A review of the importance of spines for pejibaye heart-of-palm production

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Abstract

Commercial plantations of pejibaye (\textit{Bactris gasipaes} Kunth, Palmae) are expanding in tropical America to supply the heart-of-palm market. The heart-of-palm is a gourmet vegetable composed of the tender unexpanded leaves in the palm’s crown. Both spiny and spineless germplasm is available to growers, but there are no clear data on the superiority of either. Comparisons made among populations, among progenies within populations or among alleles within progenies are of interest for different reasons. In Hawaii, the Yurimaguas population (93\% spineless; Pampa Hermosa landrace) is superior in heart-of-palm weight at one site and the Benjamin Constant (BC) population (79\% spineless; Putumayo landrace) at another. Within the BC population there is a tendency for spineless plants to be superior in heart weight at one site and spiny to be superior at another. Within BC progenies, spineless plants often have more off-shoots at both sites, but superiority of spineless or spiny in terms of relative growth rates, heart weight and total edible weight depends upon location and seldom exceeds 10\%. Although these yield components have low heritabilities there is variation amenable to selection, so that selecting within spineless germplasm should provide gains similar to those for spiny germplasm. Which is better is not a biological question but must be answered based upon comparative costs (management of spiny plants costs marginally to much more) and availability of germplasm at a given location. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: \textit{Bactris gasipaes}; Peach palm; Yields; Growth rate; Suckering

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1. Introduction

The pejibaye (*Bactris gasipaes* Kunth) heart-of-palm agroindustry is expanding rapidly throughout tropical America (Mora Urpí et al., 1997). Costa Rica has 10,000 ha and Brasil has 6000 ha in production (Bovi, 1997), and in Bolivia, Colombia, Ecuador, Nicaragua, Panama, Peru, and Venezuela small farmers and agroindustrialists are planting. The Costa Rican plantations use mostly spiny germplasm, while in Brasil the agroindustry developed only after spineless germplasm sources were found. Both growers and researchers often ask ‘are spiny pejibayes better than spineless ones for heart-of-palm production?’ The objectives of this paper are to identify and contrast the various possible comparisons, review the evidence presented to date and provide some new evidence to answer the question in one population of pejibaye.

The pejibaye is a caespitose (suckering), tall, spiny palm and is the only palm domesticated in the Neotropics (Clement, 1988, 1992). Although the native peoples of northwestern South America and southern Central America domesticated it for its fruit, today it is most widely planted for its heart-of-palm. The heart-of-palm is a gourmet vegetable extracted from the crown of the palm and is composed of the tender immature leaves above the apical meristem. These are enveloped in the tender petiole sheath of the expanding spear leaf (the newest unopened leaf in the crown). The heart is a creamy white cylinder of variable length that can be used fresh or, more commonly, processed in acidified brine (Mora Urpí et al., 1997). Fresh heart-of-palm was enthusiastically accepted by gourmet chefs in Hawaii when introduced and is thought to have greater market potential than the processed heart (Clement et al., 1996), although the latter is more widely known and available today.

A typical Latin American pejibaye heart-of-palm orchard contains 3000–6000 plants per hectare, each plant forming a clump with two to four stems. Seedlings start to sucker 4–8 months after planting and a plant may produce 0 to 18 suckers. Each sucker in turn produces more suckers, thus guaranteeing the perpetuation of the clump and making heart-of-palm production sustainable without replanting. Plantation density and sucker number can be managed to produce the desired heart-of-palm diameter at harvest: high density plantings with numerous suckers produce small hearts, similar in size to asparagus shoots; low density plantings with few suckers produce large hearts (3–5 cm), for which there is a strong demand in Latin American barbecue restaurants (Mora Urpí et al., 1997).

Wild pejibaye are spiny, but three important ‘spineless’ pejibaye populations exist as a result of domestication by Amerindians: Yurimaguas, Loreto, Peru (Pampa Hermosa ‘mesocarpa’ landrace), with 60–80% spineless plants; San Carlos, Alajuela, Costa Rica (Guatuso ‘mesocarpa’ landrace), with 15–30% spineless plants; and Benjamin Constant, AM, Brasil (Putumayo ‘macrocarpa’ landrace), with 15–25% spineless plants (Clement, 1997; Clement et al., 1988).
The variation in the percentage of spineless plants within populations reflects differences in expression due to genetic and environmental influences. There are numerous other populations, especially in western Amazonia, with lower percentages of spineless plants.

