

# Growth Responses to Wind Differ among Papaya Roots, Leaves, and Stems

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**Abstract.** ‘Sunrise’ and ‘Tainung 2’ papaya seedlings were subjected to 3 weeks of ambient winds in Guam during five experiments, and growth responses of roots, leaves, and stems were quantified to compare speed and extent of the plasticity among the organs. The cultivars responded similarly with 1 week eliciting stem growth responses and 2 weeks eliciting root responses. The timeframe of these studies was sufficient to enable adaptive responses in all three organs. Wind reduced stem and leaf expansion rate but not root extension rate, providing one example of how the form of response differed among the organs. A dose–effect was evident among the experiments with magnitude of response increasing with mean ambient wind speed. Asymmetric stem diameter and root tip density were examples of adaptive responses to directional wind load. These data on young papaya plants may be used to inform field experiments aiming to determine how chronic winds influence long-term growth and fitness.

Papaya (*Carica papaya* L.) is grown throughout the equatorial regions of the world (Crane, 2008; Morton, 1987; Nakasone and Paull, 1998), and the species is an important horticultural crop on Guam and other nearby islands. Many of the regions where papaya is grown experience chronic trade winds, and quality of papaya is improved by wind protection during orchard development (Davey, 1958). Under Guam’s conditions, wind protection improves absolute growth and increases leaf photosynthesis in young papaya plants (Clemente and Marler, 2001).

Biomechanical properties of plants improve as a result of exposure to non-catastrophic wind (Cullen, 2002; de Langre, 2008; Niklas, 1998; Schaeztl et al., 1989). Therefore, reduced absolute growth interplays with improved structural strength when plants are exposed to wind. The relative benefits of improved biomechanical properties may depend on stresses imposed after moderate wind exposure. For the regions in the northwestern Pacific Ocean, tropical cyclones are dominant forces in shaping agricultural, natural, and urban landscapes (Marler, 2001). As a result, allowing trade winds to impact a papaya orchard during establishment may decrease the extent of damage in the event of a subsequent tropical cyclone.

Phenotypic plasticity is an important means by which plants cope with environmental heterogeneity; therefore, understanding variation in plant traits is important to predict responses to variable environments. More detailed studies on crop responses to wind may improve management decisions

(e.g., Koizumi et al., 2008). Consequently, a series of experiments was conducted on young papaya plants to determine the influence of ambient wind exposure on rapid leaf, stem, and root growth responses and a second set of experiments to determine the degree of asymmetry of rapid root and stem responses to wind direction. Root physiology, morphology, and development are under genetic control (Zobel, 1975), so two cultivars derived from separate breeding programs were included in each experiment. Objectives were to compare the rapidity and extent of plasticity of growth under ambient wind exposure among papaya leaves, stems, and roots to more fully understand how these responses are coordinated among these various organs. This information may improve management decisions for establishing an orchard in windy environments, inform approaches for long-term field experimental design, and improve general understanding of biomechanical properties of this giant herb.

## Materials and Methods

*Root, stem, and leaf coordination.* Three experiments were conducted to determine growth responses of different organs to ambient wind load. These were initiated on 3 May 2009, 4 Sept. 2009, and 6 Jan. 2010. ‘Tainung 2’ and ‘Sunrise’ papaya seedlings were used, and experimental units were 8-week-old nursery transplants that had been produced in trays with 5-cm cells in a full-sun nursery. Twelve uniform plants were selected from the trays and transplanted individually into 10.5-L root chambers, which had one Plexiglas observation window displaying 520 cm<sup>2</sup> of exposed surface. Entire observation panes were covered with 2-cm thick Styrofoam sheets to exclude light and preclude

deviations from ambient temperature. Sunshine Mix 4 (Sun Gro Horticulture Canada Ltd., Vancouver, Canada) was used as the growing medium.

