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THE DEVELOPMENT OF A MUTUALISTIC RELATIONSHIP BETWEEN HUMANS AND MAYPOPS (*PASSIFLORA INCARNATA* L.) IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT.—Archaeological evidence indicates that use of *Passiflora incarnata* L. (maypops or passionflower) increased prehistorically from its earliest appearance in the Late Archaic. The intensification of the relationship between humans and this species can be understood with reference to two important components of human/plant mutualism, seed dispersal and environmental modification. Increased use of maypops is shown to have occurred along with the spread of plant husbandry and associated disturbance of existing vegetation. In addition, an extension of its range in modern times has apparently occurred despite its lack of importance as a food plant among Euroamerican populations. These findings support the notion that both anthropogenic habitat extention and seed dispersal contribute to the development of human/plant mutualism.

RESUMEN.—La evidencia arqueológica indica que el uso de *Passiflora incarnata* L. (pasionaria) aumentó prehistoricamente a partir de su primera aparición en el Arcaico Tardío. La intensificación de las relaciones entre los humanos y esta especie puede entenderse con referencia a dos componentes importantes del mutualismo entre seres humanos y plantas: la dispersión de las semillas y la modificación ambiental. Se muestra que un mayor uso de la pasionaria se dio junto con la expansión de la agricultura y la perturbación concomitante de la vegetación natural. Parece, además, haber ocurrido una extensión de su distribución en tiempos recientes, a pesar de su falta de importancia como fuente de alimento para la población euroamericana. Estos resultados apoyan la idea de que tanto la expansión del hâbitat antropogénico como la dispersión de las semillas contribuyen al desarrollo del mutualismo entre humanos y plantas.

RESUME.—L'évidence archéologique indique que l'usage de *Passiflora incarnata* L. (la passiflore) s'est aumentee prehistoriquemente de sa première apparition dans l'Archaique Dernier. On peut comprendre l'aumentation de ce rapport entre les humains et cette espèce avec la référence a deux composants importantes du mutualisme entre les humains et les plantes: la dispersion des graines et la modification de l'énvirons. On vois que l'utilisation aumentée de la passiflore s'est passée tout ensemble avec l'extension de l'agriculture et du dérangement de la vegetation naturale. En plus, l'extension de sa portée dans les temps modernes s'est passée évidemment malgré le manque d'importance comme une plante comestible entre la population euroaméricaine. Ces conclusions soutiennent l'idee que l'extension de l'environs et aussi la dispersion des graines ont contribué au développement du mutualisme entre les humains et les plantes.

INTRODUCTION

Although students of prehistory have often taken an interest in human-plant relationships, this interest has most often centered around the origin of agricultural systems and its cultural and demographic consequences. Less attention has been given to relationships between human groups and plant species of minor economic importance. Recently ethnobotanists concerned with eastern North American prehistory (e.g. Asch and Asch 1985, Fritz 1986, B. Smith 1987) have given increasing attention to indigenous domesticates such as chenopod, sumpweed, and sunflower and have recognized a number of minor commensal crops. Maypops (*Passiflora incarnata* L.) has been recognized as a weed crop on the basis of its common occurrence archaeologically and its preference for anthropogenic habitats (Yarnell 1987). Perhaps because it was a minor food plant rather than a staple, however, no attempt has been made to examine archaeological evidence for changing use of maypops over time or to discuss in any detail the relationships between this species and aboriginal North American groups.

In addition to compiling and discussing archaeological and ethnohistoric evidence for use of maypops and summarizing temporal patterns, this paper describes the geographic range of the species and relevant ecological characteristics. After reviewing ethnohistoric and archaeological evidence for increasing aboriginal use of maypops, I describe how certain propositions derived from Rindos (1984) about the roles of seed dispersal and environmental disturbance in the development of human-plant mutualism can be applied to human relationships with this species. I then compare the archaeological evidence of the use of maypops, vegetational change, and aboriginal relationships with other plant species with these propositions. Using these data, long-term changes in the use of maypops in the Southeast can be explained in part with reference to its mutualistic relationship with human populations. Probable range extension of the species in modern times is also discussed in the context of this model of domestication.

