Evaluation of Morphological Traits Associated with Productivity in F₁ Interspecific (*Cucurbita maxima* Duch. x *C. moschata* Duch.) Hybrid Processing Squash

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Abstract. Interspecific hybrids can be produced from certain cross combinations of *Cucurbita maxima* x *C. moschata*. These hybrids have been used extensively as rootstocks for melon and watermelon grafting, but only occasionally for fresh market use. The objective of this study was to assess the potential of interspecific hybrids for use in pie processing in terms of morphological traits related to productivity. We used a bush-processing inbred line of *C. maxima*, NH65, as the female parent and two vining-processing cultivars of *C. moschata*, Long Island Cheese (LIC) and Dickinson Field (DF) as pollen parents to produce two interspecific hybrids with large orange fruit, potentially suitable for processing. A greenhouse study was conducted to compare internode lengths, main stem diameters, flowering patterns, and leaf area at first appearance of female flowers in NH65, LIC, DF, and two interspecific hybrids, NH65xLIC and NH65xDF. Plants were grown in 8.7 L nursery pots, watered and fertigated with drip tubing, and trellised to a single main stem. In LIC and DF, internode lengths increased rapidly beyond the fourth node before reaching a maximum by node 12. Internodes in NH65 did not exceed 3 cm until node 15, and average lengths never exceeded 4 cm. In interspecific hybrids, internode lengths mimicked bush plants for 6 or 7 internodes, remaining below 3 cm, but then increased rapidly to lengths approaching that of the vining cultivars after internode 10. Staminate flowers were more abundant than pistillate flowers in NH65, LIC and DF; whereas the interspecies hybrids produced primarily pistillate flowers. In NH65xLIC, the first pistillate flowers appeared on nodes 9–11, on average 38.3 days after transplanting (DAT), and in NH65xDF, on nodes 9–17, 42.3 DAT. First pistillate flowers in NH65 occurred on nodes 9–11, 34.3 DAT, compared with nodes 9–13, 39.3 DAT and nodes 17–21, 50.0 DAT, respectively, for LIC and DF. A field study was conducted for comparing flowering patterns and growth habits in NH65xLIC, NH65xDF, DF, LIC, NH65, and ‘Golden Delicious’ (GD), a popular *C. maxima* processing winter squash. Stem length was short and petioles highly elongated in the two interspecific hybrids until about 34 DAT, such that plants exhibited a uniform, compact phenotype similar to NH65. Subsequently, stems elongated rapidly, with lengths approaching and occasional exceeding those in vine cultivars. In the two vining *C. moschata* cultivars, LIC and DF, 4–6 laterals developed near the base of plants, usually consisting of 12–30 nodes. NH65xLIC produced mostly short laterals (4–15 nodes) interspersed along much of the main stem, whereas NH65xDF produced numerous lateral branches, mostly ranging from 11 to 30 nodes long, between the base and about the halfway point along the main stem. Mature leaves were about twice as large in the two interspecific hybrids as in DF and GD; this together with differences in early growth habit and branching patterns contributed to a much faster leaf canopy cover in the interspecific hybrids in comparison with the vining cultigens.

In recent decades, F₁ hybrids in the genus *Cucurbita* have increasingly gained prominence over open-pollinated varieties, particularly in

summer squash, ornamental pumpkin and acorn cultivars of *C. pepo* L. and kabocha cultivars of *C. maxima* (Loy, 2012; Robinson, 2000). By contrast, open-pollinated cultivars such as GD (*C. maxima*) and strains of DF (*C. moschata*) still dominate the production of squash or pumpkin used for pie processing (Loy, 2004). Interspecific *C. maxima* x *C. moschata* F₁ hybrids may offer unique combinations of traits attractive to growers and processors. Castetter (1930) and Erwin and Haber (1929) reported that certain parental combinations of *C. maxima* x *C. moschata* set fruit and produced viable F₁ seed, and moreover, F₁ plants often produced

normal looking fruit with the aid of a pollen donor strain. Interspecific hybrid plants have been described as vigorous and highly gynoeceous, with leaf shape intermediate to parental lines, vines resembling the *C. moschata* parent, and fruit with the general appearance of the *C. maxima* parent (Castetter, 1930; Erwin and Haber, 1929; Robinson et al., 1978; Whitaker and Bohn, 1950). Interspecific hybrids are largely seedless and therefore may exhibit high pericarp yields because assimilates do not have to be allocated to seed development. Because the root systems of interspecific hybrids are highly resistant to abiotic and biotic stress, they have been used widely as rootstocks for melon and watermelon production (Davis et al., 2008). They express insect tolerance of the *C. moschata* parents, showing resistance to squash vine borers [*Melittia cucurbitae* (Harris)], and are less attractive to squash bugs [*Anasa tristis* (DeGeer)] than cultigens of *C. maxima*. In addition, we have observed that the interspecific hybrids exhibit intermediate resistance to powdery mildew disease [*Podosphaera xanthii* (Castagna) U. Braun and N. Shirshkoff].

At the University of New Hampshire, bush breeding lines of *C. maxima* squash with large, orange fruit, similar to GD, have been developed for use in hybrids for pie or baby food processing. We considered these breeding lines to be good candidate parents for producing *C. maxima* x *C. moschata* interspecific hybrids exhibiting a favorable semibush growth habit for rapid leaf canopy cover and high yield potential (Loy, 2004; Loy and Broderick, 1990). In terms of fruit set, seed yield, seed fill and germinability, initial testing indicated that two of four bush *C. maxima* lines, NH245 and NH65, exhibited good compatibility when crossed to *C. moschata* cultigens (Uretsky, 2012). For *C. moschata* parents we relied on two established processing cultivars LIC and DF. We also evaluated the open-pollinated cultivar Waltham Butternut (WBN) as a male parent, but in contrast to LIC and DF, interspecific hybrids from this parent exhibited precocious appearance of pistillate flowers (Loy and Uretsky, 2010), resulting in production of numerous fruit near the base of plants.

