

## *CARICA PAPAYA* (CARICACEAE): A CASE STUDY INTO THE EFFECTS OF DOMESTICATION ON PLANT VEGETATIVE GROWTH AND REPRODUCTION<sup>1</sup>

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Few studies have quantitatively evaluated the gender specific effects of cultivation on plant growth and reproduction. The availability of cultivated and wild populations of different genders of *Carica papaya* L. (Caricaceae) on Guam provided an opportunity to study these effects quantitatively. We compared the gender specific allometry of height vs. basal stem diameter ( $H$  vs.  $D$ ), stem slenderness ratio ( $H/D$ ), and the height at first flowering ( $H_f$ ) of carpellate and staminate plants growing under natural conditions ( $N = 150$  each) with those of carpellate and hermaphroditic plants ( $N = 250$  each) from two cultivars (Sunrise and Tainung 2). These comparisons indicated that (1) wild carpellate and staminate plants are significantly taller than either gender of the two cultivars with equivalent  $D$ ; (2) the scaling exponent governing the  $H$  vs.  $D$  relationship of both genders of wild plants is significantly higher than that of either cultivated gender; (3) cultivar type does not affect the  $H$  vs.  $D$  exponent, but gender expression does; (4) gender expression (but not cultivar-type) also affects  $H_f$  (cultivation substantially reduces carpellate plant  $H_f$ ); and (5) the onset of sexual maturity is associated with a dramatic reversal in  $H/D$  ontogeny. Cultivation therefore has “condensed” patterns of vegetative growth in a gender specific manner, whereas gender expression alters both vegetative and reproductive growth significantly more so than does cultivar-type.

**Key words:** allometry; first flowering; gender expression; Guam; papaya; plant height; scaling exponents.

The effects of domestication on plant growth, particularly on crop yield, have been extensively studied (Evans, 1993). In contrast, the effects of artificial selection on the vegetative and reproductive growth of conspecifics differing in gender have not been examined intensively, particularly in rigorous, quantitative ways. In this study, we ask whether artificial selection has resulted in gender specific differences in these two important traits, using *Carica papaya* L. (“papaya”) as the study subject. This species was selected because of its two distinct reproductive types (i.e., dioecious and gynodioecious conspecifics) and because of the accessibility of wild and cultivated populations growing in close proximity.

*Carica papaya* is a pantropical, fast-growing tree crop cultivated for its fruit, proteolytic enzyme (papain), pectin, and, to a limited extent, antibacterial substances (Morton, 1977; Emeruwa, 1982; Murthy and Natarajan, 1982). Papaya is not considered to be a weed species (OECD, 2003). However, it has naturalized in many tropical and subtropical countries (Randall, 2002). For example, cultivars, which were introduced to Guam and the rest of the Mariana Islands during the Spanish occupation of the region, have been growing spontaneously in abandoned clearings and forest gaps for at least one century (Safford, 1905; Stone, 1970). Fruit bats (*Pteropus mariannus* Desmarest) and pigeon-sized birds serve as effective seed dispersal agents. Following canopy defoliation from tropical cyclones, *C. papaya* seedlings are among the most common seedlings to emerge from the forest floor (T. Marler, unpublished data). Space et al. (2000) suggest that in Rota,

north of Guam in the Mariana Islands, papaya may be invasive in highly disturbed habitats.

As noted, among its many cultivars, there are two reproductively distinct types: dioecious and gynodioecious plants. Dioecious papaya have staminate and carpellate flowers on separate individuals; gynodioecious papayas bear carpellate flowers on some individuals and perfect (hermaphrodite) flowers on others. One cultivar (i.e., Solo) occasionally produces functionally andromonoecious (staminate and hermaphrodite flowers) on the same plant, with a terminal perfect flower subtended by a few staminate axillary flowers (OECD, 2003). These differences in floral biology are presumed to be responses to hot and dry conditions, which affect functional gender in papayas.

The genetic or chromosomal basis for papaya sex ratios is poorly understood (Villegas, 1991; OECD, 2003). However, a widely shared hypothesis is that gender is controlled by a single locus with three alleles:  $M1$  (staminate),  $M2$  (hermaphrodite), and  $m$  (carpellate) (see Somsri et al., 1998). Staminate and hermaphrodite plants are heterozygous (i.e.,  $M1m$  and  $M2m$ , respectively), carpellate plants are homozygous recessive (i.e.,  $mm$ ). Combinations of dominants, such as  $M1M1$ ,  $M1M2$ , and  $M2M2$ , lead to postzygotic ovule abortion. This hypothesis predicts that viable staminate plants can only be  $M1m$ , whereas viable hermaphrodites can only be  $M2m$ .