The seedlings were placed to receive full exposure to natural trade winds or were protected with polypropylene sheets to exclude all ambient wind as described in Clemente and Marler (2001). The root observation pane was oriented toward the wind (east) for all plants. A randomized complete block design was used with three blocks, and there were two plants for each cultivar and treatment level in each block providing six replications per cultivar. The seedlings were watered daily and fertilized weekly with complete soluble fertilizer (Excel; Grace-Sierra, Milpitas, CA). Each plant received 150 mL of the solution, which provided 7.5 mM nitrogen. Ambient wind speed was recorded with a Model 014 MET-ONE Wind Speed Sensor (Campbell Scientific, Inc., Logan, UT).

Stem height, stem base diameter, root tip density, and root extension were measured weekly. Root tip density was determined by counting the number of growing root tips in a designated 10 cm × 10-cm section of each observation pane. Diameter of the stem base was based on measurements perpendicular and parallel to wind direction and cross-sectional area was calculated from the mean. The position of each root tip was marked on the surface of the pane with a permanent marker each week and the length of each root beyond the preceding mark was measured the next week. This approach provided two consecutive measurements for root extension, which were averaged for statistical analysis.

Length of the midvein of the apical expanding leaf was measured daily for the 3 terminal days of each study. The youngest fully expanded leaf was removed from each plant, and area was measured (Model AM 100 area meter; Analytical Development Company, Hoddesdon, Herts, U.K.).

*Degree of asymmetry.* Two experiments were conducted to determine the asymmetry of rapid growth responses in relation to direction of wind exposure. Wind treatments, cultivars, preparation of transplants, container medium, and fertilization were as described previously. The experiments were initiated on 28 Jan. 2010 and 7 Jan. 2011 using 8-L root chambers, which were fitted with two parallel Plexiglas observation windows, each exhibiting 520 cm<sup>2</sup> of exposed surface. The two observation windows were oriented east (windward) and west (leeward). Stem base diameter, root tip density, and root extension rate were measured as described previously. Derived variables were calculated to quantify the level of asymmetry caused by wind direction. Stem base asymmetry was defined as the difference between diameter parallel and diameter perpendicular to wind divided by diameter parallel to wind. The asymmetry of root tip density or root extension was calculated as the difference between windward and leeward measurements divided by windward measurements. Fidelity to symmetry for these derived variables was zero, and

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as the absolute value increased to a maximum of one, there was a corresponding increase in asymmetry.

**Statistical analysis.** Measurements of stem height, area of stem base, and root tip density from Expts. 1, 2, and 3 were repeated each week. Therefore, a three-factor analysis of variance (ANOVA) with repeated measures (week) was performed using SAS GLIMMIX procedure in Version 9.2 (SAS Institute, Inc., Cary, NC). The AR(1) covariance structure was selected as the best covariance structure between repeated measures based on the minimum AICC value criterion. Root extension, leaf area, and leaf expansion from Expts. 1, 2, and 3 were measured at the end of each experiment. Response variables from Expts. 4 and 5 were asymmetry of stem base, root tip density, and root extension. These response variables were subjected to ANOVA using a randomized complete block design with cultivar, wind treatment, and their interaction as the sources of variation. ANOVA assumptions were met in all analyses.

## Results

**Root, stem, and leaf coordination.** After 3 weeks of growth under the experimental conditions, wind exerted dissimilar effects on the three papaya organs that were studied. Moreover, the mean wind speeds and corresponding plant responses from each of the three experiments were unique. In contrast, the block effect was not significant for any of the response variables within each of the experiments.

During Expt. 1, plants experienced mean daytime wind speeds of  $3.11 \text{ m}\cdot\text{s}^{-1}$  and night wind speeds of  $1.62 \text{ m}\cdot\text{s}^{-1}$ . Stem height, area of stem base, and root tip density were not influenced by cultivar, cultivar  $\times$  wind, cultivar  $\times$  week, wind  $\times$  cultivar, or cultivar  $\times$  wind  $\times$  week according to the Type III fixed-effects tests. The wind, week, and wind  $\times$  week sources of variation were significant ( $P \leq 0.0001$ ) for stem height and stem cross-section. Week and wind  $\times$  week sources of variation were significant ( $P \leq 0.0001$ ) for root tip density. Therefore, least square means between two wind treatments for each given week were computed for each variable. Wind reduced stem height by Week 2, and height of wind-exposed plants was 81% of that for protected plants by Week 3 (Fig. 1A). Wind reduced area of stem base by Week 3, when stem area of exposed plants was 89% of that for protected plants (Fig. 1B). Wind reduced root tip density by Week 2, and root tip density of wind-exposed plants was approximately half of that for protected plants by Week 3 (Fig. 1C). Leaf area, leaf expansion rate, and root extension rate were not influenced by cultivar, wind, or their interaction (Table 1).

