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Effects of Permanent and Temporary Edges on *Pinus clausa* (sand pine) Architecture and Stand Conditions

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**Effects of Permanent and Temporary Edges on *Pinus clausa* (sand
pine) Architecture and Stand Conditions**

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Abstract: Effects of permanent (i.e., maintained) and temporary edges with north- and south-facing exposures were studied in sand pine (*Pinus clausa* var. *clausa*) scrub, an open-canopied forest type in Ocala National Forest, Florida. On edges and interiors of four stands of each type, we measured canopy tree architecture in 5 x 100 m plots and stand density and basal area in 5 x 200 m plots. Edge effects were modest but often stronger on south- than north-facing edges and along permanent forest roads than temporary edges of clearcuts that were allowed to regrow. Compared to interior trees, those on edges were typically shorter, retained branches lower on their boles, oriented their first branches more towards the edge, and produced more asymmetrical crowns with the long axis extending into the opening; these trends were greater on south- than north-facing edges and along permanent than temporary edges. Contrary to expectations, there were no edge effects on total basal area, dead tree densities, proportions of sand pine trees with leaning trunks, directions of lean, or angles of lean. Instead of an edge effect, most trees leaned southwestly, which seems related to the northeastern origin of prevailing winds and wind gusts.

Keywords: edge effects, landscape ecology, clearcuts

Introduction

Edges created by fragmentation of closed-canopy forests, which are well studied (reviewed by Ries et al. 2017, Ries et al. 2014), are likely quite different from those created in more open-canopied ecosystems, which are less well studied (but see Delgado et al. 2007; Dodonov et al. 2013, Harper et al. 2015). Given that stand interior trees in sparse-canopied forests, woodlands, and savannas are exposed to wind and solar radiation from all directions, they experience comparatively minor changes in environmental conditions when exposed on an edge. Preconditioning by life-long exposure likely leads to trees in open-canopied ecosystems being more wind-firm and otherwise architecturally different from trees that grow in close proximity to neighbors. It follows, for example, that the phenomena of edge “unravelling” (i.e., high mortality rates of edge trees) of stands (e.g., Ferreira and Laurance 1997, but see Phillips et al. 2006) and development of radically asymmetrical crowns on edge trees reported for closed canopy forests (e.g., Loehle 1986, Muth and Bazzaz 2002) should be less pronounced in open canopied ecosystems.

Although many studies focus on edges created in formerly contiguous forest, some edges are more permanent, such as where forest develops adjacent to water bodies. Trees that border permanent openings, such as adjacent to infrastructural clearings, experience edge conditions their entire lives. We therefore expected that, compared to trees recently exposed on edges created by forest clearing, permanent edge trees more strongly reflect edge proximity in traits such as outward lean, branch retention, and crown asymmetry (Hallé 1978). Somewhat complicating this prediction is where forest in the clearings that created the edges is allowed to recover, such as where the silvicultural regime is clearcutting; such edges are temporary.

Regardless of the degree of canopy closure or whether an edge is permanent or temporary, edge effects are expected to vary with compass orientation. Causes of reported differences in biogeochemical processes (e.g., litter accumulation and decomposition), tree architecture (e.g., branch retention and orientation), and forest dynamics (e.g., tree growth and mortality rates) are thought to be related to the direct and indirect effects of solar radiation, which are more severe on south-facing edges in the Northern Hemisphere (e.g., Matlack 1993; Fraver 1994; Murcia 1995).

To address these contrasts, we compared tree and stand conditions on north- and south-facing edges of permanent and temporary edges in sand pine (*Pinus clausa* var. *clausa*) scrub, a sparse-canopied vegetation type endemic to Florida (e.g., Menges 1999). Sand pines are short-lived, generally not surviving more than 80 years, are especially susceptible to root rots when >40 years old, and are very vulnerable to wind damage (Duryea et al. 2007; Outcalt 1997). Based on these characteristics, we expected sand pine densities and basal areas to be lower on edges. Given the northerly latitude of the study area, we expected edge effects to be more pronounced on south- than north-facing edges. Exposure of edge trees to direct solar radiation and more wind than stand interior trees caused us to expect them to be shorter, to maintain branches lower on their boles, to produce branches that extend further out into the clearing, and to more often and more radically lean outwards, as found in other forest types (e.g., Loehle 1986; Mourelle et al. 2001; Olesen 2001; Muth and Bazzaz 2002; Dodonov et al. 2013; Lhotka and Stringer 2013). Edge effects on sand pine tree lean are expected to be particularly severe because this species is well known for its propensity to lean (e.g., Laessle 1958). In this regard, it is perhaps noteworthy that sand pine is in the same subsection of the genus *Pinus* as *P. contorta* (Gernandt et al. 2005), a species known for variations in structure including a krummholz form. We also expected the

