

## Propagule quantity and quality in traditional Makushi farming of cassava (*Manihot esculenta*): A case study for understanding domestication and evolution of vegetatively propagated crops

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### Abstract

Modeling how crop plants evolve under domestication requires estimating among-plant variation in important parameters of the reproductive system, including fecundity – the number of propagules produced – and propagule quality. Measuring these traits poses particular problems in vegetatively propagated crop plants. Unlike seeds, vegetative propagules are not intrinsic biological entities but are prepared by farmers. Propagule number and quality are thus determined by the interaction between plant traits and how farmers prepare propagules. We conducted observations, interviews and experiments to study this interaction in cassava grown by Makushi Amerindians, examining how both sources of variation, in plant traits and in farmers' practices, combine to determine the number and quality of propagules produced. Increased stake mass, determined mostly by stem diameter, leads to increased yield and also to increased asexual 'fecundity' of the resulting plant. Farmers' practices reflect knowledge of this relationship. Diameter is the key criterion in the selection of stems for stakes. Larger diameters are preferred; when thinner stems are used, stakes are cut longer, partially compensating for reduced mass. These results suggest that conscious and unconscious selection to increase 'fecundity' and propagule quality in cassava would act to favor plants with thicker stems. Mean stem diameter is greater, and variation in stem diameter is lower, in little-branched plants. Selection for increased asexual 'fecundity' can thus have led to reduction in the degree of branching, one of the most striking differences between domesticated cassava and its wild ancestors. Measuring variation in asexual fecundity is a key step in analyzing evolution of the mixed clonal/sexual reproductive systems that characterize many vegetatively propagated crop plants.

### Introduction

Ever since Darwin, domesticated plants have served as biological models for studying many questions of broad interest in evolutionary biology. Virtually all examples of such service, however, concern plants propagated by seed, in

particular grain cereals and legumes (e.g., D'Ennequin et al. 1999; Gaut et al. 2000; Gepts 2004; Ross-Ibarra 2004). In most discussions of evolution under domestication, vegetatively propagated crop plants receive short shrift. One reason for this relative lack of attention is the belief that domestication of such plants is a less complex, and less

interesting, phenomenon. It is held (Zohary 1984, 2004) that domestication essentially consists of selection and clonal multiplication of a domesticated genotype, without the repeated cycles of recombination and selection that have allowed seed-propagated crop plants to assemble suites of traits adaptive in agricultural environments, the ‘domestication syndrome’. This view of domestication of vegetatively propagated plants as a simple process is belied by work showing that, in traditional agricultural systems likely to resemble in important respects the environments in which these plants initially evolved, many of them have mixed reproductive regimes in which sex continues to play an important role via the regular incorporation of volunteer seedlings (Johns and Keens 1986; Shigeta 1996; Elias et al. 2000b; Pujol et al. 2005a). Such systems should have enabled these plants to assemble numerous new adaptations, by unconscious as well as conscious selection. Some new traits of such plants – for example, seedling functional morphology of domesticated cassava, strongly divergent from that of its closest wild relatives (Pujol et al. 2005b) – are difficult to explain in any other way.

Progress in understanding the newly realized complexity of evolution under domestication in vegetatively propagated plants depends in part on modeling the dynamics of their mixed clonal/sexual reproductive systems. What are the respective contributions of sexual and asexual reproduction to the demography and genetics of crop populations? Do genotypes differ in their allocation of resources to each reproductive pathway? Do trade-offs exist between the two pathways? Answering such questions depends on having realistic estimates of values of important parameters for each of the two pathways.

One such parameter is fecundity. Asexual ‘fecundity’ may be defined as ‘multiplication potential’, i.e., the number of clonal propagules a mature plant can supply. For the sake of brevity, and to emphasize the necessity of integrating sexual and asexual processes in a common framework to quantify the demography of clonally propagated but sexually fertile crop plants, we will employ the term ‘asexual fecundity’, henceforth without quotation marks, throughout this paper.

In seed-propagated plants, quantifying fecundity is relatively straightforward: seeds are biological entities, embryonic plants that can be

unambiguously counted, weighed, and manipulated. In some cases, vegetative propagules are also treated as discrete units. For example, farmers of the Peruvian Andes do not cut potatoes into propagules, but make use of variation in sizes of seed tubers to underpin versatile economic and ecological strategies (Zimmerer 2003). Usually, however, vegetatively propagated plants pose a problem in defining fecundity. Propagules are prepared by dividing plant organs. Even organs that appear to be discrete, indivisible entities, such as potato tubers, bulbs, or the aerial bulbils of some yams (*Dioscorea* spp.), can be divided into multiple propagules. The size of each propagule, and thus the number of propagules a given plant produces, is determined by human actions. Asexual fecundity and characteristics of clonal propagules (e.g., their size) that affect their performance, are thus not intrinsic traits of the plant but rather the product of the interaction between how farmers prepare propagules and the plant traits that influence these decisions. It is thus important to understand farmers’ criteria for selection and preparation of vegetative propagules, and to integrate them into parameter estimates that can be used to model evolution of plants under mixed reproductive regimes.

These criteria are usually linked to farmers’ observations about factors that affect propagule success. Size of propagules is one such factor, being often positively related to the survival probability, growth rate, and yield of the resulting plant. Propagules of varying size may also be used to adapt to varying ecological conditions (Zimmerer 2003). Because size of each propagule affects the number of propagules that can be prepared from a plant, farmers’ decisions on how to divide plant organs in effect integrate the two determinants of reproductive success, fecundity and the probability of success of each propagule, in a way that is impossible in seed-propagated plants.

We focus here on cassava (*Manihot esculenta* Crantz, Euphorbiaceae). Cassava is an interesting and tractable plant for studying these questions because the organ used for vegetative propagation is not the organ consumed. In many clonally propagated crops (as in many seed-propagated crops), one plant part is used for both purposes. Because higher yield of the part in question often automatically increases the number of propagules that can be prepared from it, selection acting on

fecundity cannot be distinguished from that acting on yield. In cassava, however, the tuberous roots are eaten, but vegetative propagation is effected solely using stems cut into 'stakes'. Response of the plant to selection acting on parameters of clonal reproduction can thus be partly separated from its response to selection on other functions. One of the long-term objectives of our studies of cassava (Elias et al. 2000a, b, 2001a, b; Elias and McKey 2000; McKey et al. 2001; Pujol et al. 2002, 2005a, b; Pujol and McKey 2005) is thus to examine how conscious and unconscious human selection has influenced the evolution of asexual fecundity.