During Expt. 2, ambient winds were  $3.96 \text{ m}\cdot\text{s}^{-1}$  during the daytime and  $2.15 \text{ m}\cdot\text{s}^{-1}$  during night hours. Significance of sources of variation was similar to that of Expt. 1, with wind, week, and wind  $\times$  week emerging as the only significant ( $P \leq 0.0001$ ) sources of variation for all three response variables. Wind reduced stem height after only 1 week

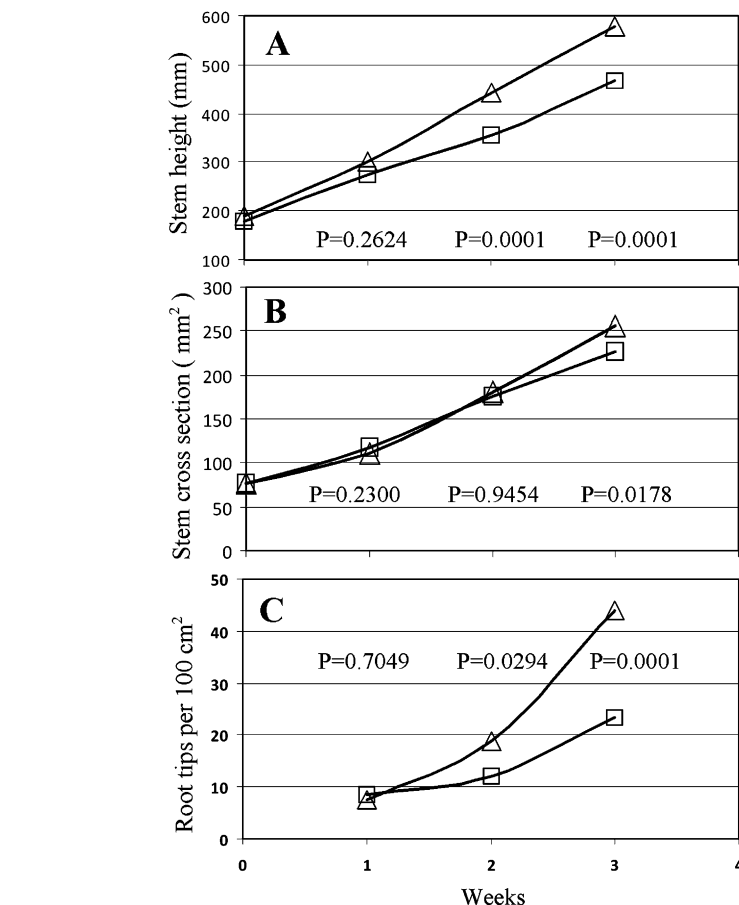


Fig. 1. Stem height (A), stem cross-section (B), and root tip density (C) of *Carica papaya* seedlings protected from (Δ) or exposed to (□) easterly ambient winds in north Guam from 3 to 24 May 2009. n = 12 (mean of six 'Tainung 2' and six 'Sunrise' plants).

of growth, and height of wind-exposed plants was 60% of that for protected plants by Week 3 (Fig. 2A). Wind reduced area of stem base by Week 2, and stem area of exposed plants was 79% of that for protected plants by Week 3 (Fig. 2B). Wind reduced root tip density by Week 2, and root tip density of protected plants was more than double that of wind-exposed plants by Week 3 (Fig. 2C).

Leaf area and expansion rates were not influenced by cultivar or the interaction of wind and cultivar. Leaf area of wind-exposed plants was 48% of that for protected plants (Table 1). Leaf expansion rate of wind-exposed plants was 71% of that for protected plants (Table 1). Root extension was not influenced by cultivar, wind, or their interaction (Table 1).