magnitude of edge influence (*sensu* Harper et al. 2005) on tree architecture (e.g., height to the first branch and branch elongation into the adjacent opening; Delgado et al. 2007, Young and Hubbell 1991; but see Mourelle et al. 2001; Muth and Bazzaz 2002) to be greater on permanent edges than on the temporary edges of clearcuts in which forest regeneration is encouraged. Finally, we expected edge effects in open-canopied sand pine scrub to be less severe than in closed canopy forest because the contrasts in environmental conditions between forest and matrix are less pronounced.

Methods

Data were collected in Ocala National Forest (29°2'N, 89°7'W to 29°0' N, 81°7'W) where annual temperature and precipitation average 21 °C and 129 cm, respectively. Sand pine scrub develops on deep, severely drained and nutrient-poor sandy entisols (e.g., Laessle 1958; Kalisz and Stone 1984; Carrington 1999, Outcalt 1997). Under an open overstory of sand pine trees (50-60% canopy closure; Laessle 1965) that ranges 15-20 m high, a more closed secondary canopy often develops of various scrub oaks (*Quercus geminata*, *Q. myrtifolia*, and *Q. chapmanii*) with other evergreen hardwoods with sclerophyllous leaves (e.g., *Ilex opaca* var. *arenicola*, *Lyonia ferruginia*, and *Persea humilis*). Due to lack of grasses and other fine understory fuels coupled with the low flammability of the oak and sand pine leaf litter, wildfires only occur under extremely hot, dry, and windy conditions (Outcalt 1997). These fires are stand-replacing, with natural fire-return intervals presumed to be of about 20-40 years (Menges 1999).

In sand pine scrub in Ocala National Forest, the U.S. Forest Service permits industrial clearcuts of up to 129 ha at 15-50 year intervals (USFS, 1999), but clearcutting mimics the natural regeneration of scrub wildfires at least in regards to its impacts on vegetation and the

herpetofauna (e.g., Greenberg et al. 1995; Greenberg 2003). After clearcutting, an understory of resprouters such as *Sabal etonia* (scrub palm), *Palafoxia feayi* (feay's palafox), and the scrub oaks initially dominate (e.g., Carrington 1999). Sand pine seeds released from serotinous cones after fires or from mechanized seeding germinate under resprouting species but dominate the overstory in a few years (Cooper et al. 1959; Marshall Mattson and Putz 2008). By 10-years post-fire or post-clearcutting, a mature scrub structure develops, with sand pines in the overstory (5-20 m), scrub oaks in the midstory (2-5 m), and a ground cover of mostly lichens (*Cladonia* spp. and *Cladina* spp.), shrubs (e.g., *Vaccinium myrsinites*), and the endemic scrub palm (*S. etonii*; e.g., Menges 1999).

We compared permanent edges of four stands that developed along major forest roads that average 14 m wide with the temporary edges of four stands that bordered 11- 43 year-old clearcuts. The eight sampled stands were 32-51 years post-clearcutting, which means that the older ones represent old growth according to the definition of Outcalt (1997). Edge data were collected 0-5 m from the edge; half the sampled edges faced south and the other half faced north. Densities and basal areas of live and dead sand pine trees >10 cm DBH were collected in 200 x 5 m plots randomly located along the edge or 50-100 m into the interiors of the same stands. Individual tree characteristics were measured on 15 randomly selected trees in each plot. On each of these trees we measured DBH, the degree and direction of trunk lean, height and azimuth of the first live branch, total tree height, and maximum crown radius into the open area (edge) and towards the stand interior. Trunk lean, measured with a clinometer, was calculated as the hypotenuse of the right triangle with height measured up to the first live branch with a 8 m height pole or digital rangefinder; the angle of the hypotenuse of the right triangle. Given that tree lean can be affected by edge proximity, prevailing wind directions, and the directions of wind gusts,

we compared lean directions with these three potential driving factors. Wind speed and direction data are daily averages and maximums for 1973-2015 recorded at the Central Weather Station in Ocala National Forest. Average wind speeds are 10-minute averages of measures recorded at 2-second intervals; gusts are the maximum wind speeds recorded within 1-hour intervals over a 24-hour period.