The first step is to know how farmers select and prepare clonal propagules. We also wished to determine how variation in propagule size affects success of the propagule, and how farmers incorporate their knowledge of such relationships in making decisions concerning the preparation of propagules. We focus here on the following questions: (1) What explicit criteria are employed in the selection and preparation of stakes? (2) How are these criteria reflected in the *actual practices* of selection and preparation of stakes? (3) What is the relationship between how stakes are prepared and the performance (yield, but also asexual fecundity) of plants resulting from them? Do criteria and/or practices in the preparation of stakes make sense? Of these questions, only the third has been the subject of much research (e.g., Oka et al. 1987; Keating et al. 1988; Raillaac 1992), and to the best of our knowledge our study is the first to consider all three simultaneously. Using data from our observations and experiments, we quantify both asexual fecundity and quality of clonal propagules, examine whether selection driven by farmers' practices could act to increase these two parameters, and discuss the plant traits that might evolve under such selection. Finally, we consider the implications of our results for analysis of the evolution of fecundity in other crop plants, and for the dynamics of the mixed clonal/sexual reproductive system of cassava.

## Materials and methods

### *Study site*

Our study was conducted in Rewa, a small Makushi community of the North Rupununi region in

Guyana. Geographical and ethnological details about the village are given in Elias et al. (2000b). Makushi are bitter cassava farmers (Makushi Research Unit 1996), and in Rewa they grow more than 76 local varieties (Elias et al. 2000b).

### *Preparation of stakes*

Information about criteria used in preparing stakes was obtained during interviews or (more frequently) during free discussions with farmers, especially when they were preparing stakes. Preparing stakes is mainly, but not exclusively, a female activity. In addition, 15 farmers (14 females and 1 male) were each provided with the entire aerial apparatus of at least five mature cassava plants, and asked to prepare stakes from their stems, as they would do if they intended to plant them. Material provided to each farmer thus included the entire range of stem diameters encountered on mature plants. To preserve anonymity of the farmers, we use in this paper gender-explicit pseudonyms. The stakes obtained from this experiment were then weighed, the length and diameter of each was measured, and the number of nodes (the Makushi call them 'eyes') was recorded. The most prominent features of 'eyes' are the leaf scar (petiole base) and the thickened areas found on either side of it, near the stipules. From the diameter we calculated the cross-sectional area ( $\pi \times (1/4) \times (\text{diameter})^2$ ). In all cases, fresh mass of the stake was highly correlated with its volume (the product length  $\times$  cross-sectional area).

When preparing stakes, farmers make two types of decisions: (1) which parts of the plant's entire branching stem system will be used for stakes, and which ones will be discarded, and (2) how long each stake will be. Our hypothesis was that these decisions might be influenced by intrinsic properties of the stem considered, such as its diameter and its density of nodes. Stem diameter should be important because thinner stems are more likely to dry out under water stress (Raillaac 1992). We thus postulated that farmers would discard stems below some minimal diameter. As determinants of stake volume, stem diameter and length (along with dry matter density and composition) determine the mass of reserves present in a stake, which is an important factor in survival, growth, and yield of stakes (Raillaac 1992). We thus predicted

that within the diameter range acceptable for stakes, farmers would compensate for differences in diameter by preparing longer stakes when dealing with relatively thin stems. We further considered that the number of nodes might be taken into account in the preparation of stakes, because above each node is an axillary bud, from which a shoot can grow. Also, located either side of the leaf scar are zones of meristematic activity that produce adventitious roots when the cutting is planted (Médard 1973; Rafaillac 1992). These roots increase the plant's capacity to assimilate water and nutrients, and also increase the number of potential sites where tubers are formed. The number of 'eyes' can thus affect survivorship, growth, and yield of the plant the stake produces (Rafaillac 1992). To test these predictions we performed for each farmer a multiple regression, using the length of stakes as dependent variable, and diameter and density of nodes as independent variables. Because the material provided to each farmer was not identical, testing for differences in the length, diameter, or number of nodes of stakes prepared by different farmers would serve no purpose. Instead, we compared how farmers treated the *relationship* between length and diameter, and that between stake length and density of nodes. We analyzed data to answer the following questions about the first relationship (and the analogous questions about the second relationship): (1) Does length of the stake prepared depend on diameter of the stem (respectively, on the density of nodes)? (2) What is the slope of the relationship, and does it vary among farmers? (3) If there is compensation for small diameters, how strong is it? Does it result in all stakes having similar mass?

To answer the last question we calculated the hypothetical mass that each stake would have in the absence of compensation (i.e., all stakes of identical length, mass varying isometrically with cross-sectional area). As hypothetical length (specific to each farmer), we used the average length of the stakes prepared by this farmer. We then compared the slopes of the regressions of mass on cross-sectional area to those of the hypothetical relationships. In all analyses, multiple tests were controlled for using sequential Bonferroni correction. To detect significant trends over the tests, we used Fisher's combined probability.

*Effect of size of stakes on performance of the resulting plant: yield of roots, production of stems, and number of 'daughter' stakes produced*

Three varieties presenting strongly contrasting architecture (principally in the extent of branching), 'siwal pîye' (henceforth termed Variety 1, moderately branched), 'tarekayapîmoi pîye' (Variety 2, highly branched) and 'zakari ye' (Variety 3, unbranched), were used in this experiment. Degree of branching is important because it affects the distribution of stems over diameter classes. A general principle of stem architecture is that stem diameter decreases with each successive ramification (Hallé et al. 1978). Much-branched cassava plants thus have a great range of stem diameters. In little-branched plants, in contrast, stem diameter diminishes little from base to apex of the stem system. For each variety, different classes of stakes were prepared, to represent typical lengths and diameters (based on the observation of local practices) as well as values smaller and larger than those usually observed. We also recorded the number of nodes present on each stake.

Four classes of length were used (A = 44 cm, B = 37.5 cm, C = 27.5 cm, D = 22 cm), in combination with different diameter classes. Given the material available, it was not possible to homogenize the different classes of diameters between varieties. The range of variation in stem diameter was greater for Variety 1, a large, moderately-branched variety, than for either varieties 2 or 3. Three diameter classes (1 = thick, 2 = medium, 3 = thin) were used for Variety 1, and two classes (1 = thick, 2 = medium) for varieties 2 and 3. Therefore, for each variety there were eight (or 12) types of stakes. Mean  $\pm$  SD of diameters of the stems used were as follows: For Variety 1, class 1:  $19.4 \pm 2.2$  mm; class 2:  $14.5 \pm 2.1$  mm; class 3:  $9.1 \pm 1.6$  mm; for Variety 2, class 1:  $16.8 \pm 4.2$  mm; class 2:  $12.2 \pm 1.3$  mm; for Variety 3, class 1:  $18.8 \pm 2.4$  mm; class 2:  $13.2 \pm 1.4$  mm. The experimental design had 14 replications of all the length  $\times$  diameter combinations of stakes for each variety. This extensive replication enabled us to minimize the effect of the environmental heterogeneity inherent to field experiments.

