Papaya (*Carica papaya* L.) Leaf Area Estimation and Single-leaf Net Photosynthetic CO₂ Assimilation Rate Following Leaf Defoliation and Fruit Thinning

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Abstract. Papaya (*Carica papaya* L.) leaves are large, up to 70 cm wide, and frequently deeply lobed, with seven to 13 major veins. The scan width of current handheld digital leaf area instruments is generally less than 15 cm. A rapid method is needed to estimate the total leaf area of a plant in the field with leaves at different stages of growth from the apex. The length of the main and side veins of papaya leaves can be used to estimate the area of a single leaf and the total leaf area of the plant. The relationship between main vein lengths and total leaf area was determined for mature leaves from the cultivars Sunset, Line-8, and Kapoho. A simple relationship exists between leaf area and the length of the two main side midribs (L3 and L4): Leaf area (cm²) = $-2280 + 87.7 \cdot L3 + 55.6 \cdot L4$ ($P > F = 0.0001$; $r^2 = 0.969$), explaining $\approx 94\%$ of the variation between estimated leaf area and leaf area. The most recently matured leaf is the third or fourth discernable leaf from the apex, with a positive net photosynthetic CO₂ assimilation rate and an average area of 2331 cm² that could fix up to 1.6 g carbon per 10-hour day under full sun. The rate of photosynthesis declined with leaf age, and the overall net photosynthetic CO₂ assimilation rate of the plant can be predicted. Following 80% leaf defoliation of the plant, the net photosynthetic CO₂ assimilation rate of the most recently matured leaf increased 30% to 50% on days 11 and 19 after treatment when the photosynthetic active radiation (PAR) was approximately half of that on day 15 under full sun when no difference in net photosynthetic CO₂ assimilation rate was seen. Fruit removal did not affect the net photosynthetic CO₂ assimilation rate. Papaya adjusts its single-leaf net photosynthetic CO₂ assimilation rate under lower light levels to meet plant growth and fruit sink demand.

Leaves normally represent the assimilating area of a plant and determine its photosynthesis and dry matter accumulation. Papaya (*Carica papaya* L.), a C₃ plant (Marler et al., 1994), develops new leaves,

flowers, and fruit continually, with 2 to 2.5 new leaves per week (Nakasone and Paull, 1998). Previous research has shown that the ratio of the leaf number to the fruit number is critical to papaya fruit growth and sugar accumulation (Zhou et al., 2000). The most significant causes of the loss of papaya leaf area are wind damage, spider mites, powdery mildew, and senescence. The loss of leaf area from high winds can significantly reduce fruit growth and sweetness (Zhou et al., 2000). Papaya leaves can range from 50 to 70 cm wide and up to 90 cm long, and they are often deeply lobed and often folded (Fig. 1) (Nakasone and Paull, 1998). Current handheld digital leaf area instruments are able to handle leaves that are generally less than 15 cm wide; therefore, the size and overlapping nature of papaya leaves mean that field digital instruments and image analysis are not viable alternatives.

Leaf area allometric models have been developed for soybean (Wiersma and Bailey, 1975), muskmelon (Panta and NeSmith, 1995), squash (NeSmith, 1992) and cucumber (Robbins and Pharr, 1987). Earlier

models of a wide range of cereals and other species have considered changes in leaf shape with position on the plant, plant age, crop density, and cultivar (Kvet and Marshall, 1971). Papaya leaf morphology differs from the morphology of plants used in previous leaf area models. Papaya leaf is frequently deeply lobed, with 7 to 13 major veins (Badiillo and Leal, 2020; IBPGR, 1988; Nakasone and Paull, 1998). As the leaf grows, the midrib length increases and leaf lobes become more deeply lobed; folds develop, with new minor ribs developing near the fifth midrib. The International Board for Plant Genetic Resources (IBPRG, 1988) listed 16 different leaf shapes, and regional variation in these different shapes have been reported in Central America (Reiger, 2009) and Nigeria (Aikpokpodion, 2012). It is difficult to measure the total leaf area of papaya without cutting the leaf into smaller pieces due to its large size and irregular shape. Campostrini and Yamanishi (2001) used the length of the central vein to calculate the log of the leaf area, with $r^2 = 0.898$ for two cultivars with deeply lobed leaves and deep indentations between the lobes used in their study. In this study, we have shown that a higher correlation is possible using the two main side veins. The greater predictive ability of the total leaf area would enable researchers to gain a better estimate of the total photosynthetic capacity of papaya plants.

