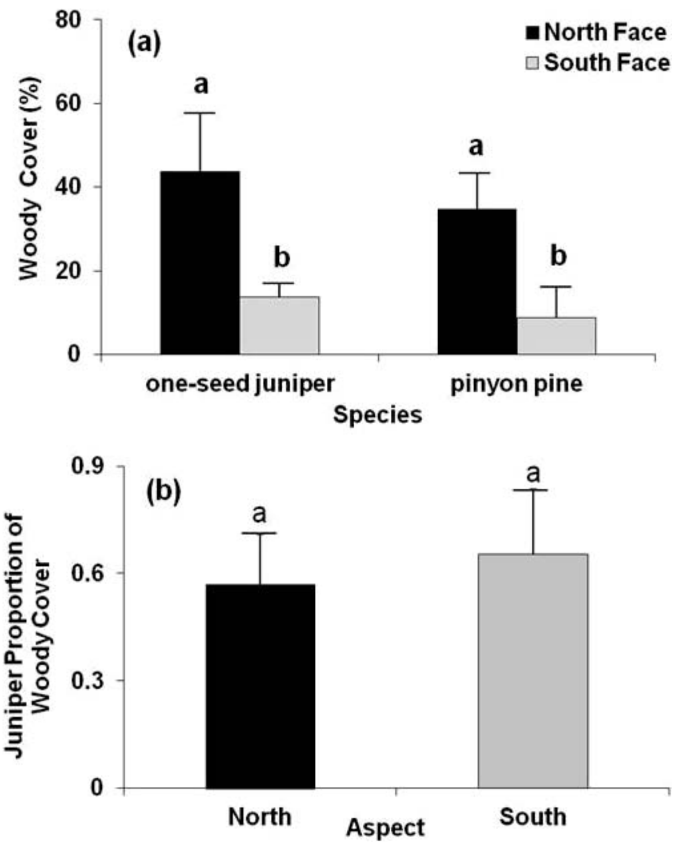

Fig. 3—Effects of aspect on the distribution of dominant woody species (pinyon pine and juniper) in Los Pinos Mountains, Sevilletta National Wildlife Refuge, New Mexico. (a) Absolute cover of woody species. (b) Ratio of juniper cover to total woody plant cover. Values are means ± 1 *SE*. Different letters indicate statistically significant differences based on Tukey HSD test in (a) and nonparametric Steel-Dwass test in (b).

of moisture in drought-prone, semi-arid landscapes of the North American Southwest; south-facing slopes receive higher incident solar radiation compared to north-facing slopes, resulting in high soil temperatures, high evapotranspiration, and relatively low soil moisture (Jenny, 1980; Klemmedson and Wienhold, 1992; Breshears et al., 1997; Clifford et al., 2013). More importantly, our results suggest that differences in soil moisture between topographic aspects are a greater environmental driver of vegetation structure than is soil nitrogen content. The lack of differences in soil nitrogen between the aspects in our study suggests that factors other than soil moisture or vegetation structure (which both differed by aspect in our study) may be affecting the decomposition of organic material and thus soil nitrogen content in semiarid ecosystems, (e.g., physical fragmentation, leaching, or photochemical degradation) (Moorhead and Reynolds, 1989; Vanderbilt et al., 2008). Additionally, our soil moisture results represent a snapshot of a highly dynamic resource and may not accurately reflect long-term differences due to topographic aspect; however, because we sampled at the end of the dry season, our measure-