After 9 months, the plants were harvested, and the yields (fresh mass) of starchy roots (WROOT) and of stems (WSTEM) were measured. In addi-

tion, the number of stakes that each plant could potentially produce (multiplication factor [MF], or asexual fecundity), as based on our results on Makushi practices in preparing stakes, was estimated. The number of stems (NBSTEM) and of roots (NBROOT) produced by each stake was also recorded. The roles of the different factors (diameter, length, and interaction between them) were explored using a two-way ANOVA for each of the varieties. We also examined the effects of fresh mass and of number of nodes of the stakes on measures of performance. We examined the effects of fresh mass of stakes on three measures (WROOT, WSTEM, MF) and the effects of number of nodes on five measures (the three above, plus NBSTEM and NBROOT), both within each variety (grouping all plants irrespective of length and diameter classes) and across all three varieties using Fisher's combined probability. We also compared the agronomical performances, the allocation ratio between stems and roots, and the ratio MF/WSTEM of the three varieties.

## Results

### *Criteria explicitly considered by the Makushi as important in the selection and preparation of stakes*

Given the type of harvest and propagation of the plant (described in Elias et al. 2000b), farmers often have the opportunity to select the plants they will use for the next generation. They prefer healthy individuals to unhealthy ones, middle-aged individuals (about 9-months-old) to plants that are too young (6-months-old) or too old (more than 1-year-old), and highly productive individuals, hoping that the daughter individuals will reproduce the maternal character. Farmers are aware of environmental effects on plant performance, but also recognize an overall correlation between parent and clonal 'daughter' individuals.

When they have selected the individuals that will contribute to vegetative propagation, they select the parts of the stem that can be used for preparing stakes. They always discard the youngest parts (surfaces of stems still green), and any additional parts with very small diameters. Farmers say that thin stakes have a higher mortality than thicker ones, and that the plants grown from such stakes

tend to have a lower production than those grown from thicker stakes. However, when they are limited by the number of stakes available (for instance, when they plant a new field, an action that requires a large number of stakes), they might use thinner diameters than those they prefer to use when not thus limited. Farmers stated that the length of the stakes prepared is rather a personal matter. Some farmers prefer to prepare rather short stakes, whereas others like long ones, with no reason for such personal preferences being offered. Some farmers stated that the length of the stakes they cut depends on the diameter of the stem, with stakes cut longer from small-diameter stems.

While the Makushi clearly consider stem diameter (and length, although the 'right' length varied among farmers) of stakes to be of importance in determining propagule quality, the number of 'eyes' was never referred to as a criterion in any of the interviews or participatory observations. One other criterion in preparation of stakes was frequently mentioned. Most plants have branching points, and farmers always manage to prepare stakes in such a way that if there is a branching point, it is located on the upper third of the stake. The reason they give for doing so is that this facilitates the planting process.

### *Preparation of stakes*

A summary of the measurements of stakes prepared by the 15 farmers given stems is presented in Table 1. The mean minimum diameter was rather consensual among farmers (mean among farmers:  $8.6 \pm 0.6$  mm; coefficient of variation among farmers: 7%). The absolute minimum diameter, 7 mm, was observed only for a single stake prepared by one farmer. Farmers never discarded stems because they were considered too large for stakes. The largest stems used in this experiment were 3 cm in diameter, and the farmer given these stems (Harry, Table 1) prepared stakes from them. Compared to maximum and minimum acceptable diameters, the minimum and maximum lengths of the stakes prepared were more variable (means among farmers:  $27.4 \pm 3.86$  cm and  $43.6 \pm 9.31$  cm; coefficients of variation: 14 and 21%, respectively), which reflects to some extent the personal preferences mentioned by the farmers.

There was also no consensual fresh mass per cutting, or number of nodes per cutting, among farmers. Both traits were highly variable, not only among farmers (fresh mass:  $F_{480}^{13} = 13.06$ ,  $p < 0.0001$ ; nodes:  $F_{480}^{13} = 66.74$ ,  $p < 0.0001$ ), but also among stakes prepared by the same farmer (average of per-farmer coefficients of variation:  $49 \pm 14\%$  and  $30 \pm 7\%$ , respectively).

The density of nodes had little effect on how farmers cut stakes, significantly influencing the length of the stakes prepared in only two cases (Table 2), both in the direction suggesting compensation (negative correlation between node density and cutting length). After Bonferroni correction, however, none of the tests were significant. There was also no trend to a relationship between density of nodes and length of stakes when tests for all farmers were combined ( $\chi^2 = 32.24$ ,  $df = 28$ ,  $p = 0.264$ ).

In contrast, stem diameter strongly influenced how stakes were cut. For 12 farmers, there was a significant negative correlation between the length and the diameter of the stem (Table 2). After Bonferroni correction, the correlation remained significant for 10 farmers. The overall relationship was highly significant when all tests were combined ( $\chi^2 = 286.08$ ,  $df = 30$ ,  $p < 0.0001$ ), showing that farmers do compensate for small diameters by increasing the length of the stake. Figure 1 shows a typical relationship for one farmer. The partial regression coefficient (slope) was highly variable among farmers (Table 2, mean  $-0.74 \pm 0.51$ , coefficient of variation 71%), reflecting once again the personal preferences often mentioned in interviews. In practice, some farmers compensated more strictly or predictably than did others.

Compensation between diameter and length did not, however, result in all stakes having a similar volume or mass. There was in fact great variation in fresh mass among stakes prepared by the same farmer (Table 1). This variation was very closely tied to the cross-sectional area of the stake (Table 3). The slope of the regression of fresh mass on cross-sectional area did not vary much among farmers (mean  $0.352 \pm 0.060$ , coefficient of variation: 17%). Figure 2 presents an example. The dashed line indicates the slope that would be observed if fresh mass varied isometrically with stem cross-sectional area (i.e., if stakes of different diameter did not vary in either length or density). In contrast, a total compensation for mass would

be a horizontal line. Figure 2 shows that stem cross-sectional area (or diameter) was the principal determinant of stake mass, while farmer compensation between diameter and length only slightly (but significantly) reduced the slope of this relationship. Stakes prepared from thin stems thus always had a low fresh mass. Such a partial compensation was observed for all of the 14 farmers for which the mass of the stake was recorded, was significant for 10 of them, and was still significant for five farmers after Bonferroni correction (Table 4). When all the tests were combined, the relationship was highly significant over all farmers ( $\chi^2 = 188.85$ ,  $df = 28$ ,  $p < 0.0001$ ).

#### *Effect of size of stakes on plant performance*

The results of the ANOVA examining the effects of dimensions of stakes on performance traits of the resulting plant – the fresh mass of tuberous roots (WROOT), total stem fresh mass (WSTEM), and number of daughter stakes obtainable (MF) are given in Table 5, and illustrated in Figure 3. Multiplication factor (MF), the number of stakes that could be prepared from the plant, i.e., its asexual fecundity, was estimated by taking into account the distribution of stem length among different diameter classes and applying Makushi rules for preparation of stakes (minimum threshold stem diameter, relationship between stem diameter and stake length). Length of the stake contributed significantly to all the performance traits of the resulting plant in all varieties, except for the multiplication factor of Variety 1. Even in this case, there was a positive trend. Increased diameter led to significant increases in all traits for varieties 1 and 3, but did not have any significant effect in Variety 2, although here again a positive trend was observed for production of both roots and stems (Figure 3). Length and diameter of the stake thus affected not only the yield of tuberous roots, but also the asexual fecundity of the resulting plant. In no case did the interaction between length and diameter affect the measured traits.

