Mechanical Abrasion and Intercrown Spacing

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ABSTRACT: The crowns of neighboring trees of similar height do not interdigitate but rather are generally separated by spaces called "crown shyness" gaps. In a black mangrove (*Avicennia germinans*) forest in Costa Rica, the width of crown shyness gaps was positively correlated with the distance pairs of trees or branches adjacent to the gap swayed in the wind ($n = 22$; $p < .01$). Abrasion of buds, leaves and branches due to trees knocking into one another seems to create and maintain the spaces around each tree crown.

INTRODUCTION

Though recent studies of forest structure and dynamics have focused on large gaps caused by single and multiple treefalls, most openings in forest canopies are extremely small (*e.g.*, Hartshorn, 1978; Runkle, 1982). Small gaps usually remain open for a short time, being temporarily closed by branch movements during winds and permanently closed by lateral growth (*e.g.*, Runkle, 1982). However, in some forests light penetrating into the canopy forms a persistent and striking border around individual crowns that are visible from the ground (Fig. 1). The term "crown shyness" (from Lane-Poole, 1927-1944, cited in Jacobs, 1955) refers to these leafless regions between adjacent crowns of similar height. Much of the light reaching the understory as sunflecks passes through crown shyness gaps. These openings may also be important insofar as they restrict intercrown movements of arboreal animals and vines (Putz, 1982). A similar sort of defense by mechanical abrasion of competitors and dislodgement of herbivores has been observed in wave-swept algae (Velimirov and Griffiths, 1979).

Two theories have been proposed to explain how crown shyness gaps are formed and maintained. One view is that abrasion of buds on wind-blown branches leads to open spaces between tree crowns (Tarbox and Reed, 1924; Jacobs, 1955; Richards *et al.*, 1962). Ng (1977), on the other hand, proposed that crown shyness in Malaysian dipterocarps (*Dryobalanops aromatica* and various species of *Shorea*) is caused by reduction in lateral growth due to mutual shading. We tested the hypothesis that crown shyness is caused and maintained by the mechanical abrasion of branches swaying in the wind. Specifically, we predicted that if mechanical abrasion causes crown shyness, then flexible trees and branches should be more widely separated than rigid trees and branches.

STUDY SITE AND METHODS

We studied crown shyness in an approximately 50-ha stand dominated by *Avicennia germinans* in the Parque Nacional de Santa Rosa, Guanacaste Province, Costa Rica (10°35′N, 85°85′W). The forest floor is inundated with sea water only when the tides are especially high. Suppressed and codominant individuals of *A. tonduzii* Moldenke are scattered through the forest but most of the canopy is occupied by *A. germinans*. Voucher specimens were deposited in the University of Florida Herbarium. The upper surface of the forest canopy is level and individual crowns do not cast dense shade (Fig. 1). Wind velocities during the dry season, when the study was conducted, were high but variable, with periods of calm interrupted by gusts to more than 11 m/sec.

If crown shyness gaps in *Avicennia germinans* are due to mechanical abrasion of branches, intercrown spaces should be proportional to the potential of adjacent branches to rub against one another. To test this we arbitrarily selected 22 pairs of trees of similar height, measured the distance between their crowns in still air, and measured the maximum horizontal distance moved by branches of each tree into the crown shyness gap when driven by gusts of wind. In other words, we compared the sum of the lateral displacements of adjacent branches towards each other with the distance between the branches in still air. The widths of openings were measured by sighting the positions of the crown edges from the ground relative to a measuring tape stretched horizontally 4 m above the ground (Fig. 2). Actual distances between adjacent crowns in still and gusty conditions were then calculated trigonometrically; heights of the crown shyness gaps were measured directly by climbing the trees. The sum of the maximum horizontal displacements of tree crowns towards each other during windy periods relative to the distance between them at rest is a measure of potential crown interactions. Wind speed variability increased the variance of our estimates of maximum horizontal distances swayed and thus introduced a conservative bias into estimates of potential intercrown collisions.

RESULTS

Flexible crowns were more widely spaced than stiff crowns ($r = .69$, $n = 22$, $p < .01$;

Fig. 1.—Vertical view into an *Avicennia germinans* canopy during calm conditions showing crown shyness gaps between trees

Fig. 3). During calm periods, adjacent crowns interlocked like loosely fitting pieces of a jigsaw puzzle (Fig. 1), but when the wind blew, they often touched and interdigitated. These results suggest that intercrown spacing is in part determined by the potential of adjacent canopies to knock into one another.

Branches bordering crown shyness gaps generally had broken twigs and few leaves while branches in more protected parts of the crown had little such damage. The absence of small twigs on many of the branches bordering crown shyness gaps makes the proportion of damaged twigs an underestimate of the amount of damage incurred. Dead branches, however, can be due to either abrasion or shading; hence, they cannot be used for distinguishing between the two causes of crown shyness.