SPECIES CHARACTERISTICS

The Passifloraceae, of which *Passiflora incarnata* L. (maypops) is a member, is a predominantly tropical family with some 23 genera, four of which are found exclusively in the New World. *Passiflora* is a pantropic genus of some 400-500 species, most of which occur in the American tropics (Hutchinson 1967, Martin and Nakasone 1970).[1] The native range of maypops covers much of the eastern United States from Virginia to southern Illinois and southeastern Kansas south to Florida and Texas (Killip 1938, 1960). *P. lutea* L. is the only other species in the Passifloraceae that occurs naturally in the continental temperate United States.

Maypops is a perennial vine with showy flowers and an edible fleshy fruit. It is frequently an aggressive colonizer of vacant lots, railroad beds, old fields, and cultivated fields in the Southeast. Maypops may also be found along roadsides and fencerows or in thickets (Radford *et al.* 1968:734). Its distribution in these kinds of habitats indicates a preference for disturbed soils and exposure to full sunlight. Judging by the species' present-day preference for anthropogenic habitats, it presumably was restricted to relatively open ground beneath canopy gaps (including stream margins, windthrow gaps, and other naturally disturbed patches in the landscape) before disruptive human activity became common within its range.

Although detailed data on the ecology of maypops are unavailable, some aspects of the morphology of its flowers and fruits allow for inferences about its reproductive biology. Maypops flowers are quite showy; in fact, the species is sometimes grown today as an ornamental in the United States. Showy flowers are nearly always characteristic of animal pollinated plants. The maypops fruit is fleshy and sweet and the numerous seeds have woody walls. Thus the fruit is likely to be consumed by animals without resulting destruction of the seed. Given these aspects of fruit and seed morphology (fruit palatability and seed durability), mammal or bird dispersal is most likely.

MODERN DISTRIBUTION

The present-day distribution of maypops is presented in Figure 1. Range information was obtained from published sources where possible and from herbarium specimens (primarily from the University of North Carolina at Chapel Hill). Occurrences were noted by county when this information was available in published sources or from herbarium specimens (see Appendix for a list of references). In addition to the county collections shown in Figure 1, published sources indicate that maypops is found throughout Louisiana, Tennessee and Georgia.

In addition to most of the states in the Southeast maypops also occurs in southern Virginia, western West Virginia, western Kentucky, southern Illinois,