All three performance traits examined were positively correlated with fresh mass of stakes (Table 6), although the relationship was no longer significant for Variety 2 after Bonferroni correction. The relationship is better explained by a log-linear model, with performance traits as a linear

Table 1. Maximum, minimum, mean and standard deviation values for length, diameter, cross-sectional area, fresh mass, number of nodes and density of nodes of the stakes for 15 Makushi farmers.

Farmer	N obs.		Length (cm)	Diameter (mm)	Cross-sectional area (mm <sup>2</sup> )	Fresh mass (g)	Number of nodes	Node density (cm <sup>-1</sup> )
Alice	16	Max	47.00	18.00	254.47	110.00	20.00	0.53
		Min	30.00	7.00	38.48	20.00	8.00	0.20
		Mean	36.44	12.09	123.81	53.13	14.44	0.40
		SD	4.69	3.48	68.77	24.26	3.56	0.09
Barbara	29	Max	40.00	19.00	283.53	100.00	23.00	0.58
		Min	29.00	8.00	50.27	12.00	5.00	0.17
		Mean	33.69	12.91	140.02	47.10	10.14	0.30
		SD	3.41	3.45	74.98	24.55	3.99	0.10
Caroline	31	Max	31.00	17.50	240.53	75.00	16.00	0.54
		Min	25.50	9.00	63.62	20.00	6.00	0.22
		Mean	28.52	12.56	128.05	39.45	10.84	0.38
		SD	1.58	2.31	48.00	15.78	2.48	0.08
Daisy	27	Max	42.00	20.50	330.06	87.00	22.00	0.60
		Min	30.50	8.00	50.27	15.00	4.00	0.13
		Mean	35.17	13.87	156.94	52.07	11.41	0.32
		SD	3.37	2.78	61.05	18.46	4.36	0.12
Emily	31	Max	43.00	25.00	490.87	140.00	18.00	0.46
		Min	29.00	9.00	63.62	20.00	6.00	0.17
		Mean	34.73	13.76	159.68	57.31	10.48	0.30
		SD	3.01	3.81	98.06	27.64	2.50	0.07
Fanny	36	Max	37.50	19.00	283.53	90.00	23.00	0.63
		Min	24.00	8.00	50.27	17.00	6.00	0.19
		Mean	30.74	12.00	119.75	40.20	11.86	0.38
		SD	3.26	2.95	61.25	18.09	3.97	0.12
Grace	24	Max	40.00	18.00	254.47	71.00	16.00	0.48
		Min	22.00	8.00	50.27	12.00	5.00	0.20
		Mean	29.46	12.10	121.34	33.67	9.25	0.31
		SD	4.03	2.89	59.53	16.70	2.77	0.08
Harry	75	Max	61.50	33.00	855.30	270.00	23.00	0.48
		Min	24.00	9.00	63.62	22.00	5.00	0.15
		Mean	36.49	15.41	213.75	76.36	10.56	0.28
		SD	8.40	5.92	183.15	55.25	3.92	0.06
Irma	126	Max	37.00	22.50	397.61	No data	No data	No data
		Min	26.00	10.00	78.54	No data	No data	No data
		Mean	31.84	14.75	176.09	No data	No data	No data
		SD	2.58	2.59	62.23	No data	No data	No data
Josephine	23	Max	56.00	19.00	283.53	115.00	18.00	0.42
		Min	36.00	8.50	56.75	25.00	9.00	0.20
		Mean	43.93	12.59	131.20	61.70	13.00	0.30
		SD	5.00	3.00	65.27	24.65	2.35	0.06
Katherine	26	Max	44.00	20.00	314.16	131.00	18.00	0.47
		Min	31.00	9.00	63.62	25.00	7.00	0.21
		Mean	36.79	13.00	141.21	53.73	11.69	0.32
		SD	3.83	3.35	73.20	27.08	2.66	0.06
Lea	26	Max	39.00	24.50	471.44	122.00	12.00	0.41
		Min	22.00	8.50	56.75	23.00	4.00	0.14
		Mean	29.65	14.81	190.46	52.54	7.77	0.27
		SD	5.32	4.92	126.27	28.17	2.25	0.08
Maria	90	Max	62.00	19.50	298.65	145.00	39.00	0.87
		Min	30.00	10.00	78.54	37.00	10.00	0.26
		Mean	45.38	14.92	177.88	87.74	24.49	0.54
		SD	7.70	2.01	47.26	22.17	6.87	0.13
Nadia	27	Max	34.00	16.00	201.06	62.00	15.00	0.49
		Min	27.00	8.00	50.27	13.00	4.00	0.13
		Mean	30.47	11.98	116.48	39.15	8.26	0.27
		SD	1.52	2.22	41.28	12.65	2.80	0.09

Table 1. Continued.

Farmer	N obs.	Length (cm)	Diameter (mm)	Cross-sectional area (mm <sup>2</sup> )	Fresh mass (g)	Number of nodes	Node density (cm <sup>-1</sup> )	
Olivia	33	Max	41.00	24.00	452.39	135.00	21.00	0.51
		Min	25.00	9.00	63.62	12.00	4.00	0.11
		Mean	34.06	13.71	162.99	55.09	8.88	0.26
		SD	3.67	4.48	111.96	31.75	2.88	0.08

function of  $\ln(\text{fresh mass})$ . Slopes of the log-linear relationships differed among varieties (Table 6). For all three performance traits, Variety 3, the least branched variety, had the highest production relative to fresh mass of the stake, while Variety 2, the most branched variety, had the lowest production relative to fresh mass of the stake for two traits (WSTEM and MF), with Variety 1, moderately branched, having the lowest production of WROOT relative to stake mass (Table 6). Differences among varieties were more pronounced for MF (2.8-fold variation in slope from smallest to largest value) than for WSTEM (1.9-fold varia-

tion) or WROOT (1.7-fold variation). Yet, given the large standard errors of the slope estimates, only the difference for MF between Variety 2 and Variety 3 was significant ( $t = 2.07$ ,  $df = 209$ ,  $p = 0.040$ ). The difference did not retain significance after Bonferroni correction.

Allocation between stems and roots also differed among varieties. Mean values of the ratio WROOT/WSTEM, across all plants of a given variety regardless of stake category (i.e., length  $\times$  diameter combination), was  $0.765 \pm 0.616$  for Variety 1,  $0.992 \pm 0.576$  for Variety 2, and  $0.642 \pm 0.377$  for Variety 3, the ratio being significantly larger for

Table 2. Multiple regression of lengths of stakes on their diameter and on their density of nodes for 14 farmers.