To more thoroughly evaluate the yield potential of interspecific hybrids, we conducted greenhouse and field research to compare flowering patterns and traits affecting leaf canopy development in two interspecific hybrids, NH65xLIC and NH65xDF, and three open-pollinated processing cultivars DF and LIC (*C. moschata*), and GD (*C. maxima*).

Materials and Methods

Plant materials. A bush *C. maxima* breeding line, NH65, with fruit type and quality approaching that of the open-pollinated cultivar GD was used as the female parent in interspecific crosses. Open-pollinated, vine cultivars of *C. moschata*, LIC and DF, were used as male parents. Interspecific *C. maxima* x *C. moschata* crosses were performed in the field during the summer of 2010 by controlled hand pollination

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using standard squash pollination protocol (Whitaker, 1960). Staminate and pistillate flowers were tied off 1 d preanthesis to prevent pollen contamination, and pollinations were performed between 0600 and 0800 hr on the morning of anthesis. Additional open-pollinated fruit were removed from plants. Fruits resulting from crosses were harvested ≈ 55 –60 d after pollination (DAP). Harvested fruits were stored in a greenhouse at 18–26 °C until ≈ 65 DAP to ensure complete seed fill. Seeds were extracted, cleaned, and dried on screens in a forced air dryer at 30 °C.

Greenhouse, 2011. A comparative study of plant growth traits was performed at the Macfarlane Greenhouses, Durham, NH in the spring of 2011 with interspecific hybrids NH65xLIC and NH65xDF and parental cultigens. Seeds were sown 17 Jan. in 50-cell plug trays containing Pro-Mix BX[®] soilless potting medium (Griffin Greenhouse Supply, Tewksbury, MA) and transplanted into 8.7 L plastic nursery pots on 3 Feb. after expansion of the first true leaf. Pots were arranged on two adjacent greenhouse benches in a randomized complete block design with six blocks, each consisting of single-plant replicates of the five comparator cultigens. The vine *C. moschata* cultivar WBN and two bush *C. maxima* x WBN interspecific hybrids were also evaluated on a bench adjacent to the main study. All plants were pruned to a single main stem and trellised. Greenhouse temperatures were maintained at 25 °C day/17 °C night. Plants were irrigated with trickle tubing and constantly fertilized with soluble fertilizer (15N–42.2P–12.4K) at an initial fertilizer concentration of 100 ppm and a final concentration of 250 ppm.

Measurements were taken from each plant, except where noted, and commenced 14 DAT. Recorded data included main stem length from the cotyledons to the shoot apex, successive internode lengths, diameter of the main stem and petioles at node 10, rate of leaf initiation, and leaf area. Cumulative leaf area of all unfurled leaves was determined at anthesis of the first pistillate flower to approximate canopy development at putative first fruit set. Individual leaf areas were estimated as leaf blade length from petiole to tip multiplied by leaf width at the basal lobes (Loy and Broderick, 1990). In addition, observations of the sex and node location of each flower reaching anthesis were recorded daily beginning at the commencement of flowering.

Field, 2011. In a study conducted at Kingman Research Farm, Madbury, NH, growth habit and productivity were compared among the interspecific hybrids NH65xLIC and NH65xDF and standard open-pollinated processing cultivars DF (*C. moschata*) and GD (*C. maxima*). Non-replicated plots of two parental lines, NH65 (*C. maxima*) and LIC (*C. moschata*), and the interspecific hybrids NH65xWBN and NH245xWBN were also observed for comparative purposes. Soil type was a Hollis–Charlton fine sandy loam (mixed mesic, Entic Lithic Haplorthod). Fertilizer was applied broadcast at a rate of 56.1 kg N and 46.6 kg K/ha

before bed formation (61 cm width $\times$ 15 cm high) and application of BioTelo biodegradable mulch (15.2 μm $\times$ 135 cm width; Dubois Agrinovation, Saint-Remi, Quebec, Canada) and drip tape (203 μm T-tape, 30 cm emitter spacing; T-Systems International, San Diego, CA). Plants were fertigated weekly for 4 weeks beginning the first week of July with soluble fertilizer at a rate of 2.8 kg N and 2.3 kg K/ha. Disease and insect control followed the general recommendations of the 2010–11 New England Vegetable Management Guide (Howell et al., 2010–2011). Weed control was achieved with mechanical cultivation between raised beds.

Plants were seeded in 50-cell plug trays containing Pro-Mix BX[®] soilless potting medium on 27 May and transplanted 10 June at the first true leaf stage. In-row spacing was 0.6 m and between-row spacing was 2.4 m (0.7 plants/m²). We used a randomized complete block design with four blocks, four cultigens as the main treatments, and 16 plants per plot of each cultigen. Each data plot contained two 8-plant rows with two guard rows on both sides and two guard plants at the beginning and end of each data row. Unhealthy or dead plants were replaced during early growth. Poor germination of GD necessitated resowing on 10 June and transplanting on 20 June.