There are two major commercial sources of seed for establishing heart-of-palm plantations. Costa Rican seed producers sell mostly spiny Occidental pejibaye germplasm of the Utilis or Guatuso landraces, while Peruvian seed merchants sell mostly spineless Amazonian germplasm of the Pampa Hermosa landrace. There are also some seed merchants and producers in Brasil, Colombia and Ecuador selling local germplasm.

In commercial high density orchards, spines are a physical and economic liability, increasing the cost of production by hindering maintenance, principally clump pruning, and harvesting — manual operations requiring a long machete and leather gloves, leggings and boots to protect the worker. Nevertheless, growers and even researchers often say that spiny pejibayes yield better and are more vigorous and robust than spineless ones, both for fruit and for heart-of-palm. During the 4th International Congress on Pejibaye (Iquitos, Peru, 1991), such comments were often made, but never substantiated. Comparisons were seldom made between spiny and spineless plants within a single progeny. Rather, the comparison most frequently mentioned was among different populations with different percentages of spineless plants. Sometimes comparisons were further complicated by different locations.

The first published comparison (Bovi et al., 1992) reported a small negative correlation between spines and heart-of-palm weight in the unidentified Costa Rican germplasm grown in Ubatuba, São Paulo, Brazil. Villachica (1996) reported a 7% yield advantage of spiny over spineless pejibaye for heart-of-palm in Peru, without, however, providing details of the germplasm or the kind of analysis used to determine this advantage.

The various comparisons imply that spines confer biological superiority or vice versa. To get at biological superiority, however, the most basic genetic level must be examined, alleles for spininess, without the confounding effects of different locations, populations or genotypes within populations. This is the comparison of interest to the plant breeder, yet even it may be irrelevant to the grower unless the magnitude of the biological superiority is large enough. The grower must weigh yield against the costs of establishing, managing, harvesting, processing and marketing spiny or spineless germplasm. In each country and each company the costs will be different. In Costa Rica, for example, the costs of extra protective clothing are thought to be less than the perceived yield advantage of spiny germplasm, although there are no data to confirm this. In Hawaii, where pejibaye was introduced recently, farm liability insurance premiums would be astronomical if spiny germplasm were used (J. Mood, pers. comm., 1994), so even a large biological superiority of spiny germplasm could be irrelevant.
Nonetheless, the question requires an answer. This paper identifies the various comparisons, reviews the evidence presented to date and provides some new evidence to answer the question in one population of pejibaye. The kind of evidence used to answer the question is also examined.

2. Spines in pejibaye

Presence of spines is thought to be primitive in *Bactris* (Mora Urpí, 1984; Uhl and Dransfield, 1987), and for this reason spininess is thought to dominate spinelessness. Spines are present on most plant surfaces: stem, leaf petiole and rachis, leaflet mid-ribs, main veins and borders, and inflorescence spathe. Spines in *Bactris* are of the emergent type (Tomlinson, 1962; Uhl and Dransfield, 1987), so-called because they emerge from the epidermal tissue layer with no vascular trace, and hence they are not modified organs as in other palms. They emerge physically because of a pulvinule at their base, which lifts the spine’s point after enclosing tissues are removed; for example, when an older leaf senesces and falls, the spines pressed against the stem behind that leaf become erect. Spines are thought to have a defensive role, principally to protect the meristem (Tomlinson, 1962), although Mora Urpí (1984) suggested that they also help channel water away from the stem and thus inhibit epiphyte establishment.