Papaya has a characteristic C₃ anatomy (Campostrini and Glenn, 2007; Marler et al., 1994). The net photosynthetic carbon assimilation rate at 2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR ranges from 25 to 35 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and it varies with variety and environmental factors (Campostrini et al., 2001; Clemente and Marler, 1996; de Oliveira Reis et al., 2006; Ferraz et al., 2016; Marler and Mickelbart, 1998; Wang et al., 2014). Leaf defoliation can severely impact papaya fruit quality (Zhou et al., 2000), although its impact on the net photosynthetic CO₂ assimilation rate has not been reported.

Efforts to model papaya plant growth and fruit development under stress and following high wind damage have been hampered by the absence of a nondestructive measure of the leaf area and information regarding the impact of leaf area loss on the photosynthesis rate and source-sink relationships. The large size of the leaves in this monopodial plant and the limited width of current field instruments showed the need to develop a mathematical model for linear leaf measurements that can predict the total leaf area with the least variation. The net photosynthetic CO₂ assimilation rate of leaves on plants that were subjected to artificial defoliation was also determined to estimate overall photosynthesis and obtain information regarding the impact of leaf area loss due to insect, disease, and wind damage.

Materials and Methods

Leaf area determination. Papaya leaves (n = 186) from flowering and fruiting cultivars

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Sunset, Line-8, and Kapoho were cut from the plant with the petioles still attached; this was performed on nine separate occasions during 1 year for Sunset and on two occasions for Line 8 and Kapoho. Leaves were obtained

from commercial papaya fields on the north shore of the Island of Oahu operated by Dole Foods Hawaii. The fields were fertilized on a monthly cycle with irrigation being at least weekly, depending on rainfall and evapotranspiration; at no time was stress due to nutrient deficiency and water stress was not observed. Leaf harvesting occurred between 9:00 AM and 12:00 PM. The leaves were deeply indented, similar to the leaf on the left of Fig. 1A. The lengths of the five major midribs of the leaf (Fig. 1B) were measured. The midribs were assigned as follows: L1, the center midrib; L2, the rib immediately to the left of the center; L3, the rib immediately to the right of center; L4, the second rib to the left of center; and L5, the second rib to the right of center. Each individual leaf was cut into smaller pieces to fit into the leaf area meter (Model L-3100A; LI-COR, Lincoln, NE).

Defoliation, fruit thinning, and photosynthesis. The net photosynthetic CO₂ assimilation rate of different aged leaves of young fruiting 'Sunset' plants were routinely measured between 9:00 AM and 12:00 PM. Plants were grown at the Poamoho Experiment Station on the Island of Oahu. The experimental field of 'Sunset' was surrounded by a tree windbreak, with the plants exposed to full sun, fertilized monthly, and irrigated on a weekly schedule. Leaves were numbered basipetally, beginning from the first leaf that had a 300-mm petiole. The first, second, third, fourth, fifth, sixth, 10th, 11th, 12th, 16th, 17th, and 18th leaves were chosen for photosynthesis measurements (Model 6200; LI-COR). Two areas in an area with no large veins toward the center of the larger lobes were marked on each leaf, and two net photosynthetic CO₂ assimilation readings were taken for each marked area. Leaves 3, 4, and 5 had the highest net photosynthetic

CO₂ assimilation; therefore, leaf 4 was chosen to measure net photosynthetic CO₂ assimilation in the defoliation and fruit thinning experiment. Thirty uniform 'Sunset' trees with a full fruit column were chosen. Ten trees were defoliated, with 80% of leaves being removed from the lowest oldest leaf. On another 10 trees, fruit were thinned by removing every third fruit from the base (oldest fruit) to the top of the fruit column (youngest fruit). The remaining 10 trees served as the control. At 11, 15, and 19 d after defoliation and fruit thinning, net photosynthetic CO₂ assimilation was determined from leaf 4. At week 3, the original leaf 4 was leaf 8. At week 5, the original leaf 4 was now ranged from leaf 9 to leaf 12.

Data analysis. The correlation and regression models were established for the linear measurement and total leaf area using the SAS stepwise regression model (SAS Institute, Cary, NC). The SAS GLM procedure (SAS Institute) was used to analyze the net photosynthetic CO₂ assimilation data.

Results and Discussion

The average individual leaf area in this study for 'Sunset' was 2331 cm² and ranged from 610 to 4267 cm². A papaya plant produces 2.1 to 2.5 leaves per week (Nakasone and Paull, 1998) and can have 10 to 50 fully expanded leaves on a plant, resulting in a total mature leaf area of up to 11.7 m²/plant. Zhou et al. (2000) found that one mature leaf can support the growth and development of three to four fruit. Therefore, a plant with a column of ≈60 fruit that are at all stages of development would require a mature total leaf area of ≈3.5 m² (Zhou et al., 2000).