During Expt. 3, ambient winds were  $4.25 \text{ m}\cdot\text{s}^{-1}$  during the day and  $3.28 \text{ m}\cdot\text{s}^{-1}$  during the night. The repeated-measures ANOVA results mirrored those of Expt. 2. Wind reduced stem height by Week 1, and height of wind-exposed plants was 56% of that for protected plants by Week 3 (Fig. 3A). Wind reduced area of stem base by Week 2, and stem area of exposed plants was 60% of that for protected plants by Week 3 (Fig. 3B). Wind reduced root tip density of wind-exposed plants by Week 3, when root tip density of wind-exposed plants was 42% of that for protected plants (Fig. 3C).

Table 1. Single leaf area, leaf expansion rate, and root extension rate of 'Tainung 2' and 'Sunrise' papaya plants exposed to or fully protected from ambient winds at the end of 3-week experiments conducted 3 to 24 May 2009 (mean wind speed =  $2.37 \text{ m}\cdot\text{s}^{-1}$ ), 4 to 25 Sept. 2009 (mean wind speed =  $3.06 \text{ m}\cdot\text{s}^{-1}$ ), and 6 to 27 Jan. 2010 (mean wind speed =  $3.77 \text{ m}\cdot\text{s}^{-1}$ ).<sup>z</sup>

| Response variable                    | Wind treatment |         | P      |
|--------------------------------------|----------------|---------|--------|
|                                      | Protected      | Exposed |        |
|                                      | <i>Expt. 1</i> |         |        |
| Leaf area (cm <sup>2</sup> )         | 199            | 196     | 0.6087 |
| Leaf expansion (mm·d <sup>-1</sup> ) | 6.83           | 5.85    | 0.0665 |
| Root extension (mm·d <sup>-1</sup> ) | 6.39           | 6.48    | 0.9252 |
|                                      | <i>Expt. 2</i> |         |        |
| Leaf area (cm <sup>2</sup> )         | 303            | 149     | 0.0001 |
| Leaf expansion (mm·d <sup>-1</sup> ) | 6.57           | 4.67    | 0.0003 |
| Root extension (mm·d <sup>-1</sup> ) | 6.58           | 6.88    | 0.9692 |
|                                      | <i>Expt. 3</i> |         |        |
| Leaf area (cm <sup>2</sup> )         | 320            | 123     | 0.0001 |
| Leaf expansion (mm·d <sup>-1</sup> ) | 7.35           | 2.71    | 0.0001 |
| Root extension (mm·d <sup>-1</sup> ) | 7.38           | 7.44    | 0.8359 |

<sup>z</sup>n = 12 (mean of six 'Tainung 2' and six 'Sunrise' plants).