Mora Urpí (pers. comm., cited by Kerr and Clement, 1980) suggested that the presence/absence of spines is a simple Mendelian trait, with various genes to modify its expression. Morera Monge (1981, 1989) reported that there are three classes of stem spine length, as well as significant variation in stem spine density, suggesting at least four genes to modify the stem spine trait. Clement (1986) reported that stem spine form also varies, with both sword-like and needle-like spines, as well as intermediate forms, suggesting at least one more gene. Leaf petiole spines vary in much the same way and also in arrangement along the petiole, with some plants presenting spines arranged in three lengthwise rows along the petiole and others with uniformly distributed spines (Clement, 1986).

Chávez Flores et al. (1990) studied the genetic structure of leaf spines in a sample of the Yurimaguas population grown in Manaus, AM, Brazil. Along with the variation previously observed, they found that the expression of petiole spine density changed with age in some plants, with older plants presenting fewer spines, suggesting yet another gene or gene complex modifying this trait. Petiole spine density presented a narrow-sense heritability of 0.35, while leaflet edge spines presented 0.25 and leaflet vein spines presented only 0.04. They found that additive genetic variances were quite low, probably because of long-term selection against spines by Amerindians followed by intensive recent selection to form the plantation studied.
Clement (1995) studied the genetic structure of leaf petiole spines in a sample of the BC population grown in Hawaii, USA. Not only did petiole spine density change with time, but different plants changed at different rates, suggesting yet another gene or gene complex modifying this trait. Petiole spine density presented narrow-sense heritabilities that ranged from 0 to 0.40, depending upon the half-sib progenies included in the analysis and the range of localities. There was good evidence that more stressful environments (especially with respect to water availability) enhanced spine density expression, resulting in plants with more spines. Petiole spine developmental expression presented narrow-sense heritabilities that ranged from 0 to 0.22 and plants in the more stressful environment were slower to develop the spineless condition.

The sum of these observations suggests that the degree of expression of stem and leaf spines is quantitatively controlled, with environment having a large effect upon phenotype. These observations do not question the recessiveness of spinelessness, which suggests that spineless plants are likely to be more homozygous than spiny plants and thus spineless plants may show inbreeding depression. This is the genetic basis for assuming that spineless plants may be less productive than spiny plants.

To examine this hypothesis, Clement (1995) looked for a positive correlation between alzyme heterozygosity (thought to reflect overall heterozygosity) and spine density in eight BC progenies in Hawaii, since a positive correlation would support the inbreeding depression hypothesis. Overall, the correlations were small, non-significant and negative (Table 1), although one progeny did present a significant negative correlation. The history of these progenies, however, precludes extrapolation of these results, because of high selection pressures that

Table 1
Correlations between progeny mean (±SD) alzyme heterozygosities and petiole spine densities\textsuperscript{a} in pejibaye (\textit{Bactris gasipaes}) of the BC population (Putumayo landrace) grown at Ninole, HI (Clement, 1995). Two mean correlations are presented: using all plants, as though there was only one population; using progeny means for each trait.

\begin{tabular}{lccccccccc}
\hline
 & 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & All & Prog. & mean \\
\hline
Heterozyg. & 0.112 & 0.052 & 0.032 & 0.091 & 0.077 & 0.091 & 0.078 & 0.077 & 0.077 & 0.077 & 0.077 & 0.077 & 0.077 & 0.077 \\
SD & 0.076 & 0.051 & 0.053 & 0.06 & 0.058 & 0.063 & 0.046 & 0.063 & 0.023 & 0.063 & 0.023 & 0.063 & 0.023 & 0.063 & 0.023 \\
Spine density & 0.93 & 1.60 & 1.70 & 1.27 & 1.62 & 1.43 & 2.52 & 1.58 & 1.58 & 1.58 & 1.58 & 1.58 & 1.58 & 1.58 & 1.58 \\
SD & 2.40 & 2.89 & 2.76 & 2.73 & 3.17 & 2.74 & 3.36 & 2.90 & 0.45 & 2.90 & 0.45 & 2.90 & 0.45 & 2.90 & 0.45 \\
r & 0.153 & 0.381 & -0.149 & 0.254 & -0.030 & -0.750\textsuperscript{b} & 0.073 & -0.024 & -0.436 & -0.024 & -0.436 & -0.024 & -0.436 & -0.024 & -0.436 & -0.024 & -0.436 \\
n & 19 & 25 & 15 & 23 & 13 & 17 & 29 & 141 & 7 & 141 & 7 & 141 & 7 & 141 & 7 & 141 & 7 \\
\hline
\end{tabular}

\textsuperscript{a} Petiole spine density was characterized on an ordinal scale (0–absent, 1–rare, 3–few, 5–moderate, 7–numerous, 9–spiny; Chávez Flores et al., 1990).

