their leaves, while those on the western slope still retained most of their canopy cover. High wind speeds increase air movement above the canopy, increasing evapotranspiration rates (Leigh 1999). As a result, it is possible that trees on windy slopes lose their leaves more readily or earlier in the dry season as a strategy to decrease water loss. Additionally, wind may physically remove leaves. A reduction in total leaf area may reduce tree productivity. For example, gross annual photosynthesis is higher in evergreen forests than deciduous forests (Leigh 1999). However, net production, while lower overall in dry forest (Leigh 1999), may not differ with leaf loss, because it is also influenced by the amount of forest respiration.

High winds may have additional consequences for ecosystem dynamics. We noted, but did not measure, an increase in temperature and humidity on the western slope. Desiccation on wind-exposed slopes lowers humidity and makes forests more susceptible to fire (E. Gonzalez, pers. comm.). Lowered humidity may also decrease soil decomposition rates (Begon et al. 1990). This may slow rates of nutrient cycling and in turn limit forest growth. As another gauge of forest growth, we observed a large number of vines, especially *Arrabidaea* spp. (Bignoniaceae) and understory plants on the western slope. These were conspicuously absent on the eastern slope. While our measurements of forest growth (height and DBH) did not show a significant difference between sides, a larger sample size might reveal a stronger trend towards smaller trees on east-facing slopes. We speculate that the water loss and physical stress of a high wind environment, such as an east-facing slope in Guanacaste, may limit forest growth in the long term.

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Water rising: the survival strategies of *Jacquinia nervosa* and possible effects on ecosystem dynamics

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Abstract: The seasonal dry tropical forest is a resource-limited environment in which plants have developed unique adaptations to cope with light and water stress. The deciduous tree *Jacquinia nervosa* exhibits several unique characteristics, including reverse leaf-loss phenology and a deep taproot. We predicted that these characteristics of *Jacuinia* would increase surface soil moisture around its base, which might in turn result in an increase in other plants growing beneath it. We found no differences in soil moisture between *Jacuinia* and comparably sized, nearby leafless deciduous trees. However, we did find significantly more neighboring plants under *Jacuinia* than under the nearby leafless deciduous trees. This suggests that *Jacuinia* may have an important effect on the microhabitat around itself. However, these effects could be due to resources other than soil moisture such as nutrients and exposure to light. Additional study is needed to elucidate the functional significance of *Jacquinia's* unique characteristics.

Key Words: hydraulic lift, phreatophyte, reverse phenology, soil moisture

Introduction

In the seasonal dry tropical forest of northwestern Costa Rica, plants use a variety of survival adaptations to deal with the limited resources of water and sunlight. Reverse phenology, leafing out in the dry season and losing leaves in the rainy season, is a strategy used by *Jacquinia nervosa* (Theophrastaceae) that may increase its access to sunlight. Because other deciduous trees lose their leaves during the dry season, *Jacquinia* can take advantage of the sunlight coming through the open canopy. The reverse phenology exhibited by *Jacquinia* may create a microhabitat around the tree by changing moisture levels, nutrient resources, or light levels.

Jacquinia adapts to water limitations by being a phreatophyte, having a deep taproot that can reach down many meters to the water table (Janzen 1983). This feature may be ecologically important in areas with high water stress by transporting water from the water table up to the surface soil through a mechanism called hydraulic lift (Caldwell et al. 1998). Hydraulic lift is based on the passive movement of water down a water potential gradient, which creates a microclimate of surface soil moisture around the plants. This water potential gradient is facilitated by surface-level roots which have a higher water potential than the surface soil and result in the passive movement of water into the surface soils (Horton and Hart 1998). A study of *Artemisia tridentata* in the southwest United States showed that one deep-rooted shrub could hydraulically lift up to 1 L/m^2 each night (Richards and Caldwell 1987). Another study by Dawson (1983) showed the proportion of hydraulically lifted water used by neighboring plants ranging from 3-60%.

We hypothesized that *Jacquinia*, with its taproot and active transpiration during the dry season, provides moisture to the surface soils that may be utilized by neighboring plants. We predicted that *Jacquinia* would have greater surface soil moisture than leafless deciduous trees at the same elevation. We also predicted that there would be more neighboring plants around *Jacquinia* than under other leafless deciduous trees, presumably due to the increase in soil moisture.

Methods

We conducted our experiment north of the OTS research station, west of the Cerros Calizos trail below the limestone cliffs, in Palo Verde National Park, Guanacaste Province, Costa Rica on 13 January 2003. We sampled 12 *Jacquinia* and 12 leafless deciduous trees (of random species, but comparable size) within 5 m of each *Jacquinia*. To control for altitudinal differences in soil moisture we sampled along a general contour line on the hillside. We measured soil moisture by taking a soil sample of approximately 100 ml within 30 cm of the trunk of each tree at a depth of 5 cm. We weighed each sample before and after drying outside until the weights stabilized, which took approximately 24 h. We calculated percent moisture from the difference in pre- and post-drying soil weights. We analyzed the difference in mean percent soil moisture between *Jacquinia* and the leafless deciduous trees using a paired t-test. We counted the number of live plants within a 1 m diameter of each tree trunk. We omitted one sample because the entire 1 m diameter was rock. Difference in mean number of plants was analyzed with a paired t-test. Data are presented as mean ± SE.