Farmer		Slope	SE	<i>p</i> -value
Alice	Diameter	-1.01	0.26	0.002*
	Density of nodes	1.89	10.32	0.857
Barbara	Diameter	-0.70	0.13	<0.001*
	Density of nodes	5.54	4.40	0.219
Caroline	Diameter	-0.15	0.13	0.261
	Density of nodes	2.47	3.61	0.499
Daisy	Diameter	-0.76	0.19	<0.001*
	Density of nodes	2.81	4.58	0.545
Emily	Diameter	-0.46	0.12	0.001*
	Density of nodes	-8.93	7.07	0.217
Fanny	Diameter	-0.68	0.15	<0.001*
	Density of nodes	1.96	3.77	0.607
Grace	Diameter	-0.22	0.30	0.457
	Density of nodes	10.36	11.26	0.368
Harry	Diameter	-0.87	0.15	<0.001
	Density of nodes	7.85	14.25	0.584
Josephine	Diameter	-0.77	0.28	0.011
	Density of nodes	-36.35	13.46	0.014
Katherine	Diameter	-0.51	0.21	0.026
	Density of nodes	3.59	11.51	0.758
Lea	Diameter	-0.86	0.12	<0.001
	Density of nodes	-17.85	7.51	0.026
Maria	Diameter	-2.29	0.34	<0.001*
	Density of nodes	-1.33	5.10	0.795
Nadia	Diameter	-0.48	0.10	<0.001
	Density of nodes	-1.92	2.30	0.411
Olivia	Diameter	-0.53	0.11	<0.001*
	Density of nodes	-1.95	6.81	0.776

\*Indicates the tests that retained significance after a Bonferroni correction.



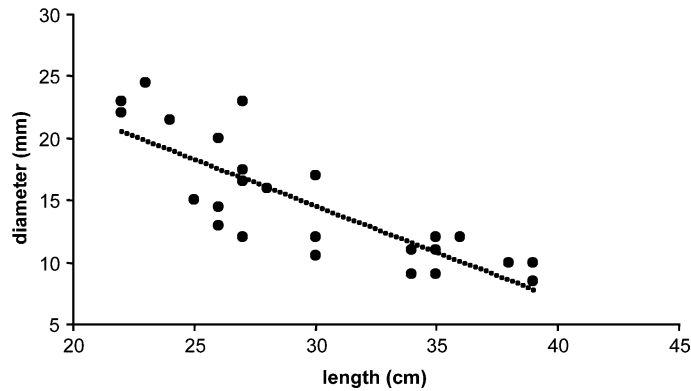


Figure 1. Relationship between length and diameter of stakes prepared by Lea ( $R^2 = 0.656$ ).

Variety 2 than for each of the other two varieties ( $t = 8.90$ ,  $df = 256$ ,  $p = 0.003$  for Variety 1,  $t = 27.26$ ,  $df = 209$ ,  $p < 0.001$  for Variety 3). Varieties also differed in the efficiency with which total stem mass can be converted into clonal propagules. The ratio MF/WSTEM was highest for Variety 3 ( $7.30 \times 10^{-3} \pm 2.88 \times 10^{-3}$ ), the least-branched variety, and lowest for Variety 2 ( $6.20 \times 10^{-3} \pm 2.97 \times 10^{-3}$ ), the most-branched variety, and this difference was significant ( $t = 7.47$ ,  $df = 209$ ,  $p = 0.007$ ). The ratio for Variety 1 was intermediate ( $6.68 \times 10^{-3} \pm 3.11 \times 10^{-3}$ ), but did not differ significantly from that of the other two varieties. This trend is accounted for by the association of extensive branching with thinner stems. Many stems of highly branched plants were too thin for stakes, and others, just above the threshold diameter, would be used to prepare a small number of long stakes.

In none of the three varieties was the number of nodes significantly correlated with any of the three measured performance traits (Table 7). In spite of weak, but positive correlation coefficients, the trend was not significant across the three varieties (combined probability: MF:  $\chi^2 = 2.640$ ,  $df = 6$ ,  $p = 0.852$ ; WSTEM:  $\chi^2 = 3.936$ ,  $df = 6$ ,  $p = 0.685$ ; WROOT:  $\chi^2 = 6.272$ ,  $df = 6$ ,  $p = 0.393$ ). Similarly, there was no relationship between number of nodes and the number of roots produced by the stake (Table 7), (combined probability:  $\chi^2 = 4.267$ ,  $df = 6$ ,  $p = 0.640$ ). A positive correlation between number of nodes and the number of stems produced by the stakes was detected for Variety 3 (Table 7), but it did not retain significance after Bonferroni correction. Over varieties, the trend was not significant ( $\chi^2 = 10.254$ ,  $df = 6$ ,  $p = 0.114$ ).

Table 3. Linear regression of fresh mass on cross-sectional area for 14 farmers (intercept set to 0).

Farmer	Slope	SE	R-square	p-value
Alice	0.408	0.017	0.840	< 0.001
Barbara	0.332	0.008	0.922	< 0.001
Caroline	0.310	0.005	0.944	< 0.001
Daisy	0.351	0.006	0.923	< 0.001
Emily	0.336	0.009	0.877	< 0.001
Fanny	0.326	0.007	0.916	< 0.001
Grace	0.302	0.009	0.896	< 0.001
Harry	0.330	0.007	0.919	< 0.001
Josephine	0.457	0.016	0.806	< 0.001
Katherine	0.375	0.010	0.911	< 0.001
Lea	0.269	0.009	0.880	< 0.001
Maria	0.482	0.010	0.335	< 0.001
Nadia	0.331	0.007	0.873	< 0.001
Olivia	0.317	0.010	0.886	< 0.001

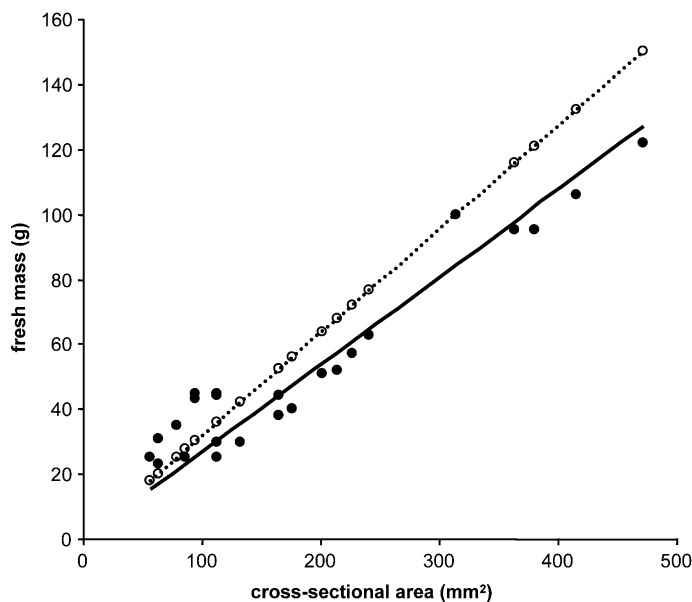


Figure 2. Relationship between fresh mass and cross-sectional area of the stakes prepared by Lea (filled circles and plain regression line,  $R^2 = 0.880$ ), and hypothetical relationship if fresh mass varied isometrically with cross-sectional area (open circles and dashed regression line). The slopes of the two regression lines (both constrained to 0), 0.269 and 0.318, respectively, are significantly different ( $p < 0.001$ ).