\textsuperscript{b} Significant at $p < 5\%$. 


resulted in extremely low heterozygosities \((H = 0.077 \pm 0.063; \text{Clement, 1995; Clement et al., 1997})\). Consequently, this subject merits further study in other populations.

3. **Spiny versus spineless**

There are several possible comparisons that involve spines: among populations, among spiny and spineless individuals within a population, and among spiny and spineless individuals within a progeny. Each is important to both growers and breeders.

3.1. **Between populations**

The comparison between populations is an important one, especially as the various seed sources currently available are essentially populations, rather than varieties or clones. Nonetheless, given that many traits affect yield, a population comparison does not give an unalloyed estimate of the influence of spininess alone on yield. Rather, it reflects population differences in a whole range of traits that adapt a given population to a given site.

In Hawaii, for example, the Yurimaguas population (93% spineless plants) yielded approximately 10% more heart-of-palm than the BC population (79% spineless plants) at Ninole, Island of Hawaii (Climate – Af, 3479 mm rainfall, no pronounced dry season, except during El Niño events; soil – Andisol, typic hydudand, pH 5.4, excellent drainage), but approximately 5% less than BC at Poamoho, Island of Oahu (Climate – Aw, 1078 mm rainfall, all months with water deficits so that supplemental irrigation is required; soil – Oxisol, rhodic eutrustox, pH 5.8, excellent drainage; Clement, unpublished data). These 5–10% differences are similar to the 7% mentioned by Villachica (1996) but vary in sign depending upon the location.

3.2. **Within populations**

The same weakness holds true for comparisons between spiny and spineless individuals within a population. Bovi et al.’s (1992) small negative partial correlation of \(-0.22\) between spininess and heart-of-palm weight yields a coefficient of determination \((r^2)\) of 0.05; in other words, spines accounted for only 5% of the variance in heart-of-palm weight in their population. Thus, the within-population comparison, while useful for selection of improved germplasm, cannot reveal differences attributable exclusively to spines.

Clement’s (1995) experiments with BC germplasm in Hawaii allow an estimate of the importance of spines within this population. Analysis of heart-of-palm
weight using petiole spines abundance (ordinal scale – 0, 1–9) as a covariate indicated that spines were a significant covariate at Ninole, but not at Poamoho (Table 2). Nonetheless, the coefficients of determination ($r^2$) were so minuscule that these equations explain no more of the variation in heart-of-palm weight than in the case studied by Bovi et al. (1992). At Ninole the relation between petiole spines and heart-of-palm weight was negative, as found by Bovi et al. (1992), but was positive at Poamoho, as found by Villachica (1996).

### 3.3. Within progenies

The comparison between spiny and spineless individuals within a progeny allows a better statement about the importance of spines with respect to yield of heart-of-palm, since the effects of locality, among- and within-populations variation, and among- and within-progenies variation can be at least partly accounted for. Within a half-sib progeny at least 50% of the variation comes from a known source — the seed (female) parent (Simmonds, 1979). Thus, the comparison is between two or more pollen sources (the male parents) that provide the genes for spininess and spinelessness. If several progenies are used, a range of pollen sources is examined over a range of maternal backgrounds, providing more information about the correlated effects of petiole spininess or spinelessness on yield. The ideal comparison, however, would be a set of full-sib progenies derived by hybridizing homozygote seed parents with heterozygote pollen sources. Unfortunately, these are not yet available, or at least no results have been published.