Domestication of carpellate and hermaphrodite plants has clearly produced cultivars differing in yield from their wild progenitors, e.g., cultivars produce seeds that are 33% larger (with less stringent requirements for germination) than their wild counterparts (see Andreoli and Khan, 1993; Paz and Vázquez-Yanes, 1998). Cultivation under irrigation and subsequent selection has likely also resulted in cultivars with growth patterns, gender expression, and floral phenologies differing from those of wild populations (e.g., under field conditions, the more vigorously growing plants are usually the

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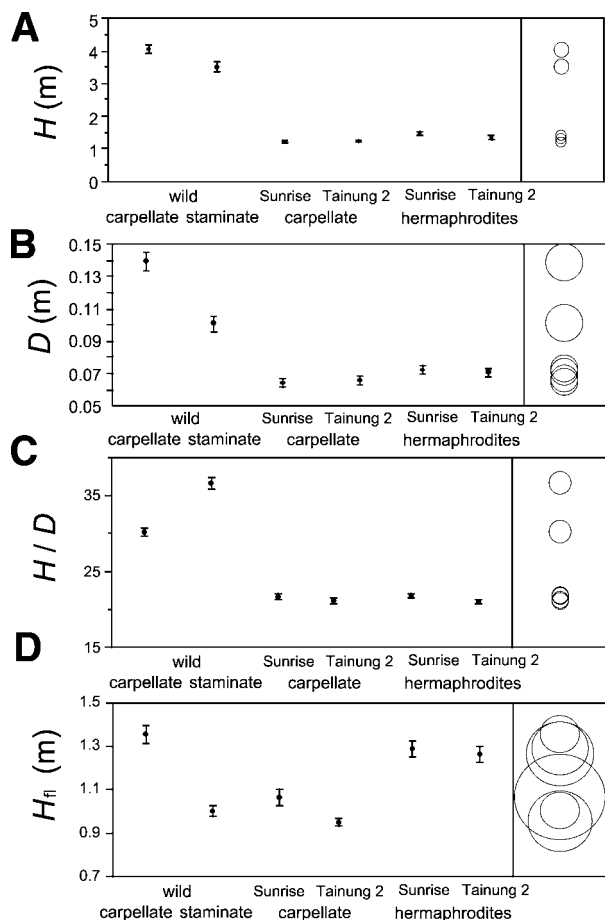


Fig. 1. Mean measurements  $\pm$  SE for *Carica papaya* for (A) height  $H$ , (B) diameter  $D$ , (C) slenderness ratio  $H/D$ , and (D) height to first flowering  $H_n$  of wild carpellate and staminate plants and of carpellate and hermaphrodite plants of Sunrise and Tainung 2. Circles denote Tukey-Kramer all pairs comparisons ( $\alpha = 0.05$ ).

staminate plants). However, the manner and extent of such alterations have not been well documented.

Here, we examine the effects of cultivation on papaya vegetative and reproductive growth by comparing staminate and carpellate plants grown under natural conditions with carpellate and hermaphrodite plants of two cultivars (Sunrise and Tainung 2). Specifically, we ask whether cultivation has altered the allometry of height  $H$  with respect to basal stem diameter  $D$  (it is reasonable to assume that  $H$  has been reduced as a consequence of domestication to facilitate fruit harvesting) and whether cultivation has changed the size at which plants achieve reproductive maturity. The allometry of plant height is often species specific and provides a convenient, nondestructive measurement of plant development and morphology (Niklas, 2004, 2006; Weiner, 2004; Niklas et al., 2006). More important, it provides a quantitatively rigorous method to compare the relative growth rates of different plant body parts. Model Type II regression of  $H$  vs.  $D$  yields two simple statistical parameters (the regression slope and y-intercept) that can be compared numerically among plants differing in gender or growing conditions. The size at which first flowering occurs is a convenient metric for plant maturity; it is a functional trait that is likely to have been altered during domestication; and it can be

pinpointed on regression curves to assess whether the scaling of  $H$  vs.  $D$  changes ontogenetically when reproduction first occurs.

## MATERIALS AND METHODS

**Data collection**—Data for cultivated plants were obtained from field studies conducted at the University of Guam Agricultural Experimental Station located in Yigo, Guam. Seedlings of the two cultivars (Sunrise and Tainung 2) were planted on 15 March 2001 in a  $2 \times 3$  m layout. Sunrise was selected to represent the Solo breeding program from Hawaii. Tainung 2 was selected for study because it is the most popular cultivar on Guam and from the Taiwan breeding program. Cultivation practices followed commercial guidelines with irrigation using drip tape and fertilizer management consisting of biweekly application per plant of 50 g (first 2 mo) or 100 g ( $>2$  mo) of a complete granular fertilizer (16 N, 7P, 13K). A second orchard of the same cultivars was planted on 3 June 2001. Height  $H$  and basal stem diameter  $D$  were measured every 2 wk for 7 mo. The data and size of plants at first flowering were also recorded; plant gender was assigned after the appearance of flowers.