The leaf width × length-based models used by other researchers for cucumbers, squash, and soybeans (NeSmith, 1992; Robbins and Pharr, 1987; Wiersma and Bailey, 1975) were not considered appropriate for Hawaii papaya cultivars due to the deeply lobed nature of the leaf that becomes partially folded during development. Campostri and Yamanishi (2001) developed a model for papaya with the log relationship from a single measurement of the central vein, with an *r*² of 0.898 for four cultivars grown in Brazil. When a single cultivar is evaluated (Posse et al., 2009), the main midrib length and estimated leaf area have a higher correlation coefficient (*r*² = 0.99); an approach to estimating the total leaf area of a papaya plant using the bottom two leaves was presented. The slope and the intercept were similar among the lines evaluated (Campostri and Yamanishi, 2001; Posse et al., 2009). The length of the central vein in our study also resulted in a slightly higher *r*² of 0.911 because of the combined data for the three varieties used in our study. The results were combined because the regression coefficients were similar for these Hawaii cultivars. However, papaya breeding lines and varieties do not always have lobed leaves with deep sinuses. The mature leaf area of Hawaii cultivars was most simply determined using

Fig. 1. Papaya leaf morphology and veins used to estimate the total leaf area. (A) Variations in papaya leaves vary from mild indentations (left) to significant indentations with deep sinuses and seven main veins (right). (B) Veins used to make linear measurements to determine the leaf area of papaya leaves.

Table 1. Stepwise regression of leaf measurements and leaf area.

Step	Variable entered	Partial <i>r</i> ²	Model <i>r</i> ²	C(p)	<i>P</i> > <i>F</i>
1	L3	0.9427	0.9427	341.674	0.0001
2	L4	0.0259	0.9687	107.0179	0.0001
3	L5	0.0059	0.9746	54.7723	0.0001
4	L2	0.0049	0.9795	11.7439	0.0001
5	L1	0.0008	0.9804	6.00	0.0060

L1, the center midrib; L2, the main side midrib to the left of the center midrib; L3, the main side midrib to the right of the center midrib; L4 and L5, the second set of midribs to the left and right of the center midrib, respectively.

Table 2. Model and parameter estimates for determining the leaf area of papaya from the leaf midrib measurement.

Variable	Parameter estimate	SE	F-value	<i>P</i> > <i>F</i>
Intercept	-2265.43	52.81	1840.04	0.0001
L2	42.82	6.50	43.40	0.0001
L3	23.15	7.60	9.27	0.0027
L4	23.46	6.23	14.19	0.0002
L5	56.90	6.66	72.92	0.0001
Leaf area = -2255.67019 + 135.0588*L3 (<i>r</i> ² = 0.94274; <i>P</i> = 0.0001)				
= -2279.95293 + 87.64602*L3 + 55.63544*L4 (<i>r</i> ² = 0.968667; <i>P</i> = 0.0001)				
= -2214.8335 + 45.05494*L3 + 56.52214*L4 + 46.91454*L5 (<i>r</i> ² = 0.97461; <i>P</i> = 0.0001)				

L1, the center midrib; L2, the main side midrib to the left of the center midrib; L3, the main side midrib to the right of the center midrib; L4 and L5, the second set of midribs to the left and right of the center midrib, respectively.

the length of the two longest side midribs (Table 1). The stepwise regression model for these two variables resulted in $P < 0.0001$ and $r^2 = 0.969$. Entering the lengths of the three other measured midribs to the model increased the r^2 to 0.980, but the P was 0.006. Our study showed that the length of the main central midrib of a papaya leaf provided the least improvement in the r^2 value compared with the leaf length, which is appropriate for linear leaves, such as in onion (Gamiely et al., 1991). There was a linear relationship between the leaf area and the lengths of the two longest side midribs (Table 2). Predictive equations may need to be adjusted for cultivars other than those used in this study, as found for cucumbers (Robbins and Pharr, 1987). However, the model may not apply to the papaya cultivars that do not have heavily lobed leaves. Because the papaya leaves ($n = 186$) for this study were collected over the course of 20 months, environmental influences, such as those found for cucumber leaf area (Robbins and Pharr, 1987), may have already been incorporated into our models.

The net photosynthetic CO_2 assimilation of papaya leaves from the apex to leaf 18 ranged from 4.1 to $16.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 2), possibly due to self-shading of the leaves in this monopodial plant. This finding provided the basis to evaluate leaf defoliation and fruit thinning. This range of the net photosynthetic

Fig. 2. Photosynthetic rate of papaya leaves at different ages from the first leaf with a 300-mm petiole. Leaf 4 was the most recently matured leaf ($n = 10$).