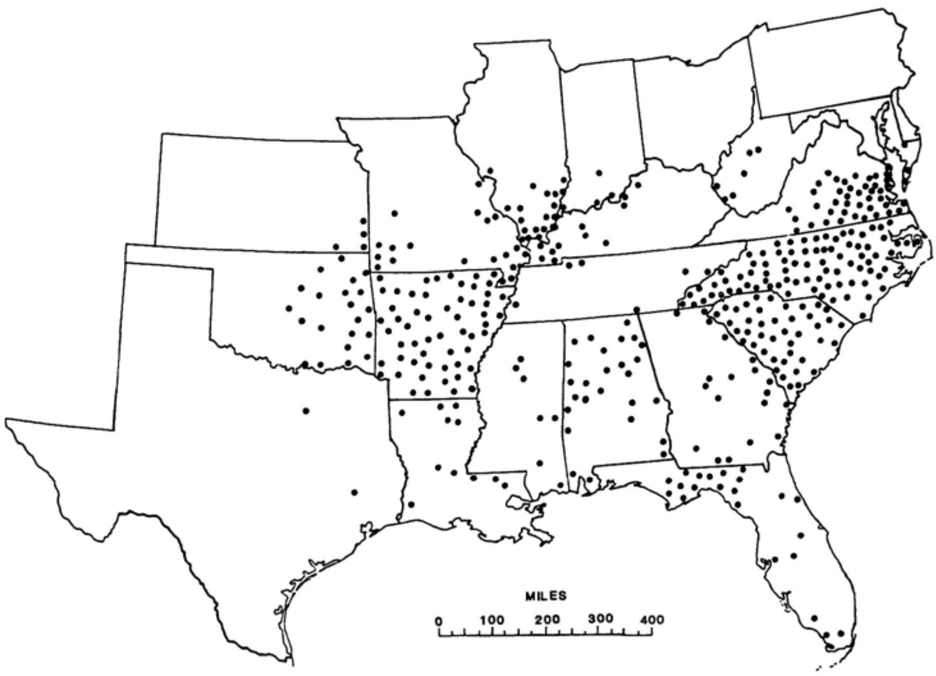

FIG. 1.—Modern distribution of maypops. Each dot represents a record of collection for a county.

southern Indiana, southern Missouri, eastern Nebraska, Oklahoma and Texas, and throughout Arkansas. Maypops occurs in southern Florida, but it shares its range there with several congenerics with Caribbean affinities (Avery and Loope 1980). The single occurrence for Pennsylvania reported by Killip (1938) is not listed by Wherry *et al.* (1979) and has therefore been omitted from Figure 1. Apparently maypops has been introduced as an ornamental north of its present natural range from Virginia west to Missouri (Killip 1938).

The western limit of the range of maypops correlates well with the western limits of the eastern deciduous forest region. This correlation is best explained as a similarity in moisture requirements between maypops and deciduous forest trees, whose growth westward is limited by low soil moisture in transitional grassland regions (Vankat 1979:132). It is unlikely that maypops' range is limited by some aspect of the environment dependent upon the presence of forest trees, since it is a vigorous colonizer of treeless areas and should be expected to thrive in them as long as conditions for growth and reproduction are met. The northern limit of the species' range is probably the result of an intolerance to cold and/or a photoperiodic requirement for flowering to occur. All collections of *P. incarnata* (with the exception of the report from Pennsylvania noted above) have been made within the area having an average frost-free period of 160 to 200 days (Espenshade 1982).

There is no reason to suspect that maypops is limited to particular kinds of substrates, since it occurs on all soil types. It does prefer disturbed soils, and as a weed, it is heliophilic and opportunistic of disturbances that remove or alter existing vegetation. Tolerance of a relatively wide range of environmental conditions is also characteristic of weeds (Baker 1974). So is a preference for anthropogenic disturbances, the frequency and extent of which influence the abundance of maypops in many areas and may have a significant effect upon its geographic range as well.

PREHISTORIC AND EARLY HISTORIC DISTRIBUTION AND USE

Documentary evidence.—Two sources, the accounts of William Strachey (Major 1849) and Robert Beverley (Wright 1947) are particularly informative about aboriginal relationships with maypops in the East. Both wrote of coastal Virginia, inhabited by Algonkian peoples. Strachey's account of early seventeenth century Indian life reports that "they plant also the field apple, the maracock, a wyld fruict like a kind of pomegranett, which increaseth infinitlye, and ripens in August . . ." (Major 1849:72). He also describes the plant and its growth habits at some length:

> Here is a fruict by the naturells called a maracock; this groweth generally low, and creepeth in a manner amongst the corne (albeit I have seene yt, planted in a gardein within our fort, at James Towne, to spred and rise as high as the pale); yt is the bignes of a queen apple, and hath manie azurine or blew karnells, like as a pomegranet, and yt bloometh a most sweet and delicate flower, and yt is a good sommer cooling fruict, and in every field where the Indians plant their corne be cart-loads of them. (Major 1849:119)

These comments indicate that maypops was abundant in Indian gardens. The latter comment even suggests that maypops and gardens were usually associated.

Although supporting the idea of a symbiotic relationship between human groups (and their managed landscapes) and maypops, Strachey's account equivocates on the question of whether or not the species was planted. In the same sentence we are told both that the plant was wild and that it was planted by the Indians. Beverly's observations of the early eighteenth century in the same area indicate that maypops was a weed rather than a crop:

> The Maracock, which is the Fruit of what we call the Passion Flower, our Natives did not take the Pains to plant, having enough of it growing every where; tho' they eat it with a great deal of Pleasure; this Fruit is about the Size of a Pullet's Egg (Wright 1947:142).