The simple question ‘which is better’ is normally answered ‘more heart-of-palm, of course!’ but should be answered ‘greater return on investment.’ Yield is involved in both answers, but is a complex trait that is significantly affected by

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**Table 2**
The importance of petiole spines as an explanation of pejibaye (*Bactris gasipaes*) heart-of-palm weight at two sites in Hawaii with BC (Putumayo landrace) germplasm, when spines are used as a covariate in an analysis of variance of heart-of-palm weight at each site

<table>
<thead>
<tr>
<th>Model</th>
<th>$F_{model}$</th>
<th>$t$-test of b</th>
<th>$p$ of $t$-test</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ninole</strong> b (n = 410)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heart wt = 181.9 – 1.86 Spines</td>
<td>4.59*</td>
<td>-2.14</td>
<td>0.033</td>
<td>0.005</td>
</tr>
<tr>
<td><strong>Poamoho</strong> c (n = 174)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heart wt = 197.0 + 2.12 Spines</td>
<td>1.79ns</td>
<td>1.34</td>
<td>0.183</td>
<td>0.002</td>
</tr>
</tbody>
</table>

a Petiole spines were characterized on an ordinal scale (0–9) (Chávez Flores et al., 1990).
b The Ninole experiment was a split-plot, with 3 densities as main-plots and 7 progenies as sub-plots, with 9 plants/plot, in a randomized complete block design with 3 replications.
c The Poamoho experiment was a randomized complete block with 6 progenies as treatments, with 9 plants/plot and 3 replications.
both genotype and environment (Simmonds, 1979). Genotypes respond differently in different environments, as observed above for the yield comparisons of Yurimaguas vs. BC populations and spiny vs. spineless individuals within the BC population at two sites in Hawaii. Additionally, yield of pejibaye heart-of-palm is only sustainable if there are enough suckers to guarantee regrowth after harvest. Clement (1995) suggested an ideotype for the BC population composed of spineless petioles, fast growth (= high relative growth rate – RGR (g/kg/day)), good sucker production and low acridity (acridity is the combination of calcium oxalate crystals with an activator enzyme that causes irritation to the mucous membranes of the mouth and throat). Heart-of-palm and total edible weight for the fresh market (total edible = heart + edible stem below heart + edible leaf above heart) were not included as a component in this ideotype because of low genetic variances, heritability equal to zero, and consequently high environmental influence, but will certainly be important with more diverse populations. Given this ideotype, evidence for the superior phenotype includes sucker number, RGR, and heart-of-palm or total edible weights. Yearly yield depends upon individual heart or total edible weights and plantation density, while decade yield (more appropriate for a sustainable plantation) depends upon sucker production, RGR, individual heart or total edible weights and plantation density.

Clement’s (1995) Hawaii dataset provides some evidence for the importance of spines. Mean values for spiny and spineless plants were contrasted at each site. At both Ninole and Poamoho the mean number of suckers (Table 3) tended to be greater in spineless plants than in spiny plants. This trend was statistically

Table 3
Percent differencea between spineless (0) and spiny (+) means (±SD) for the number of offshoots at harvest within 6 pejibaye BC (Putumayo landrace) progenies grown at Ninole and Poamoho Exp. Station, HI, between 1992 and 1995, with site means

<table>
<thead>
<tr>
<th>Spines</th>
<th>Progeny</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>5</th>
<th>8</th>
<th>9</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ninole</td>
<td>0</td>
<td>10.0 ± 2.5</td>
<td>9.0 ± 2.8</td>
<td>7.0 ± 2.2</td>
<td>9.9 ± 3.1</td>
<td>6.8 ± 2.8</td>
<td>7.7 ± 2.4</td>
<td>8.4 ± 1.3</td>
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<tr>
<td></td>
<td>+</td>
<td>9.5 ± 3.1</td>
<td>7.7 ± 2.3</td>
<td>6.9 ± 2.2</td>
<td>8.6 ± 3.1</td>
<td>6.1 ± 2.2</td>
<td>6.4 ± 2.6</td>
<td>7.5 ± 1.2</td>
</tr>
<tr>
<td></td>
<td>% diff.</td>
<td>5.1</td>
<td>16.5</td>
<td>0.7</td>
<td>5.4</td>
<td>12.9</td>
<td>19.5b</td>
<td>11.4</td>
</tr>
<tr>
<td>Poamoho</td>
<td>0</td>
<td>8.6 ± 2.1</td>
<td>8.6 ± 2.7</td>
<td>8.5 ± 2.2</td>
<td>10.1 ± 2.6</td>
<td>7.9 ± 1.7</td>
<td>8.7 ± 3.5</td>
<td>8.7 ± 0.7</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>9.3 ± 3.1</td>
<td>9.0 ± 1.4</td>
<td>7.3 ± 1.7</td>
<td>8.7 ± 3.8</td>
<td>7.1 ± 1.7</td>
<td>7.4 ± 2.1</td>
<td>8.1 ± 0.9</td>
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<tr>
<td></td>
<td>% diff.</td>
<td>−7.4</td>
<td>−4.9</td>
<td>17.2</td>
<td>16.8</td>
<td>9.9</td>
<td>17.4</td>
<td>7.3</td>
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</tbody>
</table>