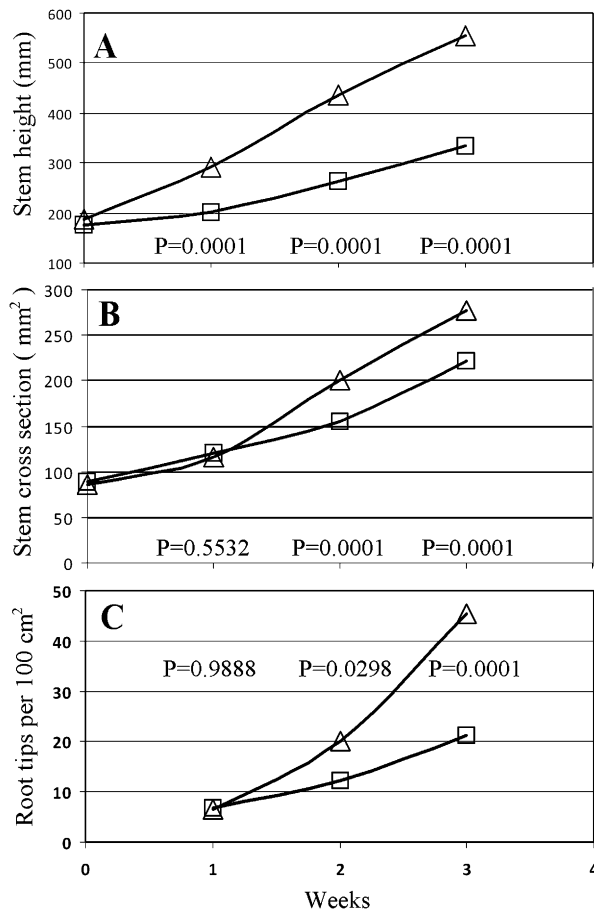


Fig. 2. Stem height (A), stem cross-section (B), and root tip density (C) of *Carica papaya* seedlings protected from (Δ) or exposed to (□) easterly ambient winds in north Guam from 4 to 25 Sept. 2009. n = 12 (mean of six 'Tainung 2' and six 'Sunrise' plants).

Leaf area and expansion rates were not influenced by cultivar or the interaction of wind and cultivar. Leaf area of wind-exposed plants was 38% of that for protected plants (Table 1). Leaf expansion rate of wind-exposed plants was approximately one-third of that for protected plants (Table 1). Root extension was not influenced by cultivar, wind, or their interaction during any week (Table 1).

**Degree of asymmetry.** Ambient winds during Expt. 4 were  $4.81 \text{ m}\cdot\text{s}^{-1}$  during the day and  $3.86 \text{ m}\cdot\text{s}^{-1}$  during the night. Ambient winds during Expt. 5 were  $4.48 \text{ m}\cdot\text{s}^{-1}$  during the day and  $3.39 \text{ m}\cdot\text{s}^{-1}$  during the night. The level of asymmetry for the stem base and root tip density was not influenced by cultivar or the wind  $\times$  cultivar interaction in either experiment. The level of asymmetry for the stem base in protected plants was a minimal 0.0055 in Expt. 4 and 0.0068 in Expt. 5. Wind exposure increased stem asymmetry to 0.1132 in Expt. 4 ( $P \leq 0.0001$ ) and 0.1236 in Expt. 5 ( $P \leq 0.0001$ ).

The extent of asymmetry of root tip density in protected plants was also minimal, 0.0013 in Expt. 4 and 0.0024 in Expt. 5. Wind exposure dramatically increased root tip density asymmetry to 0.4502 in Expt. 4 ( $P \leq 0.0001$ ) and 0.4691 in Expt. 5 ( $P \leq 0.0001$ ). The greater root tip density occurred on the windward side of the plants.

Asymmetry of root extension rate was not influenced by wind, cultivar, or their interaction in either experiment. The wind source of variation for root extension was  $P = 0.9097$  in Expt. 4 with mean of 0.0151 and  $P = 0.8734$  in Expt. 5 with mean of 0.0164.

### Discussion

This series of experiments has confirmed that plastic responses of young *Carica papaya* plants to wind exposure are rapid with stem height significantly responding after only 1 week in some cases and stem cross-sectional area and root tip density responding after 2 weeks. Adaptive responses to directional wind such as eccentric development of stem diameter and increase in root tips on the windward side of plants were significant at the first measurement after 3 weeks of wind.

This species is an interesting model species for studying biomechanics because it is not easily placed into one of the categories of plant forms that exhibit generalized characteristics of root anchorage. For example, vines and lianas that are procumbent or use the structure on which they climb for support require relatively small fibrous root systems, herbaceous annual plants generally use a tap-root system, woody trees generally use a plate system, and cereal crops rely on rigid adven-

titious root systems (e.g., Coutts, 1983; Ennos, 1993, 2000; Ennos and Fitter, 1992; Fitter and Ennos, 1989; Mickovski, 2002; Nicoll and Ray, 1996). The work on anchorage of tree root systems in particular has been limited, and more information on the anchorage of as many species as possible is needed (Ennos, 2000). Papaya is herbaceous and lacks true wood (Fisher and Mueller, 1983). Because wood is the strongest plant tissue using weight per unit volume as an index (Niklas, 2002), the papaya tree must rely on "soft" tissues for its biomechanical integrity. These peculiarities do not enable an unambiguous prediction of how papaya may approach anchorage, because the species is herbaceous but not an annual and is a tree but not woody.