## Discussion

### *Selection and preparation of propagules: congruence among stated criteria, actual practices, and agronomic performance*

Practices actually observed in the preparation of stakes reflect the criteria considered important and the practices reported by farmers. Perceptions of farmers about traits that influence production

were shown by our experiment comparing agronomic traits of plants from different categories (i.e., length  $\times$  diameter combinations) of stakes to be based on accurate observation. Stem diameter and stake length together determine mass of the clonal propagule. They are considered important by Makushi farmers, and their importance is reflected by results of the experiment. Increased mass of the clonal propagule leads to increased yield of the resulting plant. Over the range of variation

Table 4. Comparison of the slope of the linear regression of fresh mass on cross-sectional area to its hypothetical value when fresh mass varies isometrically with cross-sectional area ( $t$ -test).

Farmer	Slope	Hypothetical slope	$t$	df	$p$ -value
Alice	0.408	0.447	2.291	15	0.018
Barbara	0.332	0.357	3.150	28	0.002*
Caroline	0.310	0.312	0.408	30	0.343
Daisy	0.351	0.363	1.794	25	0.042
Emily	0.336	0.357	2.269	30	0.015
Fanny	0.326	0.345	3.046	35	0.002*
Grace	0.302	0.309	0.736	21	0.235
Harry	0.330	0.399	10.523	74	< 0.001*
Josephine	0.457	0.491	2.177	21	0.021
Katherine	0.375	0.389	1.410	25	0.085
Lea	0.269	0.318	5.337	24	< 0.001*
Maria	0.482	0.508	2.519	89	0.007
Nadia	0.331	0.339	1.143	26	0.132
Olivia	0.317	0.348	3.221	32	0.001*

\*Indicates the tests that retained significance after a Bonferroni correction.

Table 5. Two-way ANOVA: effect of diameter and length (fixed factors) on root and stem production (WROOT and WSTEM respectively), and multiplication factor (MF).

			SS	df	MS	F	p-value
Variety 1	WROOT	Length	1060626.1	3	353542.0	6.587	0.0003
		Diameter	810105.2	2	405052.6	7.547	0.0007
		Length*diameter	167283.7	6	27880.6	0.519	0.79
		Error	7567373.6	141	53669.3		
	WSTEM	Length	746945.1	3	248981.7	5.188	0.002
		Diameter	1797529.9	2	898765.0	18.729	< 0.0001
		Length*diameter	121772.2	6	20295.4	0.423	0.86
		Error	6766325.0	141	47988.1		
	MF	Length	15.2	3	5.1	1.971	0.12
		Diameter	121.7	2	60.9	23.727	< 0.0001
		Length*diameter	7.4	6	1.2	0.479	0.82
		Error	361.9	141	2.6		
Variety 2	WROOT	Length	1798483.0	3	599494.3	6.596	0.0004
		Diameter	241718.6	1	241718.6	2.659	0.11
		Length*diameter	389764.0	3	129921.3	1.429	0.24
		Error	8816583.4	97	90892.6		
	WSTEM	Length	723735.5	3	241245.2	5.644	0.001
		Diameter	70323.0	1	70323.0	1.645	0.2
		Length*diameter	87112.1	3	29037.4	0.679	0.57
		Error	4146255.2	97	42744.9		
	MF	Length	28.0	3	9.3	5.095	0.003
		Diameter	0.5	1	0.5	0.284	0.6
		Length*diameter	3.0	3	1.0	0.539	0.66
		Error	177.8	97	1.8		
Variety 3	WROOT	Length	1495995.8	3	498665.3	11.003	< 0.0001
		Diameter	339684.1	1	339684.1	7.495	0.007
		Length*diameter	44206.8	3	14735.6	0.325	0.81
		Error	4441423.5	98	45320.6		
	WSTEM	Length	1099951.5	3	366650.5	5.407	0.002
		Diameter	755694.3	1	755694.3	11.144	0.001
		Length*diameter	88948.6	3	29649.5	0.437	0.73
		Error	6645495.6	98	67811.2		
	MF	Length	95.7	3	31.9	5.725	0.001
		Diameter	26.1	1	26.1	4.684	0.033
		Length*diameter	12.6	3	4.2	0.751	0.52
		Error	546.2	98	5.6		

that farmers have to deal with, number of nodes is not considered important, and results of the experiment indicate that under the conditions of Makushi farming, number of nodes does not seem to have any significant effect on the production of either roots or stems.

We have demonstrated how asexual fecundity can be quantified in the clonal propagation of this crop plant, and have shown that it is determined not only by biological traits of the plant but also by farmers' decisions. These decisions integrate farmers' knowledge about the quality of propagules in a way that is not possible with seed-propagated plants. We hasten to add that asexual fecundity can be quantified only in relative, not in

absolute terms, because individual farmers vary in how they prepare propagules, adding a source of variation absent in seed-propagated crops.

#### *Can selection act on variation in asexual fecundity and propagule quality?*

The establishment of protocols for quantifying how farmer practices affect the asexual fecundity of an individual plant and the quality of clonal propagules now allows us to envisage studies of how plant traits affecting these parameters may have evolved over the course of domestication. Like other cassava farmers, Makushi exercise