Measurements on wild plants began in July 2005 and continued until May 2006. Wild papaya plants are a ubiquitous part of the roadside flora throughout Guam. Roadside plants were selected because they experience sunlight regimes that more closely mimic those of cultivated plants than wild counterparts growing under forested conditions. Measurements were restricted to plants for which gender could be assigned unambiguously.

**Statistical protocols**—Measurements of  $H$  and  $D$  (original units, m) were  $\log_{10}$ -transformed after preliminary statistical evaluations revealed  $\log$ - $\log$  linear relationships within each of the four juvenile and adult data-sets. Model Type II (standardized major axis, SMA) regression was used to determine the slope (scaling exponent) and y-intercept (allometric constant) of  $\log$ - $\log H$  vs.  $D$  linear functions (i.e.,  $\alpha_{SMA}$  and  $\log \beta_{SMA}$ , respectively) because functional rather than predictive relationships were sought (see Sokal and Rohlf, 1981; Niklas, 1994). These two regression parameters were computed using the formulas  $\alpha_{SMA} = \alpha_{OLS}/r$  and  $\log \beta_{SMA} = \log \bar{H} - \alpha_{SMA} \log \bar{D}$ , where  $\alpha_{OLS}$  is the ordinary least squares (OLS) regression slope,  $r$  is the OLS correlation coefficient, and  $\log \bar{H}$  and  $\log \bar{D}$  denote mean values. Note that regression of  $H/D$  vs.  $D$  or  $H$  is invalid statistically, although  $\log$ - $\log$  plots of  $H/D$  vs.  $D$  or  $H$  provide graphic tools to assess changes in stem shape as a function of changes in plant size.

The software package *Standardised Major Axis Tests and Routines* (Falster et al., 2003, see also Warton and Weber, 2002), denoted here as SMATR, was used to determine whether the numerical values of  $\alpha_{SMA}$  and  $\log \beta_{SMA}$  differed among data sets, because SMATR provides the Model Type II equivalent of OLS standard analyses of covariance (ANCOVA). Slope heterogeneity was evaluated before determining whether regression curves shared the same elevations, because numerical similarities in  $\log \beta_{SMA}$  are irrelevant for curves differing in slope. The significance level for testing slope heterogeneity was  $P > 0.05$  (i.e., slope heterogeneity was rejected if  $P > 0.05$ ). Standard  $t$ -test comparisons (at the 5% level) were used to evaluate whether mean values for  $H$  and  $D$  differed among genders and between wild and cultivated counterparts. Stem slenderness ratio (i.e.,  $H/D$ ), which is a simple descriptor of shape, was evaluated similarly.

## RESULTS

The stems of wild *C. papaya* plants were, on average, taller and thicker than those of their cultivated counterparts, based on all pairs comparisons (Fig. 1A, B). The stems of wild carpellate plants were significantly taller and thicker than those of staminate wild plants or either cultivar. No statistically significant differences were observed for either  $H$  or  $D$  between the two cultivars or their two genders, although the stems of hermaphrodites were, on average, taller and thicker than those of the carpellate cultivars (Fig. 1A, B). The stems of wild staminate plants had, on average, significantly larger slenderness ratios than those of wild carpellate plants (i.e., mean  $\pm$  SE =  $36.6 \pm 0.87$  and  $30.2 \pm 0.59$ , respectively). The slenderness ratios of the two cultivars (or their two genders) did not differ statistically (Fig. 1C).

TABLE 1. Summary of standardized major axis (SMA) regression statistics for the slope and elevations ( $\alpha_{SMA}$  and  $\log \beta_{SMA}$ , respectively) of log-transformed data for height and basal stem diameter ( $\log H$  vs.  $\log D$ ) for functional *Carica papaya* groups.