Four plants per plot were chosen at random for weekly measurements of main stem length, branching habit, and leaf initiation on the main stem. Also, petiole length, canopy height, area of the fourth and tenth leaves on the main stem, and area of leaves on mature plants were recorded. Individual leaf areas were estimated using the procedure described for the greenhouse in 2011.

Results

Vegetative traits, greenhouse. Main stem length in the bush parent NH65 did not exceed 40 cm at 42 DAT, whereas stem length in both DF and LIC vine cultivars averaged 180 cm and 275 cm, respectively, at

42 DAT (Fig. 1). Both interspecific hybrids, NH65xLIC and NH65xDF, exhibited main stem lengths similar to that of the bush parent until ≈ 25 DAT, but by 42 DAT stem length of the interspecific hybrids was intermediate to that of the bush and vine cultigens (Fig. 1).

Leaf numbers at 14, 27, and 42 DAT among the two interspecific hybrids and their parental strains were not significantly different with the exception of NH65xLIC at 14 d, a reflection of slow germination and smaller seedlings at transplant (Table 1). However, mean rates of leaf initiation for all cultigens between 27 and 42 DAT (0.67 leaves/d) was 75% higher than between 14 and 27 DAT (0.38 leaves/d). The increased rate of leaf initiation among cultigens coincided with plants entering the exponential phase of growth between 25 and 30 DAT (Fig. 1).

Because rates of leaf initiation were similar among cultigens, the differences in stem elongation were largely attributable to differences in internode lengths. Internode lengths in the bush inbred, NH65, remained below 1.5 cm for the first nine internodes and then progressively lengthened to 2.9 cm by internode 15 (Fig. 2). By contrast, internode lengths in the vine cultivars began to increase rapidly beginning with the fourth internode, until internode lengths at internode 12 more or less stabilized at ≈ 19 –20 cm for LIC and 14–16 cm for cultivar DF. In interspecific hybrids, initial internode lengths were only 2–3 cm until internode 7, resembling lengths exhibited in the bush strain. Subsequently, internode lengths elongated rapidly until internode 12–13, when the hybrids exhibited lengths comparable with the vine cultivars.

Leaf areas were measured at anthesis of the first pistillate flower to reflect potential leaf canopy formation before putative first fruit set. There were significant differences among cultigens in the number of leaves produced, the number of days from transplanting before appearance of first pistillate flowers, and also in leaf size (Table 2). The vining cultivar DF produced pistillate flowers much later than the rest of the lines and

Fig. 1. Mean main stem length (cm) in the interspecific hybrids NH65xLIC (left) and NH65xDF (right) and the respective parental cultigens by days after transplanting. Values ($\pm$ SD) are means of six plants.

therefore produced more leaves than the other cultivars and hybrids at anthesis of first pistillate flower. Separation in flowering times among the other cultivars was less clear, but bush plants tended to flower earlier than the other cultivars and at a lower node number (Fig. 3). Because of both relatively late pistillate flowering and large leaves, the interspecific hybrid NH65xDF had the greatest leaf area at first pistillate flower; however, the differences were statistically significant only in comparison with the bush strain, NH65. Leaf areas were also measured on two plants of the interspecific hybrid NH65xWBN growing adjacent to the main study. These plants produced pistillate flowers at the fifth node, and at anthesis of the first pistillate flowers, cumulative leaf area averaged only 2192 cm², considerably below that of NH65xLIC and NH65xDF.

Stem diameter of the bush line NH65 at node 10 was more than double that of the two *C. moschata* vine cultivars and was significantly larger than that of the interspecific

hybrids. Stem diameters of the interspecific hybrids were 31% to 32% larger than that of the respective *C. moschata* parental cultivars. Petiole diameters were not significantly different among cultivars with the exception of NH65xLIC, which possessed significantly thicker petioles than the other cultivars (data not shown).

Flowering habit, greenhouse. Staminate flowers were much more abundant than pistillate flowers in the parental cultivars NH65, LIC, and DF (Table 3). Only one of the two interspecific hybrids, NH65xDF, produced any staminate flowers during the course of the experiment; NH65xLIC produced staminate flower buds, but buds failed to reach anthesis. The first pistillate flowers reached anthesis on nodes 9–11 in the interspecific hybrid NH65xLIC and the parental cultivar NH65, but locations of the first pistillate flowers were more variable in LIC (nodes 9–13; Table 3). In DF, the first pistillate flowers appeared later (nodes 17–21) than in LIC, and in the hybrid NH65xDF,

location of the first pistillate flower was intermediate (nodes 9–17) to parental cultivars, but varied significantly because of bud senescence in several plants.

The bush cultivar NH65 flowered earlier than the other cultivars and staminate and pistillate flowers appeared at about the same time (34–37 DAT). Mean days to pistillate flowering in LIC and the two interspecific hybrids ranged between 39 and 42 DAT, and the values were not statistically different. On the other hand, pistillate flowering in DF (50.0 DAT) occurred significantly later than in the other cultivars. Staminate flowering was earlier in the bush inbred line NH65 (37 DAT) than in LIC (43 DAT) and DF (46 DAT). Staminate flowers were absent in NH65xLIC, and the few to appear in NH65xDF occurred late (50.6 DAT). Flowering patterns in representative single plants of the interspecific hybrids and parental cultivars observed in the greenhouse in 2011 are illustrated in pictographs (Fig. 3). In the *C. maxima* and *C. moschata* parental cultivars, staminate flowers were produced at basal nodes and pistillate flowers at more distal nodes. Basally located staminate flowers, however, did not necessarily reach anthesis before distal pistillate flowers. For example, in WBN illustrated in Fig. 3, seven pistillate flowers were produced at nodes 2–5 and 13–15 before appearance of the first staminate flowers at nodes 8 and 9. For flowers of similar sex, however, node number was positively correlated with time of flowering.