Perhaps these contradictory reports reveal a European disinclination to recognize unfamiliar types of plant management that seemed to elude a perceived dichotomy between ''wild'' and ''domesticated.'' Alternatively, the nature of the human-plant relationship involved may have changed between Strachey's time and Beverly's (although the earlier report also seems uncertain as to the status of maypops, assuming a connotation of the term ''wild'' that is similar to ours today). In any case, these two sources do indicate that maypops grew abundantly in Indian gardens, that the fruit was consumed, and that the plant was tolerated and possibly encouraged or planted in Historic times. Once planted in cultivated soil, such a persistent weed would have needed little encouragement to flourish. Its reported abundance in gardens is evidence of its success as a colonizer of human-disturbed habitats even without planting.

Archaeological evidence.—Seeds of maypops are common components of paleoethnobotanical assemblages in the Southeast and are found occasionally in adjacent regions. Incorporation of its carbonized seeds into archaeological deposits is unlikely to have occurred without human manipulation of the fruits, which otherwise would decompose and disseminate their propagules far from hearth fires. Thus their archaeological occurrence may be considered strong evidence of use of the fruit by aboriginal populations. The plausibility of consumption of the fruits is further supported by the modern-day use and cultivation of *Passiflora* throughout the tropics (Popenoe 1974:242; Hedrick 1972:409-411).

In order to explore this question of changing use over time, paleoethnobotanical data were assembled from a number of published and unpublished sources. For the Archaic and Woodland periods, original sources were consulted in conjunction with Yarnell and Black's (1985) compilation of data. For the Mississippian/Protohistoric and Historic periods, various reports were reviewed. All sources are listed in Table 1 along with the sites and components from which maypops seed counts were derived. For each component at each site, absolute quantity of maypops seeds recovered was obtained as well as total number of fleshy fruit seeds. Although acquisition of accurate totals was a priority, it must be recognized that difficulties are often encountered in synthesizing data of this kind and that differences between researchers in recovery, processing, analysis and quantification render comparisons approximate rather than precise. However, it is felt that

TABLE 1.—*Sites with maypops seeds.*

Period	Site Name	Site Number	State	County	Temporal Context	Reference
Late/Term. Archaic (3500-800 BC)	Iddins	40LD38	TN	Loudon	1800-1300 BC	Chapman & Shea 1981
	—	1FR310	AL	Franklin	Perry	Caddell 1982a
Early Woodland (800 BC-AD 200)	—	9CK(DOT)7	GA	Cherokee	Kellogg 565±75 BC-700±75 AD	Bowen 1982
Middle Woodland (100 BC-AD 550)	—	1FR310	AL	Franklin	Lick Creek	Caddell 1982a
	Icehouse Bottom	40MR23	TN	Monroe	Connestee/Candy Creek/ AD 200-500	Chapman & Shea 1981
	Eoff I	40CF32	TN	Coffee	McFarland	Faulkner 1977
Late Woodland (AD 550-1000)	Mason	40FR8	TN	Franklin	Mason/AD 600-1000	McMahan 1983
	—	1Grlx1	AL	Greene	Middle Miller II/AD 900	Caddell 1982c
	—	16WC5	LA	W. Carroll	Coles Creek	Shea 1979
	—	1JE31	AL	Jefferson	West Jefferson	Scarry 1980
	—	1JE33	AL	Jefferson	West Jefferson	Scarry 1980
Miss./Protoh. (AD 1000-1550)	Moundville		AL	Hale	Moundville I/AD 900-1000	Scarry 1986
	Martin Farm	40MR20	TN	Monroe	Miss. I and II	Schroedl *et al.* 1985
	Lubbub Creek locality	1PI33, 83, 85	AL	Pickens	Summerville I-III	Caddell 1983
	Beaverdam Creek	9EB85	GA	Elbert	Savannah II	Gardner 1984
	Gordon Mounds	22JE501	MS	Jefferson	Late Coles Creek-Plaquemines	Shea 1984