a % difference = [(spineless – spiny) ÷ spiny] × 100; hence, differences that favor spineless have a positive sign and those that favor spiny have a negative sign.

b A t-test was used to compare the means of each progeny using all plants of the progeny at the site; n varied among progenies and among spiny and spineless within progenies.
significant at Ninole for one progeny, although two progenies at Poamoho presented the opposite trend. The mean differences between spiny and spineless plants were small, 7% at Poamoho and 11% at Ninole. High CVs explain why there were so few significant differences between spiny and spineless means within progenies.

At both sites, mean RGR was essentially the same for spiny and spineless plants (Table 4). At Poamoho, spiny plants tended to have slightly lower RGR than spineless plants, while at Ninole the opposite was the case. At both sites, at least one progeny presented a trend opposite to that of the mean. The mean differences between spiny and spineless plants were small, 1% at Poamoho and 2% at Ninole, and none was significant. These differences were much smaller than the difference between mean RGRs at Poamoho (~11.25 g/kg/day) and Ninole (~8.5 g/kg/day), equivalent to 32%.

At Poamoho, spiny plants tended to have heavier hearts-of-palm than spineless plants, while at Ninole the opposite trend occurred, with one progeny presenting significantly heavier hearts from spineless plants (Table 5). The mean differences in heart-of-palm weight between spiny and spineless plants were small, 9%, similar to the 7% reported by Villachica (1996). These differences were smaller than the difference between mean heart weights at Poamoho (~200 g) and Ninole (~175 g), equivalent to 14%. Total edible weights showed the same trends as heart-of-palm weights, with similar differences.

All of these components of yield were influenced more by location than by spines. Nonetheless, the influences were inconsistent, showing no obvious trend. Consequently, the presence or absence of spines has no consistent relationship
with heart-of-palm productivity in the BC progenies studied at Ninole and Poamoho. The same conclusion is probably true for populations also, as shown by the 6-progeny mean for each yield component, so that location will play a significant role in any decision relating to selection in pejibaye germplasm.

4. Variation in yield components with spininess

The reason that yield component means for spiny and spineless individuals within any given progeny had high CVs is that there was considerable within-progeny variation for each of the traits examined. Although Clement (1995) reported generally low heritabilities for yield traits, as well as low additive genetic variances and allozyme heterozygosity, there was still considerable phenotypic variation, suggesting that some gains can be obtained from selection and hybridization among the best plants, whether spiny or spineless.

One of the best BC progenies evaluated in Hawaii was number 9 (INPA 5.5.3). It was good at both Ninole and Poamoho, had a high proportion of spiny plants and is therefore a good progeny to show variation in the spiny and spineless groups within the progeny (Fig. 1). It is clear that there is as much variation within the spiny individuals as within the spineless in this progeny. Since heritabilities and allozyme heterozygositites were low, most of the variation observed must be attributed to experimental and micro-environmental variation (see Nyquist, 1991).