Functional group	$\alpha_{SMA}$ (95% CIs)	$\log \beta_{SMA}$ (95% CIs)	$r^2$
Wild ( $N = 250$ )	0.867 (0.844; 0.891)	1.38 (1.33; 1.43)	0.817
Staminate ( $N = 150$ )	0.878 (0.846; 0.910)	1.42 (1.35; 1.49)	0.835
Carpellate ( $N = 150$ )	0.931 (0.898; 0.965)	1.41 (1.34; 1.47)	0.806
Cultivated ( $N = 900$ )	0.773 (0.766; 0.780)	1.02 (1.01; 1.04)	0.952
t carpellate ( $N = 250$ )	0.750 (0.738; 0.761)	0.98 (0.96; 1.00)	0.967
s carpellate ( $N = 250$ )	0.754 (0.739; 0.768)	0.99 (0.96; 1.03)	0.944
t herma. ( $N = 250$ )	0.785 (0.772; 0.798)	1.04 (1.01; 1.06)	0.961
s herma. ( $N = 250$ )	0.795 (0.780; 0.810)	1.07 (1.04; 1.10)	0.940
st carpellate ( $N = 450$ )	0.752 (0.743; 0.761)	0.99 (0.97; 1.01)	0.956
st herma. ( $N = 450$ )	0.792 (0.781; 0.803)	-1.31 (-1.31; -1.30)	0.950

Note: Original units = meters; t = data from Tainung 2; s = data from Sunrise; st = data from both cultivars; herma. = hermaphrodite.

Statistical comparisons of the slopes and y-intercepts of SMA regressions (i.e.,  $\alpha_{SMA}$  and  $\log \beta_{SMA}$ , respectively) indicated that wild carpellate and staminate plants share the same  $H$  vs.  $D$  allometric parameters (i.e., statistically indistinguishable numerical values for regression slopes and y-intercepts; Table 1). Regression of the combined data collected from both genders ( $N = 250$ ) indicates that  $H$  scales as the 0.867 power of  $D$ . This scaling relationship differed significantly from that of either cultivar, for which  $H$  scales as the 0.773 power of  $D$  across both (Table 1). Thus, wild plants achieve greater height than their cultivated counterparts with equivalent stem diameters.

Comparisons of the  $\alpha_{SMA}$  and  $\log \beta_{SMA}$  for cultivated plants indicated that the carpellate plants of both cultivars share the same  $H$  vs.  $D$  allometry; the hermaphrodites of both cultivars also share the same allometry; and the allometries of the two genders of cultivated plants statistically differed. Specifically, across all cultivated carpellate plants,  $H$  scaled as the 0.752 power of  $D$ , whereas across all cultivated hermaphrodite plants,  $H$  scaled as the 0.792 power of  $D$  (Table 1). Thus, gender expression affects the  $H$  vs.  $D$  relationship but cultivar type does not.

All pairs comparisons indicated that gender also influences plant height at first flowering (i.e.,  $H_{fl}$ ) and that cultivar-type does not (Fig. 1D). The  $H_{fl}$  of wild carpellate plants was significantly greater than that of the carpellate plants from either cultivar; the  $H_{fl}$  of hermaphrodites from both cultivars was significantly greater than that of their cultivated carpellate counterparts; carpellate plants of the Tainung 2 cultivar achieve, on average, reproductive maturity at the smallest  $H_{fl}$  (i.e., 0.95 m).

The height at first flowering alters both the  $H$  vs.  $D$  allometry and the stem slenderness ratios of cultivated plants (Fig. 2). Analyses of regression residuals and inspection of  $H$  vs.  $D$  bivariate plots pinpointing  $H_{fl}$  indicated that the log-log relationship becomes nonlinear for plants taller than  $H_{fl}$  (Fig. 2A). This nonlinearity is associated with an increase in stem slenderness ratios (which decrease ontogenetically before  $H_{fl}$  is achieved by the two genders of either cultivar) (Fig. 2B).

DISCUSSION

Because *C. papaya* hermaphrodites do not grow wild on Guam and because they are the only pollen donors in cultivated populations, the only legitimate direct comparisons that we can make are between wild and cultivated carpellate plants. Additionally, wild plants are descendents of early Spanish introductions that became well-established as “feral” popula-

tions at least one century before papaya cultivars, such as Sunrise and Tainung 2, were commercially introduced to Guam. Accordingly, wild and cultivated papaya populations on Guam are genetically and environmentally very different. Nevertheless, to the best of our knowledge, our study is the only one of its kind to rigorously quantify gender specific effects of cultivation on vegetative and reproductive growth. Specifically, our analyses indicate that cultivation of papaya has resulted in the reduction of three critical functional traits: (1) the average height  $H$  and basal stem diameter  $D$  of carpellate individuals, (2) the scaling exponent for  $H$  vs.  $D$ , and (3) the height of first flowering  $H_{fl}$ .