DBH, tree height, first branch height, and crown differences between edge and interior trees were compared using paired t-tests. The proportions of leaning trees were compared with chi-squared tests. Watson-Williams tests were used to compare edge and interior trees on the basis of the degree and direction of trunk lean as well as the direction of growth of the first live branch. Tree lean and first branch directions were first compared with an angular-linear test to determine whether stand age (32-51 years) was significant covariate.

Results

Sand pine tree architecture and stand characteristics in stand interiors differed in some but not all the expected ways (Tables 1 and 2). At the stand level, regardless of edge direction or edge type, there were no differences in densities of live or dead trees nor any differences in basal areas between edge and interior transects. For the traits that showed edge-interior differences, the overall magnitude of edge influences typically decreased from permanent south to permanent north edges, and then from temporary south to temporary north edges. For example, on permanent south and north-facing edges, the most pronounced edge effects on sand pine tree architecture were on crown asymmetry and height to the first live branch (Fig. 1); for temporary edges, the differences were smaller and not always significant (Table 1). Similarly, edge trees were shorter than interior trees except on south-facing temporary edges. On all but north-facing

temporary edges, the lowest branches showed a slight but statistically significant tendency to point towards the edge (Fig. 2).

Tree lean, a prominent feature of sand pine scrub, was not affected by proximity to any type of edge. Many sand pine trees leaned (48-73%), but the proportions of trees with leaning boles did not differ between edges and stand interiors, nor did the mean degrees of lean show any edge effect (Table 1, Fig. 3). Instead of leaning out of the stands into the adjacent open areas, sand pine trees in our study area predominantly leaned in a south-westerly direction (Fig. 4a). Only edge trees on north-facing permanent edges departed at all from this very strong trend, but few leaned directly outwards from the edge. Neither the extent nor the direction of tree lean varied with stand age (32-51 years; data not shown). Instead of an edge effect, the predominant south-westerly direction is leeward of the prevailing northeasterly winds (Fig. 4b & c), which is also the direction from which wind gusts are most common (Fig. 4d & e).

Discussion

Sparse-canopied sand pine scrub is susceptible to edge effects, but the magnitudes of edge impacts on the vegetation and individual trees are smaller than reported for closed-canopy forests. For example, presumably in response to increased light from the adjacent clearing, sand pine trees on edges maintained branches lower on their trunks than interior trees, but the effect was much less pronounced than in closed canopy forests. Expressing these data as crown ratios (i.e., proportion of the bole with live branches), for sand pine trees south-facing permanent edges and interiors of the same stands, the values were 0.66 and 0.63, respectively. In contrast, Sherich et al. (2007) reported edge and interior crown ratios of 0.71 and 0.58, respectively, for *Pseudotsuga menziesii* var. *glauca* (Douglas fir) trees in Idaho. Another example of modest edge

effects on sand pine is that first branch heights of edge and interior trees differed by an average of only 1 m, regardless of the direction the edge faced or its permanence. One reason for the weak edge impact on sand pine crown depth is that, unlike a few other species of *Pinus* (e.g., *P. serotina*) and many other tree species, sand pine seldom produces epicormic branches. A more fundamental difference is that due to the sparse canopy, estimated at 40-50% open (Laessle 1965), the light environments of interior and edge sand pine trees are not markedly different.