Results

The percent moisture beneath *Jacquinia* trees averaged 9.6 ± 0.59, compared to 8.9 ± 0.59 beneath leafless deciduous trees. These means were not significantly different (Fig. 1; paired-t = 1.22, df = 11, P = 0.25).

The mean number of neighboring plants was greater under *Jacquinia* trees (4.6 ± 0.76) than under leafless deciduous trees (2.3 ± 0.73). This difference was statistically significant (Fig. 2; paired-t = 2.11 df = 11, P = 0.05).

Discussion

The unique characteristics of reverse phenology and a deep taproot exhibited by *Jacquinia* may contribute to ecosystem processes in the lowland dry tropical forest. Contrary to our prediction, soil moisture was not greater under *Jacquinia* than leafless deciduous trees. However, there were more neighboring plants growing beneath *Jacquinia* than leafless deciduous trees.

Although hydraulically lifted water by phreatophytes can be an important ecological contribution to areas with high water stress (Caldwell et al. 1998, Richards and Caldwell 1987, Dawson 1993), *Jacquinia* did not show signs of using this mechanism to lift water to surface soils (Fig. 1). We do know that *Jacquinia* has a deep taproot

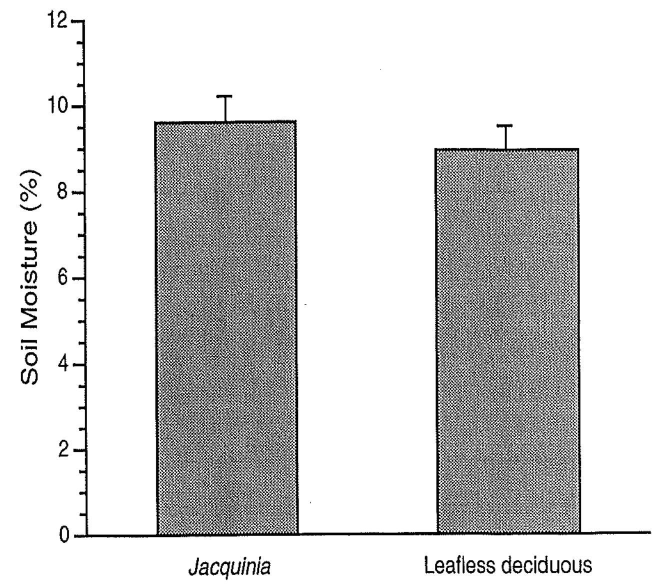

FIG. 1. Percent moisture (mean ± SE) in soil samples taken beneath *Jacquinia* (n = 12) and leafless deciduous trees (n = 12) in Palo Verde National Park, Costa Rica.

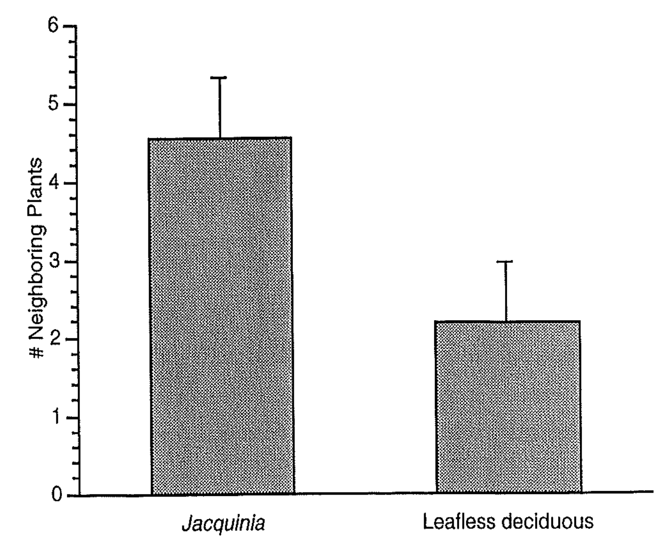

FIG. 2. Number of plants (mean ± SE) found in a 1 m diameter circle (0.79 m^2) around the base of *Jacquinia* (n = 12) and leafless deciduous trees (n = 12) sampled in Palo Verde National Park, Costa Rica.

(Janzen 1983), but not whether it has surface-level lateral root proliferation. If its lacks surface-level roots, this would account for the lack of surface soil moisture due to decreased root surface area which allows passive movement of water down the water potential gradient.

The lack of evidence for a hydraulic lift mechanism suggests that factors other than soil moisture may influence abundance of plants near *Jacquinia*. It is possible that *Jacquinia* may supply nutrients to neighboring plants when it loses its leaves at the beginning of the rainy season, corresponding to when other deciduous trees are leafing out. At the same time, neighboring plants may have greater access to sunlight due to *Jacquinia* leaf drop. Finally, *Jacquinia* may provide a protective barrier from ultraviolet deterioration of tree tissue to underlying plants during the dry season. A comparative study of the growth rates and energy stores of neighboring plants around *Jacquinia* would provide insight into effects of *Jacquinia* on ecosystem processes. The unique survival strategies of *Jacquinia* may create a microhabitat promoting interspecific relationships.

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