In the vine *C. moschata* parental cultivars, plants usually produced one flower per node (Fig. 3). On the other hand, the bush *C. maxima* breeding line NH65 sometimes produced multiple staminate flowers at one node (Fig. 3). In NH65 and the cultivars LIC and DF, pistillate flowers were separated by four or five nodes, a typical flowering pattern in *Cucurbita* species (Loy, 2004), whereas WBN produced pistillate flowers at several consecutive nodes, beginning as early as

Fig. 2. Successive mean internode lengths (cm) in the interspecific hybrids NH65xLIC (left) and NH65xDF (right) and the respective parental cultivars. Values ($\pm$ SD) are means of six plants.

Table 1. Leaf numbers at 14, 27, and 42 d after transplant (DAT) and rates of leaf initiation between 14–27 DAT and 27–42 DAT in interspecific hybrids NH65xLIC and NH65xDF and parental cultivars grown in the greenhouse in 2011.

Cultigen	Leaf no. ^z			Rates of leaf initiation (lvs/d)	
	14 DAT	27 DAT	42 DAT	14–27 DAT	27–42 DAT
NH65	4.0 $\pm$ 0.0	9.0 $\pm$ 0.9	19.0 $\pm$ 0.9	0.38	0.67
LIC	3.3 $\pm$ 0.5	8.8 $\pm$ 1.0	18.8 $\pm$ 1.6	0.43	0.67
DF	3.4 $\pm$ 0.5	7.7 $\pm$ 1.1	17.5 $\pm$ 2.0	0.33	0.65
NH65xLIC	2.2 $\pm$ 1.2	7.3 $\pm$ 2.1	16.7 $\pm$ 2.3	0.39	0.63
NH65xDF	3.5 $\pm$ 0.5	7.3 $\pm$ 0.8	18.2 $\pm$ 1.8	0.39	0.72

^zValues $\pm$ SD represent means of six plants.

Table 2. Days after transplant (DAT) to first pistillate flower, the number of leaves on the main stem, average leaf area of individual leaves, and cumulative leaf areas measured at anthesis of the first pistillate flower for the interspecific hybrids NH65xLIC and NH65xDF and parental cultivars grown in the greenhouse in 2011.

Cultigen	DAT	No. leaves	Avg leaf area (cm ²) ^z	Cumulative leaf area (cm ²)
NH65	34.3 a ^y	13.3 a	780	10,455 a
LIC	39.3 ab	16.2 ab	847	13,724 ab
DF	50.0 c	23.0 c	677	15,357 ab
NH65xLIC	38.3 ab	14.0 ab	813	11,437 ab
NH65xDF	42.3 b	18.0 bc	895	16,279 b
HSD _{0.05}	6.3	4.2	NS	5,182

^zValues estimated as the product of leaf blade width by leaf blade length.

^yValues represent means of six plants. Values within columns followed by the same letter are not significantly different according to Tukey's test ($P \leq 0.05$).

Fig. 3. Representative flowering patterns in interspecific hybrids and parental lines. Top row (left to right): NH65, and cultivars WBN, LIC, and DF. Bottom row (left to right): NH65xWBN, NH65xLIC, and NH65xDF. Numbers beside pistillate (●) and staminate (○) flowers represent time of anthesis in days after transplant.

Table 3. Node location of the first pistillate flower, commencement of pistillate (P) and staminate (S) flowering in days after transplant (DAT), and total pistillate and staminate flowers in the interspecific hybrids NH65xLIC and NH65xDF and parental cultivars at 56 DAT. Plants were grown in the greenhouse in 2011.

Cultigen	Node	DAT		Total flowers		P:S
		P	S	P	S	
NH65	9.8 ^a	34.3 a	36.8 a	3.8 b	16.2 c	0.2
LIC	11.0	39.3 ab	43.5 b	2.7 ab	9.0 b	0.3
DF	19.0	49.9 c	46.3 bc	1.3 a	9.5 b	0.1
NH65xLIC	10.3	38.3 ab	—	1.7 a	0.0 a	—
NH65xDF	14.2	42.3 b	50.6 c	2.7 ab	1.8 a	1.5
HSD _{0.05}	—	6.3	5.2	1.7	3.9	—

^aValues (means of six replicates) within columns followed by the same letter are not significantly different according to Tukey's test ($P \leq 0.05$).

node 7 (Fig. 3). However, one NH65 plant produced pistillate flowers as frequently as every two nodes, and sometimes produced flowers of both sexes from the same node (not shown). The cultivar DF produced numerous basally located staminate flowers both before and after more distally located pistillate flowers reached anthesis (Fig. 3).

Flowering patterns differed among the interspecific hybrids and reflected the flowering tendencies of the male *C. moschata* parent. For example, the strong pistillate flowering pattern in WBN was expressed in NH65xWBN, whereby plants produced successive pistillate flowers from basal nodes beginning as early as node 2, often followed

by consecutive staminate flowers and then additional pistillate flowers from more distal nodes (Fig. 3). The hybrid NH65xLIC did not produce staminate flowers, but pistillate flowers were produced much later than in NH65xWBN, beginning at nodes 9–11 (Fig. 3). Hybrid NH65xDF produced pistillate flowers similarly to NH65xLIC, but also occasionally staminate flowers on nodes between the pistillate flowers that reached anthesis much later (Fig. 3).

