Variation in Basal Sprouting in Co-Occurring Shrubs: Implications for Stand Dynamics
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Variation in basal sprouting in co-occurring shrubs: implications for stand dynamics

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Abstract. Sources of basal sprouting for five shrub species representing five plant families common to the Tamaulipan biotic province were quantified, following four intensities of top removal. Among undisturbed shrubs, *Celtis pallida* and *Zanthoxylum fagara* were somewhat arborescent, with one or two dominant primary stems per plant. *Aloysia gratissima*, *Ziziphus obtusifolia* and *Schaefferia cuneifolia* were fruticose in architecture, with more and smaller stems. Following top removal, each species exhibited a distinct regenerative hierarchy whereby shoot production following disturbance was primarily from structures immediately subtending the removed tissues, even though more distal tissues had the capacity for shoot production. Thus, removal of stems to a 5 cm residual increased the contribution of primary stems from stem bases, whereas stem removal to ground line typically induced regeneration from root crowns. *Schaefferia*, *Zanthoxylum* and *Ziziphus* were capable of producing shoots from root tissue, yet regeneration from roots was not stimulated until tissues were removed to below root crowns.

Field observations indicate that most woody species in the subtropical thorn woodlands of southern Texas, USA, are highly persistent in the face of natural and anthropogenic disturbance, owing to their ability to regenerate vegetatively. Alternative sources of stem replacement contribute to the high resilience of these shrubs following disturbance and may help explain or predict patterns of secondary succession and plant persistence following various intensities of disturbance.

Keywords: Disturbance; Resilience; Root sprouting; Succession; Thorn woodland; Vegetative regeneration; Texas

Nomenclature: Correll & Johnston (1979).

Introduction

Basal sprouting, the initiation of additional stems from at or below ground line, is a ubiquitous attribute of the woody vegetation of the Tamaulipan thorn woodlands of southern Texas, and is the predominant mode of regeneration following woodland disturbance (Scifres 1980). Observations of differences among species in survival and rates of regrowth following stand-wide disturbance (Box, Powell & Drawe 1967; Hamilton, Kitchen & Scifres 1981), suggest that interspecific differences in modes of vegetative regeneration may influence species composition.

We compared and contrasted patterns of basal sprouting for five common Tamaulipan shrub species representing five plant families: *Aloysia gratissima* (*Verbenaceae*), *Celtis pallida* (*Ulmaceae*), *Schaefferia cuneifolia* (*Celastraceae*), *Zanthoxylum fagara* (*Rutaceae*), and *Ziziphus obtusifolia* (*Rhamnaceae*). Our objectives were to (1) determine the sources of sprouting, (2) quantify effects of different intensities of top removal on shoot origin and (3) quantify canopy regeneration following stem removal. These data constitute a first step toward explaining and predicting shifts in species abundance following various types or intensities of disturbance.

Methods

The study was conducted on the Texas Agricultural Experiment Station's La Copita Research Area, 20 km southwest of Alice in Jim Wells County, Texas (27° 40' N, 95° 12' W). The climate is subtropical with warm winters and hot summers. Mean annual rainfall is 65 cm. The vegetation was a savanna woodland dominated by a *Prosopis glandulosa* overstory with *Zanthoxylum*, *Celtis*, *Aloysia*, and *Condalia hookeri* prominent in the understory. Soils were sandy clay loams. See Scifres & Koerth (1987) for more complete site descriptions.

Target species received four intensities of stem removal: (1) none recorded for 20-30 yr, (2) all aerial stems removed to ground line in 1979, (3) stems removed to a 5 cm residual above ground in January 1984, and (4) all tissues (stem bases and root crowns) removed to below the first woody lateral root in March 1984.

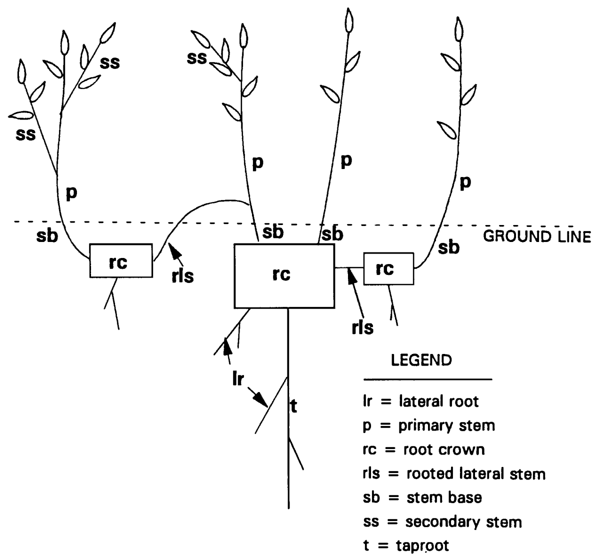

Fig. 1. A schema based on form and function for characterizing regenerative structures of shrubs examined in this study.