CO_2 assimilation rate (Fig. 2) agreed with the published range of 8 to $17 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the photosynthetic photon flux compensation of $\approx 35 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ with saturation more than $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Allan and de Jager, 1978; Marler et al., 1993). At PAR of $2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, the net rate is approximately double at 25 to $35 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Campostrini et al., 2001; Clemente and Marler, 1996; de Oliveira Reis et al., 2006; Marler and Mickelbart, 1998; Wang et al., 2014). The net photosynthetic CO_2 assimilation declined from a maximum near the recently mature leaf (leaf 4) of $16.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to $4.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at leaf 18 (Fig. 2). An average leaf area of 2331 cm^2 would fix 1.6 g carbon per leaf per day.

Defoliation can lead to an increase of 30% to 40% in the leaf net photosynthetic CO_2 assimilation rate (Table 3) on two of the three dates after defoliation treatment was imposed. On day 15, the PAR light levels were nearly twice that of days 11 and 19 (1621 vs. 753 and $871 \mu\text{mol}$ quanta/ $\text{m}^2\cdot\text{s}$), with no difference in the leaf net photosynthetic CO_2 assimilation rate due to defoliation. The impact of leaf defoliation on other species has similarly shown an increase in the net photosynthetic CO_2 assimilation rate of the remaining leaves (Avery, 1977; Jeong et al., 2017; Petridis et al., 2020; Poni et al., 2006; Wareing et al., 1968). This increase may be due, in part, to greater light penetration and its availability to the remaining leaves and modification of the temperature environment, in addition to the increased rate per unit leaf area, as reported here. In a separate study that we conducted, we showed that leaf defoliation has an altered flower abscission rate and fruit sugar levels (Zhou et al., 2000). These defoliation effects can last for up to 6 weeks under severe defoliation of 75%, which is not an uncommon level of defoliation for papaya in tropical areas subject to cyclonic high winds or severe powdery mildew. Similarly, severe *Papaya ring spot virus* infection can significantly reduce leaf net photosynthetic CO_2 assimilation through leaf yellowing and stunting of new leaf development (Decker and Tió, 1958; Marler et al., 1993). Pruning of older leaves had been practiced in Hawaii to facilitate spraying and harvesting, with no significant effect on fruit yield or soluble solids reported (Ito, 1976). Removal of 50% of the leaves did not significantly reduce fruit size (Zhou et al., 2000), and this might be due, in part, to partial compensation by increased net photosynthetic CO_2 assim-

ilation per unit area of the remaining leaves. The delay in the fruit sugar level returning to predefoliation levels is critical for fruit marketing. The presence on the papaya stem of fruit at all stages of growth and development once flowering commences (Campostrini and Glenn, 2007; Zhou et al., 2003) is coupled to a small amount of photosynthate being allocated to the roots, where less growth is observed (Marler and Discekici, 1996, 1997). Photosynthate is preferentially allocated to new leaf and flower growth and fruit and seed development. Fruit thinning did not significantly alter net photosynthetic CO_2 assimilation (Table 3). It is possible that fruit thinning or complete fruit removal from the plant could lead to the diversion of photosynthate to renew root growth. Papaya root growth, once flowering and fruiting start, declines sharply (Marler and Discekici, 1996, 1997). It has been observed that following heavy rains and flooding, root rot becomes a major problem that is often followed by plant death. Fruit removal from the plant leads to a higher tree survival rate, possibly due to increased root growth, with photosynthate formerly going to fruit and seed development now available for new root growth.

The availability of a rapid measure of papaya leaf area coupled with the knowledge of photosynthate rates provide tools to develop papaya growth models. These models could provide insight regarding source-sink relationships and the allocation of resources between new leaf, flowering, fruit and root growth, and development for this single-axis plant.

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Table 3. Photosynthetic rate of the most recently matured papaya leaf (4), at 11, 15, and 19 d after one of every third fruit was removed from the base of the fruit column or 80% of the leaves were removed.

Treatment	Days after treatment		
	11	15	19
	Photosynthetic rate ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		
Control	7.5 B	7.1 A	6.4 B
Fruit thinned	8.0 B	8.3 A	5.6 B
Defoliated 80%	11.3 A	8.0 A	9.7 A
<i>PAR</i> average ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	754	1621	872

Means (Duncan/Waller); $n = 10$.

PAR = photosynthetic active radiation.

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