Main stem development, field. Quantitative data on stem thickness were not taken in the field during the summer of 2011, but as in the greenhouse study, bush plants of NH65 (*C. maxima*) were observed during early growth to have extremely thick main stems. Nonetheless, bush main stems eventually vined out and appeared phenotypically similar to those of the vine processing cultivar GD, but with shorter internodes. Main stems of both GD and NH65 were thicker and more succulent than stems of the *C. moschata* cultivars DF and LIC. In the interspecific hybrids, main stems resembled those of the *C. moschata* cultivars but were slightly thicker.

At 45 DAT, mean main stem length in GD was 280 cm (not shown), compared with 210 cm in LIC, 148 cm in DF, 161 cm in NH65xLIC, and 173 cm in NH65xDF (Fig. 4). Main stem length in the hybrids resembled the bush parent until 30–34 DAT, but progressive and rapid increase in elongation of internodes resulted in main stem lengths in NH65xLIC and NH65xDF approaching or exceeding those of the respective vine parents by 45 DAT (Fig. 4).

Lateral shoot development, field. The main shoot in the bush parent NH65 was highly dominant, and plants produced only short lateral shoots (not shown). Figure 5 depicts representative growth habits of the interspecific hybrids NH65xLIC and NH65xDF and the vine parental cultivars. The vine parent LIC produced between three and four laterals of substantial length, followed by a few short to moderately long laterals, all located near the base of the plant (Fig. 5). Branching was more pronounced in DF plants, which produced up to five long lateral shoots from basal nodes and a few shorter branches about midway along the main shoot (Fig. 5). The interspecific hybrid NH65xLIC produced a dominant main stem, on average several internodes longer than in either LIC or DF, but with less lateral development, usually characterized by one or two lateral vines of moderate length near the plant base and several short lateral shoots along the length of the main shoot (Fig. 5). Hybrid NH65xDF plants not only produced a long main stem, but also the most lateral branches of all cultigens observed, with numerous moderately long to long shoots distributed along the main stem for some distance from the plant base (Fig. 5).

Petiole length and canopy height, field. Petiole length and canopy height differed substantially among interspecific hybrids and processing cultivars (Table 4). Petiole lengths for leaves initiated from the first 10

Fig. 4. Mean main stem length (cm) in the interspecific hybrids NH65xLIC (left) and NH65xDF (right) and the respective parental cultigens by days after transplanting in field plots in 2011. Values ($\pm$ SD) represent means of four randomly selected plants in each of four blocks in NH65xDF, DF, and NH65xLIC, six plants in NH65 and four plants in LIC.

nodes of plants averaged 67.9 cm in NH65xLIC and 71.9 cm in NH65xDF, while petiole length in GD and DF was 44.5 and 47.3 cm, respectively. LIC displayed similar petiole lengths and canopy height to DF, but no data were taken. Long petioles in interspecific hybrids translated to leaf canopy heights of 111.2 cm in NH65xLIC and 116.4 cm in NH65xDF, compared with canopy heights of 60.5 cm in GD and 83.5 cm in DF. Once interspecific hybrids began to vine out beyond nodes 9–11, leaf petiole lengths were reduced correspondingly to between 15 and 25 cm, only marginally longer than the vining cultivars.

Leaf size, field. There were significant differences in leaf size among cultigens; however, leaf areas varied within cultigens depending on the stage of plant growth (Table 5). For example, area of the fully expanded fourth main stem leaf in GD was 284 cm², significantly larger than that of all other cultigens. In DF plants, area of the fourth main stem leaf was 116 cm², and in hybrids NH65xLIC and NH65xDF areas were 197 and 232 cm², respectively (Table 5). As vines began running off of raised beds and between plant rows (after 10–12 nodes), leaf areas for NH65xLIC (1918 cm²) and NH65xDF (1668 cm²) were about double those of GD (881 cm²) and DF (826 cm²), and these relative differences remained throughout development. The large leaf size in mature interspecific hybrid plants was comparable with that of the bush parent NH65 (1603 $\pm$ 219 cm²; not shown in Table 5).

Flowering habit, field. Pistillate flower production preceded staminate flower production in the *C. maxima* processing cultigen GD and in the interspecific hybrids NH65xLIC and NH65xDF during the summer of 2011 (data not shown). In GD plots, pistillate flowering commenced at 35 DAT and staminate flowers appeared at 40 DAT. Pistillate flowering commenced at 37 and 33 DAT in NH65xLIC and NH65xDF, respectively. The hybrid NH65xLIC initiated staminate flower

buds, but all senesced before anthesis. In NH65xDF, plants produced several staminate flowers after 50 DAT, but the anthers were shriveled, lacked pollen, or both. In plots of the processing *C. moschata* cultivar DF, staminate flowers appeared at 43 DAT, whereas pistillate flowering commenced at 51 DAT.

The first pistillate flowers in GD, NH65xLIC, and NH65xDF were located between nodes 7–9, and in GD, and these early pistillate flowers resulted in fruit set near the plant base. On the other hand, in NH65xLIC, the first pistillate flowers failed to develop normal ovaries and senesced within 1 week after anthesis. In NH65xDF, fruit that set early were misshapen, but developed to a moderate size before aborting between 10 and 14 d after anthesis. In addition, some fruit produced later in development in NH65xDF senesced even after reaching full size but before harvest. In the interspecific hybrids, fruit that reached maturity developed from pistillate flowers initiated at $\approx$ 45–50 DAT, whereas fruit set in DF occurred later, between 50 and 60 DAT.