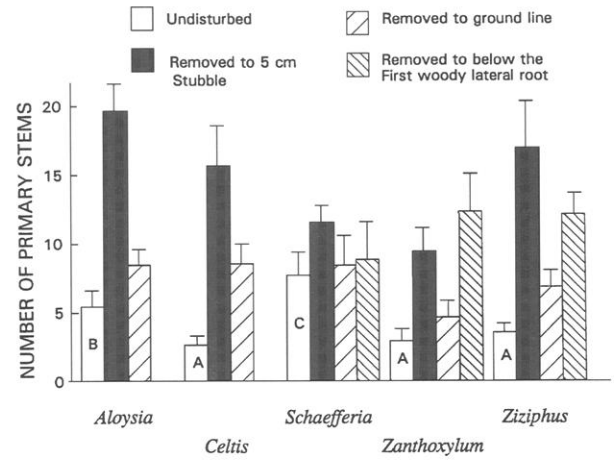

Fig. 2. Mean (± SE) number of basal stems per plant in August 1984 for *Aloysia gratissima*, *Celtis pallida*, *Schaefferia cuneifolia*, *Zanthoxylum fagara*, and *Ziziphus obtusifolia*, following various intensities of top removal. Species means for the undisturbed treatment marked with the same uppercase letter were not statistically different ($P \leq 0.05$). Statistical comparisons between treatments were not made because of differences in time since disturbance.

All stems originating at or below ground line were counted and their diameters were measured for 10 to 20 randomly selected individuals of each species in August 1984. Canopy diameters of 10 to 20 individuals from treatments (1) and (3) above, were measured in August 1984 and March 1985, respectively. Differences ($P \leq 0.05$) in the mean number of basal stems on plants in undisturbed stands and differences in mean canopy diameter for plants in treatment (3) were assessed with one-way analysis of variance and means were separated using the Student-Newman-Keuls test (Steel & Torrie 1980). Differing lengths of time between treatments and data collection precluded formal analysis of variance for effects of time and intensity.

Soil was cleared from regenerating structures (minimum depth of 25 cm) of 10 individuals of each species in each treatment and the origin of primary stems was noted. Differences between disturbed and undisturbed shrubs in primary stem origin and evenness of stem distribution between sources of origin were compared by use of X^2 ($P \leq 0.05$).

Results

Patterns of primary stem origin and species characteristics

Terms used to describe patterns of stem origin are defined and illustrated in Fig. 1. The schema is based on form and is not intended as a morphologically rigorous model. 'Root crowns' were regions of tissues accumulated at the junction of roots and shoots. 'Primary stems' arose at or below ground line, whereas 'secondary stems' arose above ground, directly from primary stems. Secondary stems could become primary stems by layering. The downward extension of primary stems from ground line to their junction with root crowns or other stems were termed 'stem bases'. 'Rooted lateral stems' arose by layering or sympodial branching below ground.

Undisturbed plants of the five species exhibited a range of growth habits. Average primary stem diameters for *Aloysia* (5.0 cm), *Schaefferia* (7.3 cm) and *Ziziphus* (10.2 cm) were smaller ($P \leq 0.05$) than those of *Zanthoxylum* (20.5 cm) and *Celtis* (19.8 cm).

Undisturbed *Aloysia* and *Schaefferia* had more stems per plant than *Celtis*, *Zanthoxylum* and *Ziziphus* (Fig. 2). The latter three species typically had one or two dominant primary stems and several smaller stems per plant, and hence larger coefficients of variation (CV) in mean stem size (range = 67 - 88%). Stems of *Aloysia* and *Schaefferia* were uniformly smaller (CV = 22 and 39%, respectively). With the exception of *Schaefferia*, plants subjected to top removal supported more stems than non-manipulated plants.

15 months following stem removal, mean canopy diameters of *Aloysia* (74 cm) and *Celtis* (88 cm) were significantly larger ($P \leq 0.05$) than those of *Schaefferia* (24 cm), *Zanthoxylum* (45 cm) and *Ziziphus* (41 cm). In