The influence of wind on plant development is also an interesting subject to study. Some components involve leaf and stem movements and contact so some growth responses are thigmomorphogenic, some components place stems and roots under bending tension or compression, and responses are to improve anchorage and tissue strength, yet some components are desiccating and elicit physiological responses that decrease water loss. Furthermore, the tension and compression forces are exerted on canopy and root components, yet the direct desiccating components of wind stress are exerted only on the canopy organs. For example, Smith and Ennos (2003) showed that plant responses to wind loading drastically differed from those to stem flexure alone. Very few studies have used a similar approach in attempts to disentangle the respective components of wind exposure and how each is perceived. Therefore, when a growth response to wind is quantified, what is initially perceived as the stimulus, what is the responsive signal, and how is the signal deployed for timely activation of plant responses? The means by which the cause of a response can be assigned to one component of wind stress is poorly understood.

These ambiguous characteristics of wind stress may explain why stem growth responses were generally more rapid than root growth responses. A reduction in height is a typical response of plants to wind (Kaufman et al., 1989; Kozłowski et al., 1991), and this reduced stature (Figs. 1A, 2A, and 3A) and more compact leaf size (Table 1) decreases wind-induced drag on the crown (Sellier and Fourcaud, 2005). The rapid reduction in papaya stem height may have been a response to the signals exerted by direct desiccating effects of wind exposure, whereas the slower root responses may have been a reaction to the signals elicited by indirect mechanical perturbations to the plant body.

Speed of response was not the only difference between canopy and root variables. For example, stem extension was highly responsive to wind exposure, yet root extension was unaltered by wind in every experiment. Furthermore, wind-induced reduction in root tip density was the most consistent response among the experiments in that the least windy conditions of Expt. 1 reduced root tip density

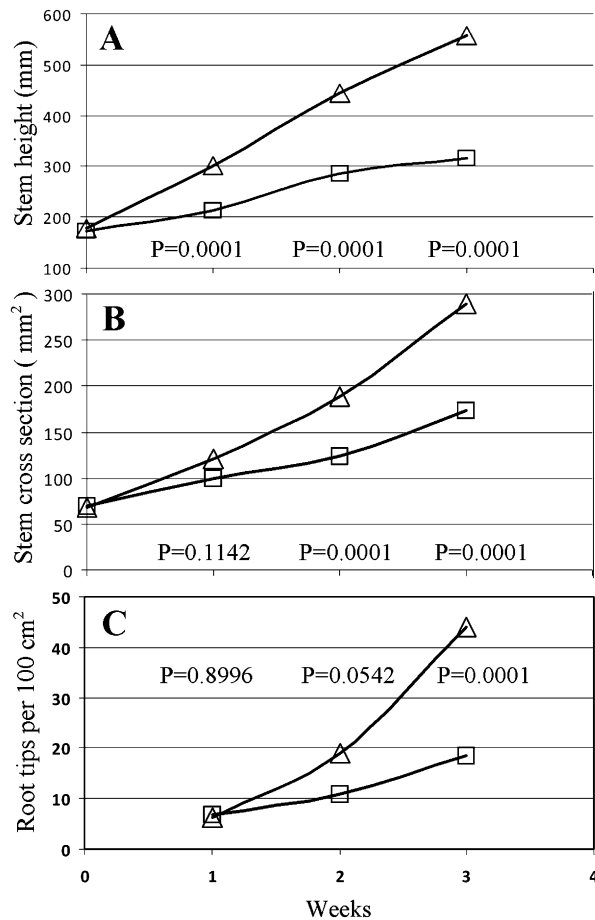


Fig. 3. Stem height (A), stem cross-section (B), and root tip density (C) of *Carica papaya* seedlings protected from (Δ) or exposed to (□) easterly ambient winds in north Guam from 6 to 27 Jan. 2010. n = 12 (mean of six 'Tainung 2' and six 'Sunrise' plants).

to 53% of that for protected plants, yet leaf area and leaf expansion rate were unaffected by wind. The opposite occurred in the more windy conditions of Expt. 3, when leaf area and expansion rate were reduced by wind to a greater degree than was root tip density.