We hypothesized that the height of domesticated papaya would be significantly less than that of wild plants, because it is

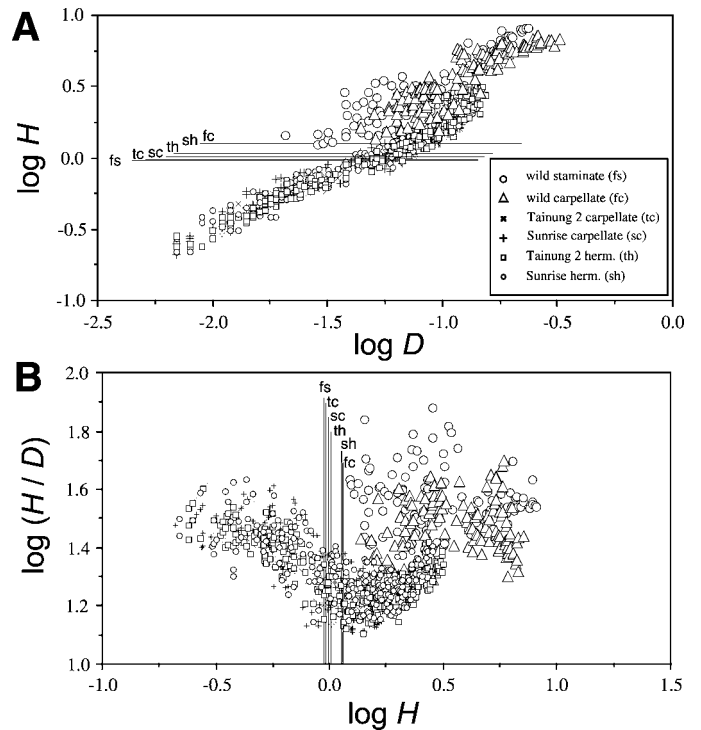


Fig. 2. Bivariate log-log plots of (A) plant height  $H$  vs. stem diameter  $D$  and (B) stem slenderness ratio  $H/D$  vs.  $H$  for *Carica papaya*. Average height to first flowering ( $H_{fl}$ ) is indicated by horizontal and vertical lines in A and B, respectively. See insert for symbols denoting gender and cultivar type.

logical to assume that shorter plants would be selected for the ease of harvesting fruits. The reduction in  $H$  reported here is not an artifact of sampling or population demography because wild populations of carpellate plants are significantly taller than their cultivated counterparts with equivalent basal stem diameters. This observation is implicit from the observation that the  $H$  vs.  $D$  relationship among wild carpellate plants is governed by a numerically larger scaling exponent than that of their cultivated counterparts, because the scaling exponent is numerically the rate of change in  $H$  with respect to the rate of change in  $D$ . It is notable in this context that the  $H$  vs.  $D$  scaling exponent for cultivated carpellate plants is statistically indistinguishable from 0.75, which theoretically obtains the mechanical condition known as elastic self-similarity, i.e., elastic deflections that are indifferent to the magnitudes of bending forces across columnar support members differing in size (McMahon, 1973; Niklas, 1994). Although papaya stems can reorient themselves by means of reaction wood (see Fisher and Mueller, 1983), shortened stems bearing large fruit clusters in their upper canopies (i.e., "terminal loads") would benefit mechanically from this scaling relationship. A reduction in plant height would also theoretically reduce the drag forces exerting bending moments at the base of stems.

The conclusion that gender expression dictates reproductive size as well as patterns of vegetative growth emerges from two observations. First, regardless of cultivar type, cultivated carpellate plants (and their hermaphrodite counterparts) have statistically indistinguishable  $H$  vs.  $D$  scaling exponents, and, second, the hermaphrodites of both cultivars reach reproductive maturity at statistically indistinguishable average heights. Cultivar type may influence the height at first flowering for carpellate plants. However, cultivated carpellate plants reach reproductive maturity at significantly shorter heights than cultivated hermaphrodites with equivalent stem diameters in addition to being dramatically shorter than their wild counterparts. These observations suggest to us that the life cycle of carpellate individuals has been "condensed" under domestication, perhaps as a consequence of irrigation and other cultivation practices (see Evans, 1993).

Future research into phenomena like "condensation" would benefit greatly from statistical models for mapping the specific quantitative trait loci (QTLs) that underlie scaling relationships like those reported here. This approach, which is called "functional mapping," has been used successfully for animal systems, e.g., mouse  $F_2$  progeny for which two QTLs detected on different chromosomes determine the scaling relationship between growth rate and body mass (Long et al., 2006; Wu and Lin, 2006). Unfortunately, to the best of our knowledge, this approach has not been used for any plant system. It is nevertheless clear that the effects of domestication on plant vegetative and reproductive growth have been manifold and often profoundly allometric, as revealed by the scaling of papaya.

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