



**Identification of Annual Rings in an Arid-Land Woody Plant, *Prosopis Glandulosa***

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indicates significant clumping (based on Poole and Rathcke's [1979]  $\chi^2$  test), Min is still indicating significant displacement. Arita's Case IV for eight species (his Fig. 1) also shows significant clumping according to Var although Min and  $G_{1(n-1)}$  show competitive displacement.

### Conclusion

My computer simulations have shown that the communitywide parameter Var is superior to the non-communitywide test statistics  $G$  and Min. Not only are  $G$  and Min less able to detect displacement in the vicinity of even spacing, they can also misidentify random or clumped communities as having displacement. Although Arita's criticism of my original methods is valid, my original conclusion still remains; the  $G$  test statistics, and I now also include Min, should *not* be used to analyze communities to test the competitive displacement hypothesis.

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## IDENTIFICATION OF ANNUAL RINGS IN AN ARID-LAND WOODY PLANT, PROSOPIS GLANDULOSA

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*Prosopis glandulosa* var. *glandulosa* Torr. (honey mesquite) is an arborescent leguminous species in the southwestern United States and northern Mexico, where it dominates many plant communities (Simpson and Solbrig 1977). Depending on the context, *P. glandulosa* may be viewed as an invasive pest (Fisher et al. 1973), a commercial wood producer (Weldon 1986), or a potential fuel and fodder crop for arid lands (Felker 1979). The ability of *P. glandulosa* to invade grasslands and, in some circumstances, facilitate the ingress and es-

tablishment of other woody species, appears to have been an integral factor in the conversion of southwestern grasslands and savannas to woodlands in recent history (Johnston 1963, Buffington and Herbel 1965, Archer et al. 1988). A knowledge of *P. glandulosa* population biology is therefore crucial to reconstructing and understanding vegetation change in many dry-land ecosystems.

Successional changes involving *P. glandulosa* have been inferred from historical observations (Inglis 1964), permanent plots (Buffington and Herbel 1965, Goldberg and Turner 1986, Turner 1990), sequential aerial photography (Archer 1989), and stable carbon isotope ratios of organic carbon (Tieszen and Archer 1990). However, such records may provide only infrequent "snapshots" and qualitative, coarse, and/or indirect assessments of vegetation change and are not available for most landscapes. Tree ring analysis of *P. glandulosa* would allow more precise quantification of plant growth rates and population age structure in relation to soils, disturbance, succession, and climate (e.g., Henry and Swan 1974, Stewart 1986) than has been previously possible for this species. However, for tree rings to be useful for age determinations, plants must produce distinct, annual growth rings. Species vary widely in the extent to which growth rings are discernible and growth anomalies such as "missing rings" and "false rings" are possible (Fritts and Swetnam 1989). It is, therefore, desirable to verify the annual nature of ring deposition if techniques in dendrochronology are to be reliably applied. This would be particularly important for woody

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plants such as *Prosopis*, whose ranges extend into tropical and subtropical environments where exogenous factors might strongly influence patterns of ring deposition (Jacoby 1989). Studies in other dryland systems have verified the annual nature of growth rings in trees and shrubs of some species (Ferguson 1964, Roughton 1972, Arno and Wilson 1986, Wyant and Reid 1992, Keeley 1993). Here we examine cross sections of *P. glandulosa* stems from stands of known age to ascertain the relationship between stem age and number of growth rings and describe a preparative technique.

#### Methods

Seven stands of *P. glandulosa* of known age were located in five areas of Texas, USA. The sites spanned a climatic gradient ranging from temperate (33°28' N; 100°51' W) to subtropical (27°40' N; 98°12' W) and encompassed a wide range of mean annual precipitation, temperature, and frost-free period. Six of the stands consisted of *P. glandulosa* plants known to have regenerated vegetatively immediately following stand-wide cutting. Plants in the seventh stand had been grown from seed in experimental plots.

Cross sections ( $n = 5-19$  per stand) of 3-5 cm thickness were taken 10-20 cm above ground level. Cross sections were sanded with successively finer grained sand paper (50 through 1000 grit), then buffed with 0000 steel wool placed over the nozzle of a vacuum cleaner to remove dust from vessel cells. The sanded surfaces were darkened with a black, permanent, broad-tip marking pen and air-dried 24 h. White blackboard chalk was then rubbed over the cross sections and excess chalk brushed away, leaving chalk in vessel cells.

Rings were counted along three radii per cross section and were rectified for false and missing rings (Schweingruber 1988). When differences in ring counts between radii could not be resolved because of scars or anomalous wood near the pith, an average of the three radii was used.

#### Results and Discussion

**Efficacy of surface preparation.** *P. glandulosa* xylem is ring porous (Meyer and Meola 1978). Vessels of early wood were distinctly larger than those of late wood and formed a well-defined zone or ring in stem cross sections. Darkening the surface of stem cross sections with a black marker pen and highlighting the vessel cells with white chalk greatly accentuated the distinctness of this xylem structure over sanding and vacuuming alone. The enhanced contrast between vessels and the surrounding tissue was particularly helpful when following growth rings in an effort to identify false and locally indistinct rings. Several types of marker pens were tried. Those with thick ink tended to clog vessel cells so that they would not hold chalk.

TABLE 1. Average number of rings counted on *Prosopis glandulosa* trees in seven stands of known age from five regions in Texas, USA. Mean annual temperature (Temp, °C), and precipitation (PPT, mm) are shown for each region.