Discussion

In the present study, several horticultural traits associated with plant architecture and productivity were compared in interspecific hybrids, parental lines, and traditional processing squash cultivars, including growth rates, flowering patterns, and branching patterns. Because the interspecific hybrids were derived from a bush *C. maxima* breeding line crossed to vine *C. moschata* cultivars, they were expected to express a phenotype intermediate to the bush and vine growth habits. In plants heterozygous for the *Bu* gene and often referred to as semibush, plants initially display a bush growth habit, followed by successively longer internodes and a more spreading growth habit typical of vine plants (Denna and Munger, 1963; Zack and Loy, 1981), a phenomenon that Shifriss (1947) labeled “developmental reversal of

dominance.” In the present study, interspecific hybrids displayed this phenotype in both the greenhouse (Fig. 1) and field (Fig. 4) due primarily to a progressive lengthening of internodes during development. Lengths of internodes one through six or seven were short, resembling those of the *C. maxima* bush parent. This was followed by rapid expansion, and by internodes 10 or 11, lengths approached those of the vine cultigens (Fig. 2). The differences in internode length and stem elongation between a bush line and semibush hybrids were almost identical to that reported in a comparison of growth of a bush *C. maxima* processing strain (NH30-11-26-6) related to NH65 and a *C. maxima* hybrid resulting from NH30-11-21-6 crossed to the vine cultivar Pink Banana (Zack and Loy, 1981). It was shown further that fruit development suppressed subsequent leaf initiation in the bush strain but not the semibush hybrid. In the present study, continued vegetative growth late into the growing season was evident in the semibush interspecific hybrids as indicated by the large number of main stem internodes that surpassed those of even the vine cultivars (Fig. 5).

All of the interspecific hybrids we have evaluated to date are highly gynoeious, agreeing with previous reports (Castetter, 1930; Erwin and Haber, 1929; Robinson et al., 1978). Nonetheless, node location of the first pistillate flower, numbers of pistillate flowers, and presence or absence of staminate flowers on interspecific hybrids is highly dependent on parentage and appears especially dependent on the flowering habit of the male, *C. moschata* parent (Uretsky, 2012). In a greenhouse study (Loy and Uretsky, 2010), WBN initiated female flowers 2 weeks before staminate flowering and produced more pistillate than staminate flowers. When used as a male parent in producing interspecific hybrids with bush *C. maxima* lines as female parents, the interspecific hybrids were highly gynoeious and produced successive pistillate flowers as early as node 2 or 3 both in the greenhouse and field (Uretsky, 2012). In the field, this flowering pattern resulted in development of numerous fruit near the crown of plants and a consequent reduction in vine and leaf canopy development as compared with plants with later fruit set, presumably because of competition for photosynthate between vegetative and reproductive organs (Wien, 1997). In the present study, the processing cultivars LIC and DF produced more staminate than pistillate flowers, and pistillate flowering appeared later than staminate flowers in DF (Table 4). In the greenhouse, hybrids using these parents produced pistillate flowers at much later node numbers than NH65xWBN, resulting in a much greater leaf area and photosynthetic capacity at time of appearance of first pistillate flower (Table 3). Thus, flowering habit appears to be a crucial criterion in selecting *C. moschata* parents for developing productive interspecific hybrids.

The bush gene or genes affect not only internode lengths but the entire architectural phenotype in squash plants. Other traits

Fig. 5. Representative branching habit in ‘Long Island Cheese’ (*C. moschata*, top left), NH65xLIC (*C. maxima* x *C. moschata* ‘Field’ (*C. moschata*, bottom left), and NH65xDF (*C. maxima* x *C. moschata*, bottom right). Numbers indicate node of initiation on main stem followed by nodes per shoot in parentheses.

Table 4. Petiole length (cm) and canopy height (cm) in the interspecific hybrids NH65xLIC and NH65xDF and processing cultivars Golden Delicious (GD, *C. maxima*) and Dickinson Field (DF, *C. moschata*), measured within 10 nodes of the base of plants. Plants were grown in the field in 2011.

Cultigen	Petiole (cm)	Canopy (cm)
GD	44.5 ± 5.5 a ^z	60.5 ± 2.2 a ^z
DF	47.3 ± 5.8 a	83.5 ± 6.4 b
65xLIC	67.9 ± 8.7 b	111.2 ± 14.1 c
65xDF	71.9 ± 4.2 b	116.4 ± 9.7 c
HSD _{0.05}	13.9	19.1

^zValues (±SD) represent mean of four replicates in four blocks arranged in a randomized complete block design. Values within columns followed by the same letter are not significantly different according to Tukey’s test ($P \leq 0.05$).

associated with the bush growth habit include thicker main stems with reduced tendril production, longer petioles contributing to an

Table 5. Estimated areas (cm²) of fully expanded fourth, tenth, and mature leaves on the main stem in the interspecific hybrids NH65xLIC and NH65xDF and standard processing cultivars Golden Delicious (GD, *C. maxima*) and Dickinson Field (DF, *C. moschata*) grown in the field in 2011.