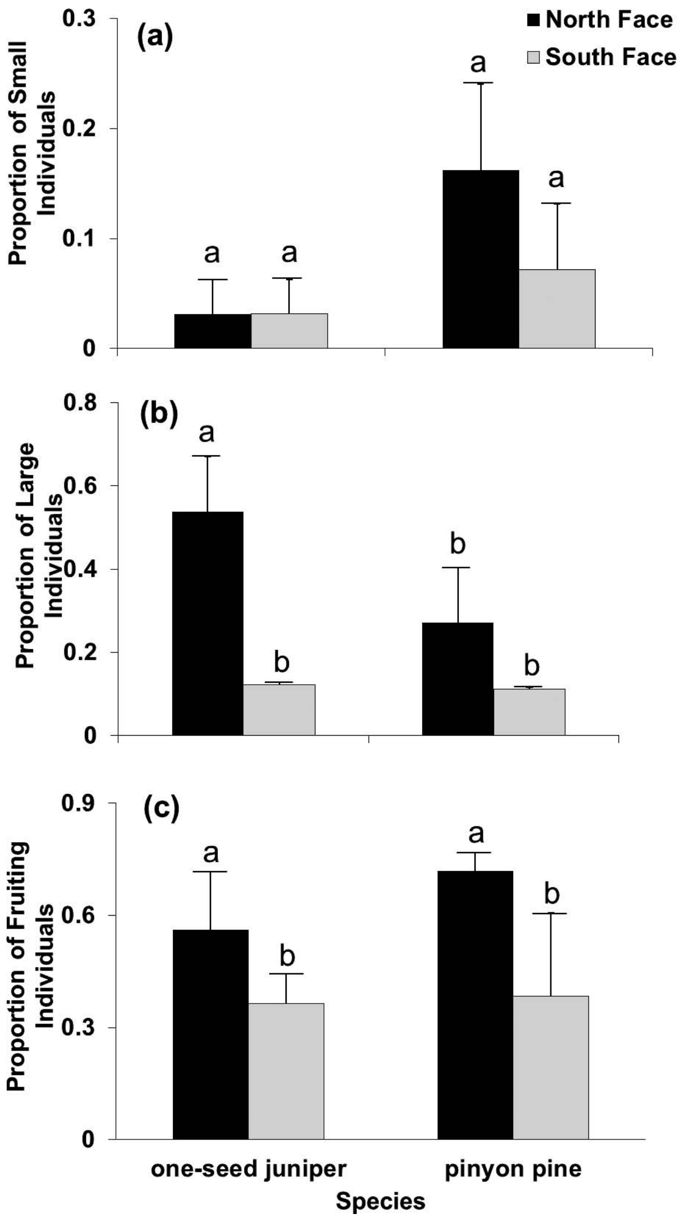

FIG. 4—Effects of aspect on population structure (demography) of dominant woody species (pinyon pine and juniper) in Los Pinos Mountains, Sevilletta National Wildlife Refuge, New Mexico. (a) Proportion of small individuals (crowns ≤100 cm wide). (b) Proportion of large individuals (crowns >500 cm wide). (c) Proportion of fruiting individuals. Values are means ± 1 *SE*. Different letters indicate statistically significant differences based on Tukey HSD test in (a) and (c) and nonparametric Steel-Dwass test in (b).

ments are likely to reflect cumulative soil moisture conditions of the dry season.

Soil-Plant Interactions—Aspect-related differences in soil environment and microclimate can considerably influence population processes of woody plants in semiarid environments, contributing to differences in community composition and physiognomy between aspects (Johnson and Miller, 2006). Our results corroborate relevant studies by suggesting that north-facing aspects in semiarid ecosystems maintain environments considerably more favorable for woody plant establishment and survival than do south-facing aspects, resulting in greater tree cover on moist, north-facing aspects than on dry, south-facing aspects (Sternberg and Shoshany, 2001). Because low soil moisture can decrease germination rates, growth, and survival, particularly in woody species (Fekedulegn, et al. 2003), as tree abundance increases, shade from the tree canopy should promote tree seedling establishment and survival (Mueller et al., 2005; Alvarez-Yepiz et al., 2014) resulting from increases in soil moisture. Johnson and Miller (2006) observed decreased establishment of western juniper (*Juniperus occidentalis*) with increasing southerly exposure, and Clifford et al. (2013) found that pinyon pine mortality was strongly related to low precipitation and high temperature (high vapor pressure deficit). At our study site, Gaylord et al. (2013) documented higher mortality in pinyon than in juniper when both were exposed to an experimental drought treatment. Indeed, higher soil moisture and lower temperatures on north-facing vs. south-facing slopes have been shown to influence plant community composition in woodlands composed of Mexican pinyon (*Pinus cembroides*) and Johannis pines (*Pinus johannis*) (Romero-Manzanares et al., 2012). We note that while changes in plant cover may be used to monitor species-specific responses to changes in resource availability, comparisons of species richness may provide a more accurate reflection of differences in community composition due to topographic aspect.

Highly variable and generally low summer monsoon precipitation, characteristic of the pinyon-juniper woodland, can affect soil-plant and plant-plant interactions by favoring species that are able to draw water from deeper soil horizons (Williams and Ehleringer, 2000). Thus, decreased summer precipitation resulting from increasing regional aridity could have a larger negative impact on species that are more responsive to summer precipitation pulses, such as pinyon pine (Huxman et al., 2004). Conversely, trees that compete better with herbaceous vegetation for soil moisture should become more dominant across the landscape than would less-competitive species. Chambers et al. (1999) describe juniper as being more highly competitive for soil moisture than pinyon.

Soil nitrogen and water availability usually interact to limit plant growth and primary productivity in arid environments (Lajtha and Whitford, 1989). Soil nitrogen can have positive effects on maximum net photosynthesis and water use efficiency (and thus productivity) in both pinyon pine and juniper woodlands (Lajtha and Getz, 1993). While litter from woody vegetation should increase nitrogen availability (Scholes and Archer, 1997), semiarid woodlands can experience considerable runoff and erosion (Ludwig and Tongway, 1995); thus higher tree cover may not be necessarily positively correlated with soil nitrogen concentration (c.f., the lack of variation in soil nitrogen content in our study). Law et al. (2012) also found no differences in soil nitrogen among areas that differed in the amount of canopy cover within a pinyon-juniper woodland and attributed it to rapid plant uptake in this nitrogen-poor ecosystem.