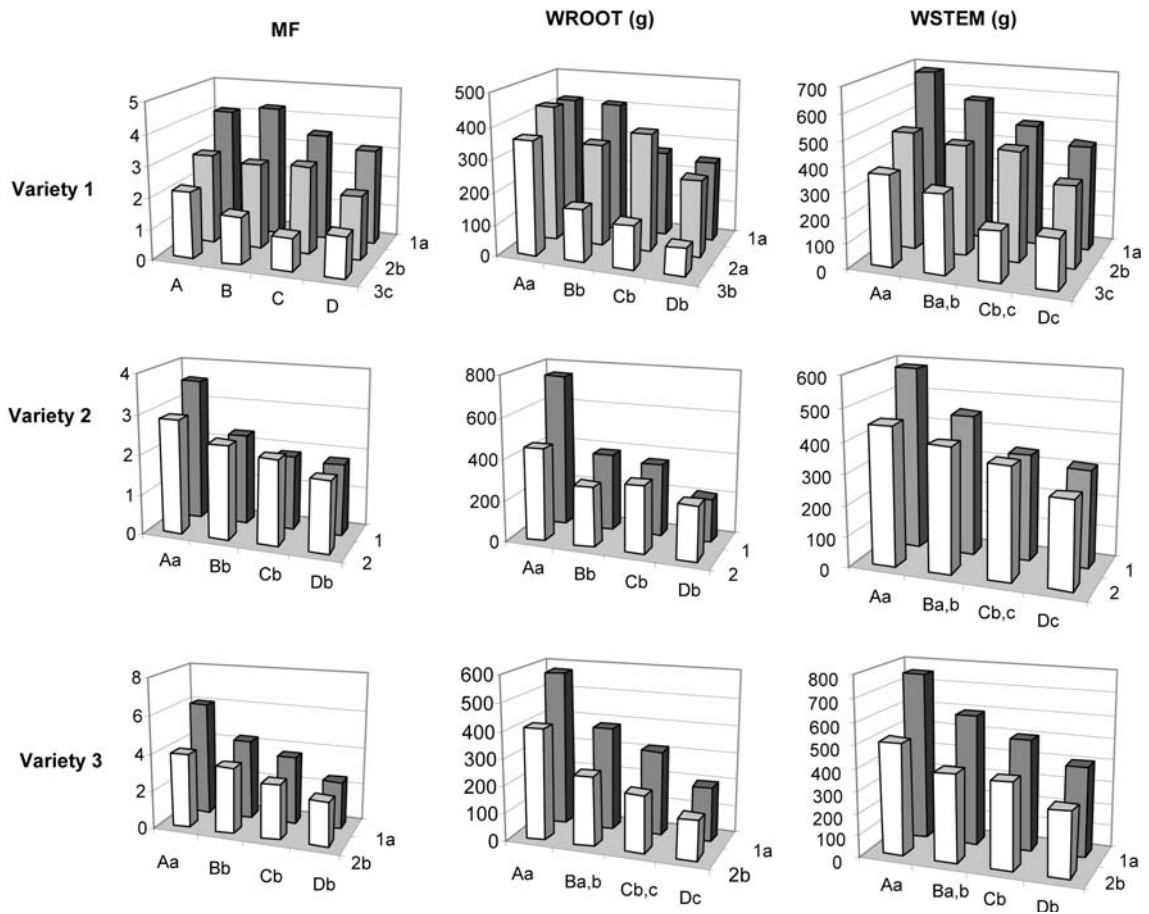


Figure 3. Mean values for each variety of MF (in number of 'daughter' stakes), WROOT and WSTEM (both in g) for each of the length categories (A, B, C, D) and diameter categories (1, 2, 3). Significant differences between different categories are indicated by different lower case characters.

selection among plants, making a large number of propagules from some, and none at all from others. There is thus the potential for selection to favor plants that, in addition to their performance in terms of consciously selected traits (e.g., root

yield), can also provide a large number of high-quality stakes. Farmers might also consciously favor plants because they are highly productive of stakes, although we found no evidence for this in our study of the Makushi.

Table 6. Log-linear regression of the agronomical traits on fresh mass of the stakes.

		Slope	SE	R-square	p-value
Variety 1	WROOT	104.58	26.02	0.096	< 0.001*
	WSTEM	131.61	25.10	0.154	< 0.001*
	MF	1.13	0.18	0.210	< 0.001*
Variety 2	WROOT	147.88	59.07	0.057	0.014
	WSTEM	92.17	39.66	0.050	0.022
	MF	0.58	0.26	0.047	0.026
Variety 3	WROOT	178.49	39.74	0.162	< 0.001*
	WSTEM	175.18	47.63	0.115	< 0.001*
	MF	1.60	0.42	0.121	< 0.001*

\*Indicates the tests that retained significance after a Bonferroni correction.

Table 7. Coefficient of correlation ( $r$ ) and their significance level ( $p$ ) between the number of nodes and five agronomical traits.

	WROOT		WSTEM		MF		NBSTEM		NBROOT	
	$r$	$p$	$r$	$p$	$r$	$p$	$r$	$p$	$r$	$p$
Variety 1	0.095	0.244	0.054	0.510	0.032	0.695	0.071	0.382	0.062	0.446
Variety 2	0.073	0.461	0.076	0.441	0.076	0.442	0.086	0.380	0.067	0.496
Variety 3	0.085	0.387	0.049	0.621	0.016	0.869	0.199	0.041	0.061	0.535

NBSTEM and NBROOT are the number of stems and roots, respectively, produced by the stakes.

Measuring asexual fecundity and propagule quality is pertinent to understanding evolution only if there is heritable variation in traits affecting these parameters. What traits affect the number and quality of clonal propagules that can be obtained from a plant, and does genetic variation exist for these traits? Our observations and experiments accord with the literature (Oka et al. 1987; Keating et al. 1988; Jennings 1995) in showing that the architecture of the stem system, in particular the extent of branching, is the most important determinant of asexual fecundity in cassava. This is because the extent of branching affects the distribution of stems across diameter classes. In plants generally, the primary diameter of stems decreases with each subsequent ramification (one of ‘Corner’s rules’ (Hallé et al. 1978)). Thus, the stems of highly branched cassava plants are subdivided into modules of a great range of diameter classes, with a significant proportion of total stem volume in diameter classes too small to yield high-quality stakes. In contrast, little-branched plants show less diminution of diameter from base to apex of the plant’s stem system, and a larger proportion of total stem volume should be in diameter classes that yield high-quality stakes. A little-branched plant should thus have a higher asexual fecundity than a much-branched plant of comparable total stem mass. These predicted differences are reflected in the results of our experiment. With increasing fresh mass of the initial stake, the MF of the least-branched variety, Variety 3, increased most rapidly, whereas the MF of the most-branched variety, Variety 2, increased least rapidly. Also, the ratio of MF/WSTEM was greatest for the least-branched variety and lowest for the most-branched variety.

Extent of branching of cassava plants is affected by many factors, including propagation practices and environmental conditions, but it also shows high heritability when such factors are controlled

(Okogbenin and Fregene 2003). Extent of branching is considered to be reduced in domesticated cassava relative to its wild ancestors, and selection for increased success in vegetative propagation may have driven the evolution of this trait during domestication (Jennings 1995). The results of our experiments, along with those of previous studies of performance of plants produced by stakes prepared from different parts of cassava plants (‘position effects’: Oka et al. 1987; Keating et al. 1988), suggest how such a selective process might operate. Stakes prepared from the thinner stems of the more distal modules of highly branched varieties give low root yields and poorly developed stem systems. Such plants are unlikely to be selected as planting material by farmers, and even if they are, they should supply even poorer-quality stakes than the parent plant. Such cycles of diminishing returns from highly branched plants could lead to a rapid decrease in the representation of much-branched clones relative to little-branched clones, which continue to produce, generation after clonal generation, a larger number of high-quality stakes. This scenario is consistent with results of two studies that independently compared position effects on propagule quality, in cassava varieties differing in their degree of branching (Oka et al. 1987; Keating et al. 1988).