DISCUSSION

Crown shyness is most easily observed in monospecific stands of similar-size trees but seems to be common in forests of all types. Closely spaced trees in plantations often

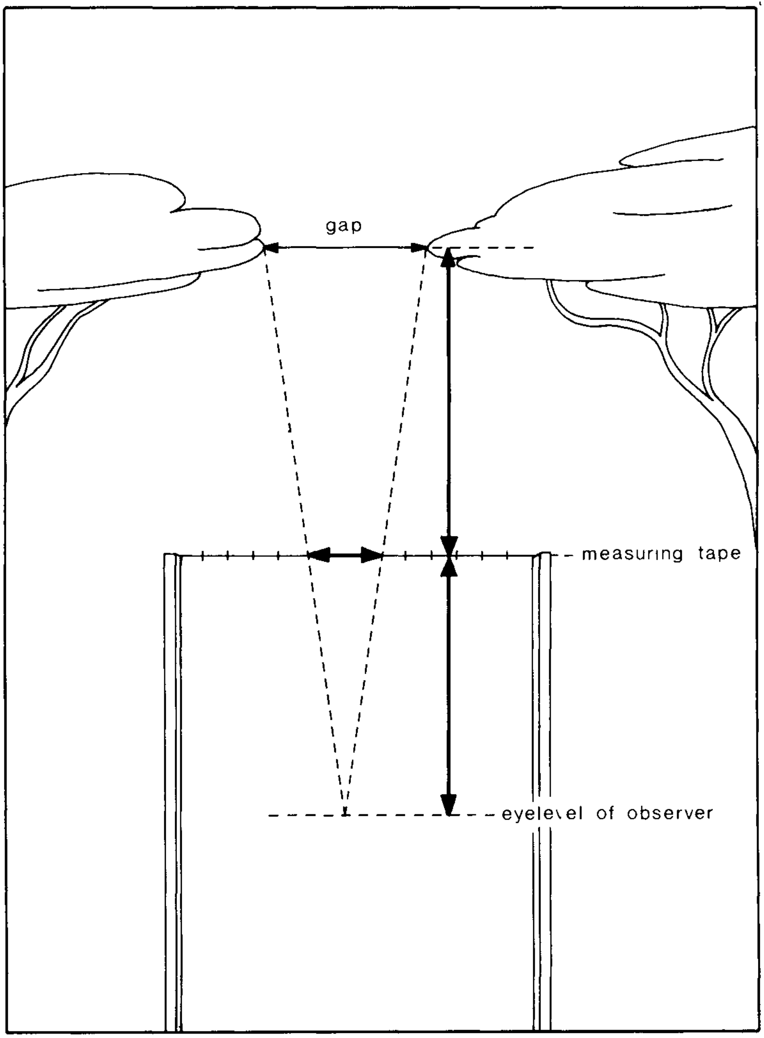

Fig. 2. —Sketch showing method for measuring gap widths

show distinct crown shyness (Richards *et al.*, 1962), but this may be because plantations have little understory to obscure observations of crown shyness as well as because the trees are even-aged. Crown abrasion apparently leads to reduced yields in overstocked pine plantations (Tarbox and Reed, 1924). We expect crown shyness to be present in all forests but to be prominent in (1) forests in windy areas; (2) monolayered forests (where the gaps are not obscured by overlapping crowns); (3) stands of flexible trees, and (4) early successional forests, comprised of flexible trees with limited abilities to produce branches in lateral openings (De Castro e Santos, 1980). We observed crown shyness between independently swaying branches on the same tree as well as between trees. Indeed, branch, rather than whole tree, flexibility may sometimes determine crown shyness gap size.

Crown shyness gaps may in some cases be due to reciprocal shading of adjacent trees with similar light compensation points. We have no data on this alternative hypothesis, but our observations of damaged leaves and twigs cannot be explained on the basis of shading effects alone. While crown shyness may have other causes, our study supports the importance of reciprocal pruning by mechanical abrasion in forming crown shyness gaps in an *Avicennia germinans* forest.

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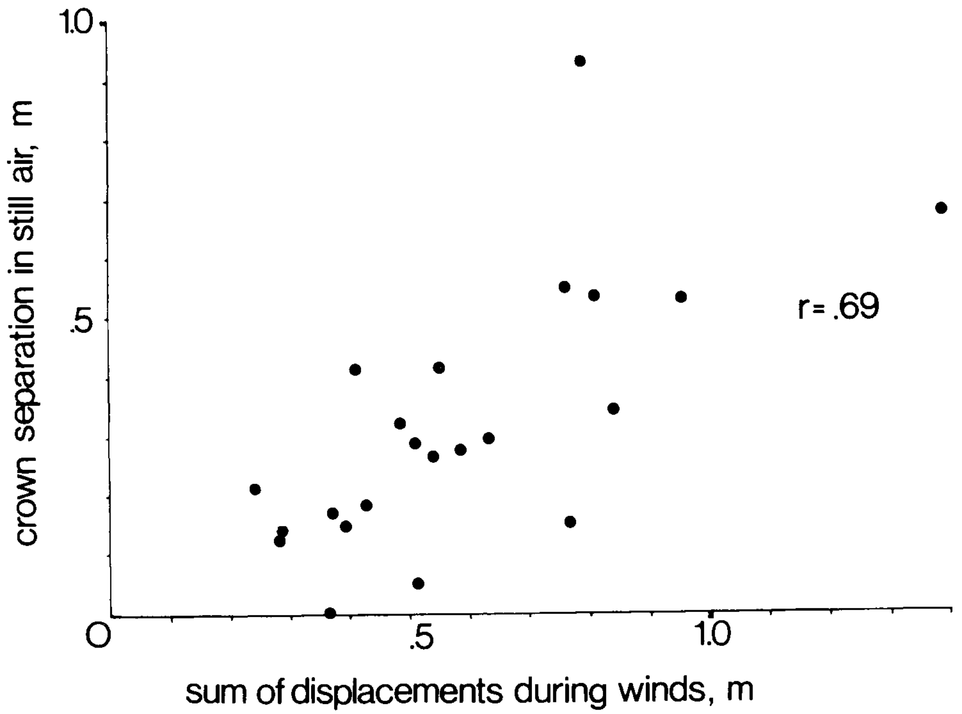

Fig. 3.—Intercrown distance in still air is significantly positively correlated with the sum of the distances adjacent branches swayed towards each other when blown by the wind ($r = .69$, $p < .01$)

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