The disparity in plastic responses to wind among the papaya organs provides an example of modularity (Watkinson and White, 1986). The integrative mechanisms underlying these modular responses have broad ecological and evolutionary implications. Several mechanisms may account for the modular coordination of specialized functions, including resource-based functional equilibrium, metabolic control, and chemical signals (Brouwer, 1983; Friend et al., 1994). Although the root and shoot systems function complementarily to meet the needs of the whole plant, they also compete for resources (Brouwer, 1983; Russell, 1977). Certain tradeoffs must therefore exist between different plant functions (Givnish, 1995). This competition for resources is more evident during changes in environmental conditions. Our understanding of how these properties interact with each other over space and time and the tradeoffs that occur among various organs is limited (Read and Stokes, 2006). Berthier and Stokes (2005) suggest that crosstalk occurs among different pathways in plants and that the stimulation of sensors through mechanical

stimulus may cascade to other reactions. The disparity in how these signals were sent then received by the various organs and/or the competition for limited resources may explain the discussed differential responses to wind among the papaya organs.

This study also provided evidence of a dose-effect. Wind speed was least during Expt. 1, intermediate during Expt. 2, and greatest during Expt. 3. Stem height, stem cross-sectional area, and root tip density of wind-exposed plants averaged 74% (Expt. 1), 62% (Expt. 2), and 53% (Expt. 3) of protected plants. Moreover, leaf area and leaf expansion rate were not reduced by wind in Expt. 1, were significantly reduced by wind in Expt. 2, and were significantly reduced to a greater degree in Expt. 3.

Critical information to inform management decisions related to how exposure to trade winds influences subsequent tropical cyclone damage is lacking. Growers would benefit from a better understanding of how chronic trade winds influence plant responses than how those responses increase or decrease damage during subsequent cyclones. Phenotypic plasticity is adaptive if the response increases the plant's fitness to its environment (Sultan, 2000). Wind-induced reductions in stem height and leaf size are common avoidance strategies because they minimize the

forces encountered by the plant. Zimmerman (2010) defined plant height as the major characteristic behind disparity in damage among papaya cultivars during Hurricane Omar with shorter cultivars experiencing less damage than taller cultivars. Exposure to trade winds during orchard development would directly improve this character. Although stem cross-sectional area was reduced by wind exposure, the magnitude of this reduction was less than that of stem height. This disparity in growth reduction increased the relationship between plant height and stem basal area, which also directly improved biomechanical properties. The asymmetric stem cross-section and root tip density were clear adaptive responses to directional wind load because this response improved mechanical design and increased root surface area and root-soil friction on the windward side (Stokes et al., 2005). The increase in stem diameter parallel to the direction of sway increases the second moment of area, which improves the flexural stiffness of a stem. These responses are common tolerance strategies because they maximize resistance to mechanical failures. Windward roots are primarily under tension (Coutts, 1983), so papaya roots are adept at signaling a rapid plastic adaptive response when tension is imposed. The contributions of these plastic responses to reducing damage during a tropical cyclone, however, may depend on the direction of damaging winds during the tropical cyclone event.

In summary, leaves, stems, and roots of young papaya plants exhibited rapid adaptive responses to wind. Wind stress of only 1 week was sufficient to elicit significant responses. Stem responses were the most rapid, but the root tip density responses exhibited the greatest magnitude among all wind conditions. The asymmetry index in Expts. 4 and 5 translated to the windward side exhibiting 1.8 to 1.9 times more root tips than the leeward side. The form of a root system becomes increasingly variable with tree age as it responds to a number of stimuli and the bulk of the plant body increases (Sutton, 1969). For example, Retuerto and Woodward (1993) report a marked influence of plant age on responses to wind for the herbaceous *Sinapis alba* L. Therefore, these data on young papaya plants may inform experimental protocols for long-term field experiments designed to determine if these profound, rapid responses at the seedling stage are sustained as the plants increase in stature.

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