Tree-Grass Coexistence—Local competition for resources and resource (niche) partitioning among plant functional groups, such as trees, shrubs, and grasses, lead to their different spatial distributions on global and regional scales (Silvertown, 2004). Semiarid woodlands are low-density forests that grow slowly, accumulate soil organic matter slowly, and shift toward shrublands and grasslands in more-arid areas (Whittaker, 1975). Similar grass cover on northern and southern aspects, coupled with the higher tree cover and tree-grass ratio on moister northern aspects in our study, suggest that tree-grass coexistence in this system is at least partially mediated by soil moisture availability and likely due to partitioning of soil water among woody species and grasses. Woody species, and especially trees, are able to access water from deeper soil horizons than are grasses, leading to tree-grass coexistence via niche separation, especially on more-stressful, moisture-limited southern aspects (Breshears and Barnes, 1999; Sankaran et al., 2004). Trees appear to benefit more from lower heat stress and moister microclimates on northern aspects than do grasses. The lack of a significant difference in the tree-grass ratio may be due to facilitation, as grass performance (e.g., productivity, survivorship) can be positively influenced by tree canopy shade that ameliorates heat stress and decreases evapotranspiration (Scholes and Archer, 1997). Thus, the increased tree cover on northern aspects may offset negative effects of tree competition for soil water and provide an alternative explanation for the lack of differences in both the tree-grass ratio and grass cover between north-facing and south-facing slopes. North-facing slopes appear to be generally more biologically productive than are south-facing slopes in these semiarid landscapes; they experience greater soil moisture and support larger tree cover without a corresponding decline in grass cover.

Soil Moisture Influence on Woody Species Demography—The population structure of the codominant trees, two-needle pinyon pine and one-seeded juniper, was significantly influenced by aspect at our study site. Compared to southern aspects, north-facing aspects had a significantly greater proportion of large individuals of juniper, indicating that tree cover and recruitment may be positively influenced by available soil moisture. North-facing aspects also had a greater proportion of small individuals when species were pooled, but this result was not statistically significant. Additionally, the proportion of small pinyons on north-facing aspects was on average four times greater than the proportion of small junipers, suggesting that small pinyons may experience higher survival, recruitment, or both on north-facing aspects while junipers perform equally well on north- or south-facing aspects. Because one-seeded juniper has a higher water use efficiency compared to pinyon pine, it can maintain a net positive carbon balance at lower water potentials than can pinyon pine (Lajtha and Barnes, 1991). Thus, interspecific differences in water use efficiency and lower susceptibility to xylem cavitation (Koepke and Kolb, 2013) may explain why large junipers responded more favorably to increased soil moisture on north-facing aspects than did similarly sized pinyon. With increasing regional aridity and the expansion of grasslands into pinyon-juniper woodlands, we predict that the more drought-tolerant juniper will become the dominant tree species in our study area.

Tradeoffs between plant reproduction and growth suggest that reproductive output should be lower under stressful conditions of low soil moisture and high heat stress (Zlotin and Parmenter, 2008). Our results support previous studies in that the proportion of fruiting individuals was significantly influenced by aspect (and thus moisture status) in our study. A higher proportion of fruiting individuals should result in greater recruitment rates on north-facing aspects and agrees with our finding that overall tree cover is significantly higher on north-facing aspects. The overall production of reproductive structures (cones) or seeds per individual has been shown to respond to moisture stress in semiarid landscapes (Zlotin and Parmenter, 2008).

Conclusions—Topographic aspect plays a large role in determining the distribution of plants in resource-limited, semiarid landscapes because it affects the coexistence of plant functional groups (such as trees and grasses) and dominant tree species (such as pinyon pine and juniper). Our results corroborate that aspect-mediated differences in soil moisture can affect tree population structure (by affecting reproduction, recruitment, and survival) and cover in this moisture-limited environment. We found no evidence that soil nitrogen, an important limiting nutrient, is influenced by topographic aspect, and no evidence of a tradeoff between tree and grass cover. Physiological adaptations may explain interspecific differences in population structure and reproduction (i.e., juniper has been shown to be more resistant to drought-prone environments than is pinyon). Increased aridity due to global climate change will influence plant-soil interactions, leading to the increasing dominance of species adapted to arid conditions (e.g., grasses or perhaps one-seeded juniper rather than pinyon pine) and likely to a generally sparser plant community characterized by low cover of woody species (Breshears et al., 2005).

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