Cultigen	Fourth leaf	10th leaf	Mature leaf
GD	284 ± 66 c ^z	754 ± 117 b ^z	881 ± 98 a ^z
DF	116 ± 29 a	412 ± 56 a	826 ± 66 a
NH65xLIC	197 ± 23 bc	981 ± 85 c	1,918 ± 128 c
NH65xDF	232 ± 12 ab	1,028 ± 39 c	1,668 ± 86 b
HSD _{0.05}	84	191	109

^zValues (±SD) represent means of four randomly selected plants in four blocks arranged in a randomized complete block design. Values within columns followed by the same letter are not significantly different according to Tukey’s test ($P \leq 0.05$).

upright canopy, cupped leaf morphology and, often, earlier flowering (Broderick, 1982; Denna and Munger, 1963; Loy, 2004). In the present study, interspecific hybrids displayed not only thicker stems and longer petioles during early development than the *C. moschata* parental lines (Table 4), but also

larger leaves (Table 5), an apparent dominant trait contributed by the *C. maxima* bush parent.

Leaf numbers on the main stem among the processing cultigens and the interspecific hybrids were not significantly different under greenhouse conditions (Table 1). However,

as pointed out by Wareing and Patrick (1975), plant growth and photosynthetic capacity are determined not only by rates of leaf initiation but also by degree of branching or number of shoot meristems and by rate of leaf expansion and final leaf size. There were appreciable differences in growth patterns and branching habits among the *C. moschata* processing cultivars and the interspecific hybrids (Fig. 5), but it is not easy to draw conclusions as to which plant architecture is most efficient based on patterns of lateral branching and leaf numbers. Most of the major secondary lateral branches in the cultivars LIC and DF occurred close to the base of plants and were often over 20 nodes in length (Fig. 5), suggesting that such a pattern of development would contribute to early canopy development. By contrast, NH65xLIC had several laterals distributed for some distance along the main stem, but the laterals tended to be short (5–15 nodes; Fig. 5). Plants of NH65xDF had the greatest capacity for leaf development, having numerous branches, with many longer than 20 nodes (Fig. 5). Based on branching habit and length of lateral branches as judged from a small sample of plants, the two vining cultivars appear relatively more efficient at producing leaves than NH65xLIC, but less efficient than NH65xDF. On the other hand, leaf areas of both interspecific hybrids were about twice that of the vining cultivars, and initial growth was more uniform and the leaf canopy denser because of shorter internodes. Because of these morphological differences and the more random orientation of prostrate vines in the vining cultivars, full leaf canopy development appeared much later in the vining cultivar DF (Fig. 6A) than in either of the semibush hybrids (Fig. 6B and C). Rapid development of the leaf canopy and attainment of optimum leaf area indices are developmental features that contribute to more efficient light interception (Shibles and Weber, 1965, 1966) and, in turn, greater photosynthetic efficiency and crop growth rate (Brougham, 1958; Gifford and Jenkins, 1982). In addition, the pattern of early compact growth followed by more vining growth in interspecific hybrids allowed for effective weed control by mechanical cultivation before leaf canopy cover between the mulched beds.

Differences in growth habit among the processing cultivars may affect optimum planting densities for maximizing fresh weight yield. The field planting density used in 2011 (2.4 m row spacing and 0.6 m between plants) was within the range of densities reported for high productivity of squash (Botwright et al., 1998; Loy and Broderick, 1990), but within-row spacing may have been too close for the vigorous interspecific hybrids. It was observed that the first fruit set in the interspecific hybrids at this spacing often abscised after initial development, and in NH65xDF, some fruit were highly misshapen. High plant populations have previously been noted as producing small and misshapen fruit in a bush processing squash (Broderick, 1982), and

Fig. 6. Leaf canopy development in (A) 'Dickinson Field', (B) NH65xDF, and (C) NH65xLIC at 44 d after transplanting (DAT).

high plant populations in kabocha squash (*C. maxima*) result in excessive pistillate flower abortion (Botwright et al., 1998). Excessive canopy development and shading has been shown to have an adverse effect on fruit set in *Cucurbita pepo* (Wien et al., 2002), but poor pollination can also lead to abortion of early fruit (Stephenson et al., 1988). Interspecific hybrids used for commercial squash production require a pollenizer cultivar, usually a *C. maxima* cultivar, occupying 10% to 20% of the cultivated area (de Mendonça, 2006). In the present study, the pollen source was provided by a variety of *Cucurbita* cultigens planted adjacent to the experimental plots and presumed to be sufficient. In a 2012 field study of productivity among interspecific hybrids and a processing strain of *C. moschata* (Uretsky and Loy, 2013), within-row spacing was increased from 0.6 to 0.9 m. Fruit set in interspecific hybrids did not appear to be an issue, and the plant morphology of interspecific hybrids resulted in a rapid leaf canopy development and high fresh weight fruit yields.