Asymmetrical crowns due to differential extension growth of branches that faced edges did develop on sand pine trees. Also as expected, the extent of edge effects on architectural characteristic tended to be larger for trees on south-facing than north-facing edges and greater on trees on permanent than temporary edges. It should be noted, however, that the mean difference in crown radii into the opening and towards the stand interior was only 1.4 m on permanent, south-facing edges, which is modest given that the longest branch measured 4.7 m. The minimum crown radius difference (i.e., towards the edge minus towards the interior), which was also statistically significant, was only 0.19 m for trees on temporary north-facing edges. Comparison of these values with those in the literature is difficult because in many reports, differences in crown dimensions result from the combination of bole lean and branch length (e.g., Umeki 1995) or the data are presented in terms of crown areas and not maximum branch extension (Young and Hubbell 1991, Mourelle et al. 2001). We do not know how rapidly sand pine crown eccentricities developed, but reported rates of crown expansion into treefall gaps in closed canopy forests typically average 8-15 cm per year (Hibbs 1982; Runkle 1998; Ye and Comeau 2009). One generalization that emerges from this literature that helps explain the development of only modest crown asymmetry on edges by sand pine trees is that this response is more characteristic of shade tolerant species (Mourelle et al. 2001), whereas sand pine is light-

demanding. Furthermore, as for the other traits, the differences in light environments on sand pine stand edges and interiors are small, given the openness of the canopy.

In sand pine scrub, edge direction and type showed no effect on live tree density, densities of dead-standing or fallen trees, or basal area (Table 1). Other studies, in contrast, report that high rates of tree fall and damage along edges results in lower canopy tree densities and reduced basal areas (e.g. Mesquita et al. 1999; Harper et al. 2005; Ferreira and Laurance 1997; Delgado et al. 2007). Again, it is not clear whether this difference is due to the openness of sand pine scrub canopies or some characteristic of sand pine trees.

Tree lean, which is a striking characteristic of sand pine scrub (Laessle 1958), is evidently not an edge effect. Whereas trees on forest edges typically lean outwards (Hallé 1978; Loehle 1986; Young and Hubbell 1991; Muth and Bazazz 2002; Delgado et al. 2007; Sherich et al. 2007), the angles and directions of sand pine trunk lean were more related to wind direction than edge proximity. Sand pines' predominant lean towards the southwest may provide them with a degree of streamlining that helps them avoid susceptibility to wind-induced crown damage and stem breakage (Hedden et al. 1995) from the prevailing northeasterly winds.

Conclusions

Edge effects are apparent in sand pine scrub and follow the frequently reported trends, but are modest relative to those reported for closed canopy forests. For example, sand pine trees that grew up on permanent edges retained branches lower on their boles and extended their crowns further into the adjacent opening than trees on temporary edges or in stand interiors, but both edge responses were of much lower magnitude than reported for edges of closed canopy forests. The modest edge effects observed in sand pine scrub are apparently due to stand interior trees in

this open-canopied forest type being illuminated from all sides and their neighbors providing little protection from wind.

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Table 1. Sand pine trees (>10 cm DBH and 30-50 years old) on permanent and temporary edges that faced either north or south compared with similar aged trees in the interiors of the same stands 50-100 m from the edge. Individual tree data are from a random sample of 15 trees from each plot. Means $\pm$ 1 standard deviation and the corresponding probabilities of edge versus interior differences for each edge type (N = 4) are based on t-tests. SP = south-facing permanent edge; NP = north-facing permanent edge; ST = south-facing temporary edge; NT = north-facing temporary edge.