Does variation in asexual fecundity and propagule quality affect reproductive success in field environments? Does such variation result in strong selection? Both automatic (natural) and conscious artificial selection could favor genotypes that produce clonal propagules in larger numbers than do other genotypes. For herbaceous plants, such as yams (*Dioscorea* spp.), or relatively short-lived woody plants, such as cassava, the rate of multiplication that can be attained using traditional means of vegetative propagation is notoriously slow compared to seed-propagated crops (e.g., Thro et al. 1999), and farmers should often face

situations in which the number of high-quality propagules is limiting. Any plant which satisfies other criteria, such as yield, but also produces more clonal propagules, could be strongly favored in reproduction. The advantage of plants with greater asexual fecundity might be especially great during episodes when stakes are present in limited supply, e.g., after crop failures, or in periods when the area planted is expanding. Propagule quality is also an important determinant of fitness in field conditions. Higher-quality propagules result in higher survivorship and growth, and thus often higher yield. Farmers learn to recognize plant traits that confer high quality to propagules prepared from them; human selection thus magnifies natural selection favoring these traits.

Thus, if heritable variation exists for traits affecting them, both fecundity and per-propagule reproductive success are likely to evolve under domestication. Propagule quality is in part based on developmental traits – e.g. the number and activity of buds, affecting the ability to sprout – that are different from those influencing fecundity, so that the two can evolve to some extent independently. They are not completely independent, however. Fecundity can be increased by increasing the plant's allocation of resources to producing the organs used as propagules, or by dividing the same amount of resources into more propagules, i.e., decreasing the size of propagules. Because smaller propagules are often less successful, it is unlikely that both propagule number (fecundity) and quality can be maximized simultaneously. A prediction worth testing is that farmers' practices will tend toward propagule quality/number combinations that maximize yield of the crop population.

*C-effects: their importance in the clonal propagation of cassava*

Like previous authors (Oka et al. 1987; Keating et al. 1988), we have emphasized position effects on propagule quality due to the decreasing size of cassava stakes prepared from increasingly distal portions of the plant's stem system. Position effects are an example of 'C-effects', i.e., nonrandom parental or environmental effects, transmitted to clonal descendants, that cause ramets to resemble each other more than they would be expected according to only their genetic similarity (Haissig

and Riemenschneider 1988). Not only size, but many other traits of clonal propagules can vary with the position on the parent plant of the stem from which they were prepared. The stem system of a plant is comprised of parts that vary greatly in chronological and developmental age, displaying complex gradients in concentrations of starchy reserves, mineral nutrients, nitrogen, hormones, and other constituents, all of which affect the performance of propagules prepared from them. Oka et al. (1987) found that dry matter content decreased, and respiratory rate increased, from basal to apical stems in cassava, both gradients becoming stronger as plants aged. Dry matter content is considered an important factor influencing the greater yield of roots (and production of stems) of plants prepared from basal sections of stem systems (Enyi 1970; Oka et al. 1987; Raffailac 1992). Composition of dry matter – nutrients as well as hormones and other molecules affecting development – is also likely to vary among different parts of the stem system. Work on clonal propagation by stem cuttings of forest trees has shown the important influence of developmental gradients on the performance of daughter plants originating from stems of different positions on the parent. The general conclusion of this work is that adventitious rooting ability is a juvenile trait, and that cuttings prepared from basal stem sections generally have greater rooting ability than those prepared from upper, ontogenetically mature, stem sections (for recent examples, see Schroeder and Walker 1991; Rieckermann et al. 1999; Fishel et al. 2003; Zalensny et al. 2003). Recent work (Busov et al. 2004) is beginning to elucidate the hormonally mediated mechanisms responsible for such variation. C-effects can be very long-lasting indeed, if they reflect epigenetic changes over plant development. One plausible example is the plagiotropic growth of plants produced by cuttings from plagiotropic branches, in tree species with marked dimorphism between orthotropic and plagiotropic axes (Ng 1996; McCown 2000). The agronomic literature on cassava includes observations of some curious C-effects. For example, Médard (1974) showed, for one particular variety only, that plants prepared from stems of different positions on the parent plant differed in their architecture. Those stakes prepared from the apex of the parent plant's basal-most module (i.e., near the branching point) branched precociously much

more often (85% of cases) than did stakes prepared from the base of the same module (6%). Médard (1974) wrote of the ‘memory’ of branching in this variety. It would be interesting to study, using modern techniques, the mechanisms behind such effects.

It would be surprising if farmers have not noticed some of these C-effects that result from the complex heterogeneity of the population of stems used for preparing stakes. However, farmers’ knowledge about C-effects and other complex aspects of vegetative propagation appears to be completely unplumbed.

#### *Implications for analysis of the evolution of asexual fecundity in other domesticated plants*

Our analysis suggests the interest of pursuing analogous questions with other crops. Most directly comparable are other vegetatively propagated plants in which the organ consumed is different from that used for propagation, such as sweet potato (*Ipomoea batatas* L., Convolvulaceae), where tubers are eaten and the plant is usually propagated by stem cuttings, as in cassava, or bananas (*Musa paradisiaca* L., Musaceae), where sterile, parthenocarpic fruits are eaten and propagation is by means of basal corms. Seed-propagated plants in which seeds are not the edible organ (e.g., carrots) would also be interesting to explore in this regard. Plants in which the same organ is both eaten and used for propagation (either clonal or sexual) should be affected by the same pressures on fecundity, but in these plants the evolution of fecundity and yield will probably be impossible to tease apart.

#### **Conclusions**

Makushi practices in the selection and preparation of stakes are guided by knowledge of the parameters that affect plant performance. Our results confirm earlier work in showing that stem diameter is an important factor in both the selection of stakes and the performance of plants resulting from them. Our results also extend those of previous studies by documenting two important sources of variation. First, we show how variation among plants affects their capacity to produce

high-performance stakes. The asexual fecundity of a plant varies with its degree of branching, because this trait affects the distribution of diameters in the population of stems produced by the plant. Second, instead of reporting ‘usual’ practices, we document how practices in the selection and preparation of stakes *vary within a population of farmers*. Farmers’ practices show not only variation among individuals, but also regular patterns in this variation. For example, when given comparable stems, farmers varied in the length of stakes they prepared. But while this aspect was variable among farmers, another feature of their behavior was almost invariant. Given stems of varying diameter, almost all farmers cut shorter stakes from thicker stems than they did from thin stems. Both sources of variation, that among plants and that among farmers, affect the demography of clonal propagation.

We have emphasized the positive effect of reduced branching on asexual fecundity as a selective pressure favoring the evolution of less branched architecture in domesticated cassava. Reduced branching has several other consequences, however, and some of these may have helped drive selection of this trait. Reduced branching leads to increased harvest index and higher yield (Cock et al. 1979). Furthermore, because branching is associated with flowering in cassava (Médard 1973; Jennings 1995; Alves 2002), reduced branching could increase yield by reducing the plant’s allocation to flowers and fruits. Incidentally, this points to a potential trade-off between asexual and sexual fecundity among differentially branched phenotypes in cassava. The implications of this trade-off will be considered in detail in a subsequent paper.

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