Table 5
Percent difference\(^a\) between spineless (0) and spiny (+) means (±SD) for heart-of-palm weight (g) at harvest within 6 pejibaye BC (Putumayo landrace) progenies grown at Ninole and Poamoho Exp. Station, HI, between 1992 and 1995, with site means

<table>
<thead>
<tr>
<th>Spines</th>
<th>Progeny</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>5</th>
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<td>Ninole</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>179 ± 52</td>
<td>168 ± 54</td>
<td>189 ± 52</td>
<td>201 ± 63</td>
<td>177 ± 62</td>
<td>179 ± 44</td>
<td>182 ± 11</td>
<td></td>
</tr>
<tr>
<td>+</td>
<td>148 ± 63</td>
<td>156 ± 49</td>
<td>176 ± 50</td>
<td>160 ± 55</td>
<td>178 ± 66</td>
<td>182 ± 49</td>
<td>167 ± 13</td>
<td></td>
</tr>
<tr>
<td>% diff</td>
<td>21.2</td>
<td>7.9</td>
<td>7.6</td>
<td>26.2 (^b)</td>
<td>-1.0</td>
<td>-1.7</td>
<td>9.4</td>
<td></td>
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</table>

| Poamoho |        |     |     |     |     |     |     |      |
| 0      | 197 ± 66 | 160 ± 49 | 215 ± 67 | 213 ± 64 | 203 ± 61 | 169 ± 83 | 193 ± 21 |
| +      | 205 ± 81 | 213 ± 69 | 205 ± 32 | 222 ± 68 | 231 ± 42 | 192 ± 52 | 211 ± 13 |
| % diff | -3.8 | -25.0 | 4.9 | -4.3 | -12.1 | -11.8 | -8.7 |

\(a\) % difference \(= [(\text{spineless} - \text{spiny}) \div \text{spiny}] \times 100\); hence, differences that favor spineless have a positive sign and those that favor spiny have a negative sign.

\(b\) A \(t\)-test was used to compare means of each progeny using all plants of the progeny at the site; \(n\) varied among progenies and among spiny and spineless within progenies.
Thus, while the response to selection in either spiny or spineless plants will be slow because of the low heritabilities and genetic variances, either group of plants within the progeny will provide a response. It follows, therefore, that continuing work with spineless germplasm is completely justified, rather than concentrating on spiny germplasm, as suggested by Villachica (1996). Imar C. Araújo (pers. comm., 1996) reports that two cycles of mass selection for off-shoot number in a very restricted sample of spineless Yurimaguas germplasm resulted in all plants with off-shoots (plants with no off-shoots are a frequent complaint about unselected Yurimaguas germplasm). The response obtained by Araújo is what would be expected if spineless germplasm were as viable as spiny germplasm for heart-of-palm improvement. Araújo is worried about fruit yield potential, however, since the Yurimaguas germplasm in his plantation is more susceptible to precocious fruit drop (see Couturier et al., 1991 for a description of this problem). Antonio N. Vieira (pers. comm., 1996) has decided that spininess is not an important negative criterion in his selections for heart-of-palm in BC germplasm in Acre, partly because of lower seed yields from the spineless plants.

5. Conclusions

‘Are spiny pejibayes better than spineless ones for heart-of-palm production?’ Biologically, spiny and spineless germplasm have approximately the same heart-of-palm yield potential, and the superiority of one or the other depends upon both genotype and environment; in other words, upon factors other than spines. Consequently, the simple question ‘which genotype, spiny or spineless, is better?’ cannot be answered with ‘the one that yields more heart-of-palm,’ because the biological answer to the question is ‘it depends upon your germplasm and where you are.’

Since the biological comparisons do not clearly resolve the above question, a more appropriate answer is ‘the one that yields greater return on investment.’ The grower must decide based upon local experiences with available germplasm and the relative costs of working with spiny plants when spiny versus spineless yields are so similar. Spineless plants are much easier to work with, which makes plantation installation, management and harvesting easier and certainly reduces worker discomfort and accidents with spines.

Selection for heart-of-palm, however, cannot ignore fruit yield, especially those components related to precocious fruit drop. Consequently, the answer for the seed producer may be different than for the heart-of-palm grower. There are clear indications that gains from selection are obtainable even in germplasm with a narrow genetic base, so that by combining selection for heart-of-palm criteria with good fruit yield criteria it should be possible to select high quality heart-of-palm germplasm that will satisfy both the grower and the seed producer.
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