Variable	Edge (0-5 m)				Interior (50-100 m)				p-Value
	SP	NP	ST	NT	SP	NP	ST	NT	
Dead Tree Density (#/ha)	131 $\pm$ 40	130 $\pm$ 56	80 $\pm$ 64	153 $\pm$ 88	153 $\pm$ 153	85 $\pm$ 72	102 $\pm$ 96	215 $\pm$ 64	ns (for all)
Live Tree Density (#/ha)	443 $\pm$ 446	182 $\pm$ 16	506 $\pm$ 153	352 $\pm$ 112	665 $\pm$ 490	352 $\pm$ 129	415 $\pm$ 40	352 $\pm$ 48	ns (for all)
DBH (cm)	20.2 $\pm$ 4.8	24.9 $\pm$ 5.6	23.2 $\pm$ 4.9	20.7 $\pm$ 5.2	20.8 $\pm$ 4.8	21.2 $\pm$ 4.1	21.5 $\pm$ 5.2	21.3 $\pm$ 4.7	0.051, <0.001, 0.07, ns
Tree Lean Direction (°)	226 $\pm$ 45.0	292 $\pm$ 50.0	197 $\pm$ 43.9	188 $\pm$ 60.7	233 $\pm$ 47.0	224 $\pm$ 43.5	248 $\pm$ 70.2	227 $\pm$ 50.3	ns, <0.001, ns, ns
Trunk Lean Degree (°)	11.5 $\pm$ 5.4	8.8 $\pm$ 3.8	11.2 $\pm$ 5.5	7.1 $\pm$ 5.0	9.9 $\pm$ 5.2	9.6 $\pm$ 4.6	10.6 $\pm$ 5.4	8.8 $\pm$ 3.5	ns (for all)
First Branch Height (m)	10.4 $\pm$ 2.5	10.4 $\pm$ 2.5	13.0 $\pm$ 2.2	11.0 $\pm$ 2.1	11.4 $\pm$ 3.0	11.4 $\pm$ 3.0	14 $\pm$ 2.5	12.0 $\pm$ 1.93	<0.001, ns, <0.01, <0.001
First Branch Direction (°)	198 $\pm$ 64.0	347 $\pm$ 58.9	150 $\pm$ 70.6	19 $\pm$ 67.4	286 $\pm$ 77.0	136 $\pm$ 77.7	173 $\pm$ 70.6	179 $\pm$ 78.3	<0.05, <0.001, <0.05, ns
Tree Height (m)	15.4 $\pm$ 1.6	16.4 $\pm$ 1.8	17.6 $\pm$ 1.7	16.4 $\pm$ 2.3	16.1 $\pm$ 2.2	17.1 $\pm$ 2.1	18.6 $\pm$ 2.4	16.4 $\pm$ 2.1	<0.001, 0.062, <0.01, ns
Crown Radius Difference (cm)	137.0 $\pm$ 134.6	70.4 $\pm$ 79.0	83.4 $\pm$ 105.4	19.6 $\pm$ 94.1	90.9 $\pm$ 118.2	60.4 $\pm$ 79.0	42.1 $\pm$ 108.1	56.9 $\pm$ 110.5	<0.001, <0.001, 0.061, ns

Table 2. Stand-level data are from 5 x 200 m plots on stand edges and in stand interiors (N = 4 stands per situation). The proportions of leaning trees (out of 60 trees per edge and interior type) on stand edges and interiors, are compared with chi-squared tests. For basal area, means±1 standard deviation and the corresponding probabilities (based on t-tests) are presented; abbreviations as in Table 1.

Variable	Edge				Interior				p-Value
	(0-5 m)				(50-100 m)				
	SP	NP	ST	NT	SP	NP	ST	NT	
Number of Trees	70.0	73.3	48.3	70.0	70.0	63.3	51.6	70.0	ns (for all)
Leaning (%)									
Basal Area (cm²/m²)	11.3	7.7	17.9	12.6	14.2	11.5	13.0	12.4	ns (for all)

FIGURE LEGENDS

Fig. 1. Height to the lowest live branch on sand pine trees on permanent and temporary edges and in the interiors of the same stands. North and south-facing edges are at 0-5 m from roads or clearcuts, while interior trees are 50-100 m from the nearest edge. Data for each panel from four replicates with 15 trees each. Note that the labels for edge types appear on the right side of all panels.

Fig 2. Directions of lean of sand pine trees >10 cm DBH on north and south-facing permanent and temporary edges compared to stand interior trees. Data for each panel from four replicates with 15 trees each. Note that the labels for edge types appear on the right side of all panels.

Fig. 3. Compass direction of growth of the first live branch on sand pine trees on permanent and temporary edges compared to interior trees. Data for each panel from four replicates with 15 trees each. Note that the labels for edge types appear on the right side of all panels.

Fig. 4. Sand pine tree lean, prevailing winds, and the directionality of wind gusts: (a) compass directions of sand pine tree lean (n=334 trees), (b) wind rose for directions of average daily wind origins, where the average origination is $68.64^{\circ} \pm 74.85$ and the data lack circular uniformity ($p < 0.001$), and (c) wind rose of daily gust wind speeds. Data are from the US Forest Service's Central Weather Station in Ocala National Forest. Avg. wind speeds are 10-minute averages of wind intensity measures recorded at 2 second intervals. Peak wind gusts are the maximum wind speeds recorded within 1-hour intervals.

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