Literature Cited

- Botwright, T., N. Mendham, and B. Chung. 1998. Effect of density on growth, development, yield and quality of kabocha (*Cucurbita maxima*). *Austral. J. Expt. Agr.* 38:195–200.
- Broderick, C.E. 1982. Morpho-physiological factors affecting plant productivity in bush and vine forms of winter squash (*Cucurbita maxima* Duch.). PhD Dissertation. University of New Hampshire, Durham. 8227426.
- Brougham, R.W. 1958. Interception of light by the foliage of pure and mixed stands of pasture plants. *Austral. J. Agr. Res.* 9:39–52.
- Castetter, E.F. 1930. Species crosses in the genus *Cucurbita*. *Amer. J. Bot.* 17:41–57.
- Davis, A.R., P. Perkins-Veazie, Y. Sakata, S. López-Galarza, J.V. Maroto, S.G. Lee, Y.C. Huh, Z. Sun, A. Miguel, S.R. King, R. Cohen, and J.M. Lee. 2008. Cucurbit grafting. *Crit. Rev. Plant Sci.* 27:50–74.
- Denna, D.W. and H.M. Munger. 1963. Morphology of the bush and vine habits and the allelism of the bush genes in *Cucurbita maxima* and *C. pepo* squash. *Proc. Amer. Soc. Hort. Sci.* 82:370–377.
- Erwin, A.T. and E.S. Haber. 1929. Species and varietal crosses in *Cucurbita*. *Iowa State Agr. Exp. Sta. Bull.* 263:344–371.
- Gifford, R.M. and C.L.D. Jenkins. 1982. Prospects of applying knowledge of photosynthesis towards improving crop production, p. 419–457. In: J.D. Hesketh, J.T. Woolley, and D.B. Peters (eds.). *Photosynthesis: Development, carbon metabolism, and plant productivity*. Academic Press, New York, NY.
- Howell, J.C., A.R. Bonanno, R. Hazzard, and M.B. Dicklow. 2010–2011. 2010–2011 New England vegetable management guide. Univ. Massachusetts Extension Office of Marketing and Communications, Amherst, MA.
- Loy, J.B. 2004. Morpho-physiological aspects of productivity and quality in squash and pumpkins (*Cucurbita* spp.). *Crit. Rev. Plant Sci.* 23:337–363.
- Loy, J.B. 2012. Breeding squash and pumpkins, p. 93–139. In: Y.H. Wang, K. Behera, and C. Kole (eds.). *Genetics, genomics, and breeding of cucurbits*. CRC Press, New York, NY.
- Loy, J.B. and C.E. Broderick. 1990. Growth, assimilate partitioning, and productivity of bush and vine cultivars of *Cucurbita maxima*, p. 436–447. In: D.M. Bates, R.W. Robinson, and C. Jeffrey (eds.). *Biology and utilization of the Cucurbitaceae*. Cornell Univ. Press, Ithaca, NY.
- Loy, B. and J. Uretsky. 2010. Vegetative growth in bush *Cucurbita maxima* x vine *Cucurbita moschata* interspecies hybrids, p. 105–108. In: J.A. Theis, S. Kousik, and A. Levi (eds.). *Cucurbitaceae 2010 Proc. Amer. Soc. Hort. Sci.*, Alexandria, VA.
- de Mendonça, R.U., F.X. Mangan, M. Moreira, S. Criswell, S. del Vecchio Nunes, and W.R. Autio. 2006. Adaptation of tropical pumpkin cultivars (*Cucurbita* spp.) for production in the northeastern United States. *Proc. Interamer. Soc. Trop. Hort.* 50:1–6.
- Robinson, R.W. 2000. Rationale and methods for producing hybrid cucurbit seed, p. 1–47. In: A.S. Basra (ed.). *Hybrid seed production in vegetables: Rationale and methods in selected crops*. The Haworth Press, Inc., New York, NY.
- Robinson, R.W., M.A. Boettger, and J.W. Shail. 1978. Gynoeious sex expression in *Cucurbita* resulting from an interspecific cross. *Cucurbit Genet. Coop. Rpt.* 1:31–32.
- Shibles, R.M. and C.R. Weber. 1965. Leaf area, solar radiation interception and dry matter production in soybeans. *Crop Sci.* 5:575–577.
- Shibles, R.M. and C.R. Weber. 1966. Interception of radiation and dry matter production by different soybean planting patterns. *Crop Sci.* 6:55–59.
- Shifriss, O. 1947. Developmental reversal of dominance in *Cucurbita pepo*. *Proc. Amer. Soc. Hort. Sci.* 50:330–346.
- Stephenson, A.G., B. Devlin, and J.B. Horton. 1988. The effects of seed number and prior fruit dominance on the pattern of fruit production in *Cucurbita pepo* (zucchini: squash). *Ann. Bot.* 62:653–661.
- Uretsky, J. 2012. Development and evaluation of interspecific *Cucurbita maxima* x *Cucurbita moschata* hybrids for processing squash. MS Thesis, University of New Hampshire, Durham, NH. 1518016.
- Uretsky, J. and B. Loy. 2013. Interspecific processing hybrids of *Cucurbita maxima* x *Cucurbita moschata* display high biomass yields. *HortScience* 48:S7 (abstr.).
- Wareing, P.F. and J. Patrick. 1975. Source-sink relations and the partitioning of assimilates in the plant, p. 481–499. In: J.P. Cooper (ed.). *Photosynthesis and productivity in different environments*. Cambridge Univ. Press, Cambridge, England.
- Whitaker, T.W. 1960. Breeding squash and pumpkins. *Sonderdruck aus Handbuch der Pflanzenzüchtung* 4:331–351.
- Whitaker, T.W. and G.W. Bohn. 1950. The taxonomy, genetics, production and uses of the cultivated species of *Cucurbita*. *Econ. Bot.* 4:52–81.
- Wien, H.C. 1997. Correlative growth in vegetables. In: H.C. Wien (ed.). *The physiology of vegetable crops*. CAB International, Cambridge, UK.
- Wien, H.C., S.C. Stapleton, D.N. Maynard, C. McClurg, R. Nyankanga, and D. Riggs. 2002. Regulation of female flower development in pumpkin (*Cucurbita* sp.) by temperature and light, p. 307–315. In: D.N. Maynard (ed.). *Cucurbitaceae 2002 Proc. ASHS Press*, Alexandria, VA.
- Zack, C.D. and J.B. Loy. 1981. Effect of fruit development on vegetative growth of squash. *Can. J. Plant Sci.* 61:673–676.