Stand location	Mean annual		Stem origin*	Stand age (yr)	Mean (SD) number of growth rings	Number of trees sampled
	Temp (°C)	PPT (mm)				
Alice	24	660	v	12	10.4 (0.7)	19
Uvalde Stand 1	22	610	v	23	22.4 (0.9)	9
Stand 2			v	23	17.9 (1.6)	11
Stand 3			v	30	28.4 (2.3)	11
Spur	17	533	v	20	16.4 (3.6)	5
Palo Pinto	18	711	v	7	6.5 (0.5)	10
College Station	21	965	s	17	12.5 (0.8)	10

\* v = vegetatively regenerated following stand-wide cutting. s = stand established from seeds; no known disturbance.

*Are P. glandulosa growth rings produced annually?* Ring counts were, on average ( $\pm 1$  SD), within  $2.5 \pm 1.9$  yr of known stand age (Table 1). In no case did ring numbers exceed the known stand age, suggesting that false rings were not produced and that ring production was relatively unresponsive to exogenous factors. This was true even for trees from the southernmost stands, where climate was subtropical and where ring production may either not occur or may occur in response to exogenous factors such as climatic fluctuation rather than endogenous annual growth cycles (Jacoby 1989). We examined other common woody species from the Alice stand (ring-porous *Acacia farnesiana* and diffuse-porous *Celtis pallida*, *Condalia hookerii*, and *Zanthoxylum fagara*) and could not distinguish annual rings using the same method. Thus, the technique was species specific. Although little is known of the biology and seasonal growth dynamics of these species, the timing of leaf initiation, radial growth, and dormancy from southern and northern ecotypes of *P. glandulosa* appears to be regulated primarily by photoperiod rather than temperature or moisture (McMillan and Peacock 1964), as is typical for most *Prosopis* species in the section *Algarobia* (Mooney et al. 1977). Cambial activity in *P. flexuosa*, *P. alba*, *P. nigra*, and *P. caldenia* from arid and semiarid regions of Argentina also appears to be annual and controlled endogenously (Villalba and Boninsegna 1989).

Ring counts on three of the five plants in the 20-yr-old Spur stand indicated stems were 19 yr old. However, two plants had stems with ages of 12 and 13 yr.

As a result, the relative variability in stem ages in this stand (coefficient of variation = 0.22) was more than twice that of the other stands ( $cv = 0.04\text{--}0.09$ ). The magnitude of these within-stand disparities was clearly unusual relative to that of other stands and cross dating did not indicate anomalies in ring deposition.

Variability in stem ages may reflect within-stand differences in shoot initiation after planting or disturbance. Thus, while stand age was "x," stem initiation may not have occurred on some plants until year  $x + 1$  or  $x + 2$ . In addition, the consistent underestimation of stem age by ring counts of *P. glandulosa* (Table 1) should partially reflect variability in the time required for stems to reach sampling height (Norton and Ogden 1990). Ages of stems cut at 10–20 cm above ground at the undisturbed College Station stand were, on average, underestimated by 4.5 yr. This agrees with reported field measurements of plant height on *P. glandulosa* seedlings in central Texas (S. Archer, unpublished data) and *P. juliflora* seedlings in southern Arizona (Glendening and Paulsen 1955), which averaged 20 and 12 cm, respectively, at 4 yr of age. Smaller differences in actual and estimated ages for stems regenerated vegetatively following disturbance, in comparison to stems from undisturbed plants, are consistent with observations that *P. glandulosa* stems regenerating after top removal develop more rapidly than those that arise from seeds (Hamilton et al. 1981).

### Conclusions

The utilization of woody plants for dendroecology requires species that produce distinguishable rings in most years, that possess ring features that can be dated dendrochronologically, and that attain sufficient age to provide the time control required for a particular investigation (Fritts and Swetnam 1989). Our survey suggests that *P. glandulosa* plants from a range of climatic regimes produce true annual rings and that the surface preparation technique described here was effective in highlighting these rings for analysis. Models of *P. glandulosa* size/age relationships based on plant growth rate analysis (Archer 1989) suggest stems of some trees may exceed 200 yr in age. Thus, tree ring analysis of *P. glandulosa*, which is sufficiently long lived to be a canopy dominant in the vegetation over much of its range, appears to be a promising tool for reconstructing climatic events, disturbance, stand development, and successional history in many arid and semiarid ecosystems of the southwestern United States and Mexico.

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## FOREST DISTURBANCE BY LARGE BLOWDOWNS IN THE BRAZILIAN AMAZON

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Wind defoliation and large blowdowns are important and frequent disturbances for tropical forests of islands and coastal areas in the hurricane belts 10°–20° north and south of the equator (Sousa 1984, Whitmore 1984). In the Caribbean, hurricane repeat cycles may be  $\leq 15$ –20 yr and effects on the forest can range from

minor defoliation to large-scale tree mortality (Tanner et al. 1991). In contrast, little is known about the importance of windstorms in tropical forests outside the hurricane belt. Large blowdowns from convectional storms have been reported for tropical forests in South America (Dyer 1988) and southeast Asia (Whitmore 1984). However, there has been no continental-scale quantification of blowdown occurrence.

This study describes and quantifies for the first time the widespread occurrence of large (more than  $\approx 30$  ha) blowdowns in mature Amazonian forest. In Landsat Thematic Mapper (TM) images of the Brazilian Amazon, anthropogenic clearings and secondary forests are readily detected by their spatial patterns and their reflectances in the different TM wavelengths (spectral properties), which contrast with those of the mature forest (INPE 1992). However, other patches of secondary forest, far from sites of human occupation and apparently of natural origin, have also been detected. For example, Braun and Siegl (1990) noted large fan-shaped patches of secondary forest in a remote area south of Tefé. Here, we present evidence that these and other similar patches of secondary forest visible on Landsat images across the entire forested Brazilian Amazon ( $3.9 \times 10^6$  km<sup>2</sup>) are similar in origin to recent, confirmed blowdowns that we discovered north of Manaus using Landsat images and observations from aircraft and on the ground.

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