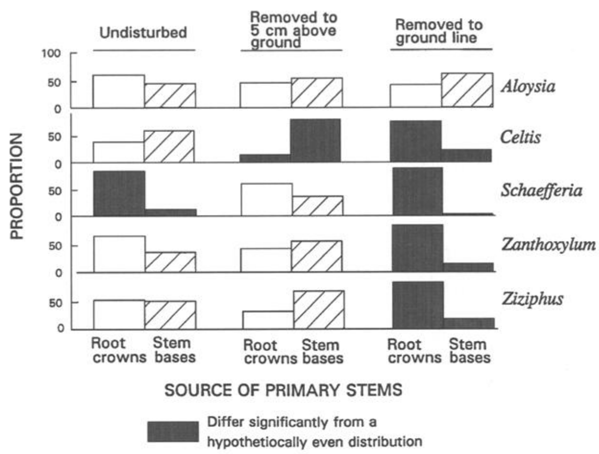

Fig. 3. Proportion of basal stems originating from root crowns and stem bases, for *Aloysia gratissima*, *Celtis pallida*, *Schaefferia cuneifolia*, *Zanthoxylum fagara*, and *Ziziphus obtusifolia* in August 1984. Plants had been subjected to either no top removal, removal to a 5 cm residual above ground or removal to ground line. Based on X^2 comparisons with untreated plants, relative contributions of root crowns and stem bases were different ($P \leq 0.05$) for all species following both treatments except for *Schaefferia cuneifolia* removed to ground line. Shaded bars indicate that source of stems differed significantly from a hypothetical even distribution for that species/treatment combination.

addition, regrowth canopy cover expressed as a percentage of mean canopy diameters for undisturbed plants was higher for *Aloysia* (154%) and *Celtis* (135%) than it was for *Schaefferia* (27%), *Zanthoxylum* (51%) and *Ziziphus* (58%).

The gross form of regenerative structures varied considerably among species. In contrast to the root crowns of *Schaefferia*, *Zanthoxylum*, and *Ziziphus*, the root crowns of *Aloysia* and *Celtis* were much enlarged relative to stems and roots. *Aloysia*, *Schaefferia* and *Zanthoxylum* did not produce rooted lateral stems. *Ziziphus* stems often exhibited a decumbent habit.

Intensity of top removal and stem origination

For non-disturbed plants, proportions of primary stems arising from stem bases and root crowns were comparable in all species except *Schaefferia*, which produced 86% of its primary stems from root crowns (Fig. 3). Stem removal to a 5 cm residual increased the proportion of sprouts arising from stem bases in all species relative to untreated plants. However, root crowns continued to contribute a higher proportion of primary stems than stem bases for *Schaefferia*. Regeneration following stem removal to ground line was primarily from root crowns in all species except *Aloysia*, for which stem bases continued to contribute a greater-than-expected proportion of primary stems. *Schaefferia*, *Zanthoxylum* and *Ziziphus* regenerated from roots following the removal of all stem and root crown tissue, but *Aloysia* and *Celtis* did not. Shoots arising from taproots comprised 91, 82, and 84% of such sprouts in *Schaefferia*, *Zanthoxylum* and *Ziziphus*, respectively.

Discussion

Stem removal increased the number of primary stems on plants relative to untreated controls, and increasing stem numbers may increase root crown size via thickening at the junction of root crowns, stems and roots. Keeley & Keeley (1988) observed the development of large root crowns induced by repeated sprouting in response to fire for several species from the California chaparral. Intensity of top removal also influenced patterns of stem origination by removing potential sprouting structures. A regenerative hierarchy occurred, whereby shoots typically arose from structures immediately subtending the excised tissues, even though tissues further removed had the capacity for shoot production. *Schaefferia*, *Zanthoxylum* and *Ziziphus*, the species which root sprouted, only did so when roots had been severed from the main plant. Jones & Raynal (1988) similarly found that disturbance was required to stimulate sprouting from *Fagus grandifolia* roots.

Common sources of canopy and primary stem damage and mortality among Tamaulipan shrubs include frost (Lonard & Judd 1985), drought (Carter 1964), fire (Box, Powell & Drawe 1967) and mechanical manipulation (Scifres 1980). Each of these may disturb shoot systems at differing intensities. As a result, shrub species composition and successional patterns in this vegetation may be closely linked to the sprouting characteristics of component species. For example, *Celtis* and *Aloysia* possessed the most morphologically distinct variants of the root crown sprouting trait, and developed larger canopies than the other species following stem removal. Other studies in the region have documented similar and longer-term increases in relative canopy cover for *Celtis* and *Aloysia* in stands regenerating from simple top removal (Scifres, Mutz & Durham 1976; Koerth et al. 1989). The relatively large root crowns of these two species, may provide increased surface area for subterranean meristems as well as an increased volume of stored nutrients required for regrowth. Conversely, the inability of *Aloysia* and *Celtis* to regenerate from root tissues may result in their disappearance from stands subjected to more intense disturbances which effectively damage or destroy below ground stem and root crown tissues (e.g. severe frosts, hot fires, or range management practices such as grubbing or root plowing). Following these kinds of disturbances, plants with the capacity to sprout from root tissue (*Schaefferia*, *Zanthoxylum* and *Ziziphus*) might be most likely to persist on the site and subsequently attain dominance (e.g. Flinn & Wein 1977).

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