TABLE 1.—*Sites with maypops seeds. (continued)*

Period	Site Name	Site Number	State	County	Temporal Context	Reference
	Cemoche-chobee	9Cla62	GA	Clay	Mississippian	Dunn 1982
	Toqua	40MR6	TN	Monroe	Dallas	Shea *et al.* 1986
	—	38AN8	SC	Anderson	Late Miss.	Gardner 1982
	—	44HA22	VA	Halifax	Protohistoric	Trinkley 1976
	Yarborough	22CL814	MS	Clay	Protohistoric	Caddell 1982b
	Wall	31OR11	NC	Orange	Protohistoric	Gremillion 1987b
Hist. (AD 1550-1800)	Little Egypt	9MU102	GA	Murray	Barnett/AD 1550-1700	Hally 1981
	Tanasee	40MR62	TN	Monroe	Cherokee	Schroedl & Shea 1986
	Chota	40MR2	TN	Monroe	Cherokee/AD 1746-1774	Schroedl & Shea 1986
	Lamar Village	GP-HK-08	GA	Hancock	early 1600s	Gardner 1985
	Mialoquo	40MR3	TN	Monroe	Cherokee	Russ & Chapman 1983
	Upper Saratown	31SKla	NC	Stokes	late 1600s	Wilson 1977
	Mitchum	31Ch452	NC	Chatham	1600s	Gremillion 1987b
	Fredricks	31OR231	NC	Orange	late 1600s	Gremillion 1987a
Misc.[1]	Spoonbill	41WD109	TX	Wood	AD 750-1350	Perttula & Bruseth 1983
	Calahan-Thompson	23MI171	MO	Mississippi	AD 1300-1500	Byrd & Neuman 1978
	Towasahgy	23MI2	MO	Mississippi	L. Mississippi?	Cottier 1971
	Nuyaka Vil.	1HB3	AL	Tallapoosa	AD 1000-1200	Crawford 1975
	Spiro	34LE46	OK	LeFlore	AD 1000-1400	Fritz 1982, 1984
	Duncan Tract	40TR27	TN	Trousdale	prehistoric	Shea 1983
	—	22HI500	MS	Hinds	AD 1200-1400	Cutler & Blake 1976

[1]Used only for constructing Figure 3 (not included in quantification.)

the database is large enough to make comparisons among time periods useful for assessing change. Quantitative data were drawn only from sites in the Southeastern states (here including Alabama, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, and Virginia).

Two quantitative methods were employed in arriving at a measure of the frequency of use of maypops for each time period. The first involved calculating the proportional contribution of maypops seeds to total numbers of fleshy fruit seeds[2] for each site and each time period based upon sources listed in Table 1. The same operation was performed on data presented in Chapman and Shea (1981) to create a sequence showing changes in the archaeological occurrence of maypops in a particular region, the Tellico Reservoir area of the lower Little Tennessee River valley. For sources listing fragments, numbers of whole seeds were added to half the number of fragments in order to estimate numbers of whole seeds.

The other method used was calculation of ubiquity as the percentage of sites of each time period from which maypops seeds were recovered. The same dataset was used as for calculation of seed percentages. However, the total number of sites from which the percentage containing maypops was calculated is the total number of sites for each time period for which a report on paleoethnobotanical remains was reviewed by the author. These data were obtained by consulting Yarnell and Black (1985) for the Archaic and Woodland periods and by reviewing published and unpublished reports on plant remains for the Mississippian, Protohistoric and Historic periods. Thus ubiquity values are in part a function of the quality and quantity of research done in various regions and of the completeness of the author's survey of available data. Since ubiquity is less subject to biases produced by differential preservation than are manipulations based upon seed quantities, this measure is probably a more reliable indicator of change.

Table 2 presents the proportional contribution of maypops seeds to the total number of fleshy fruit seeds recovered from Southeastern archaeological sites through time. A general trend toward comprising a greater percentage of fleshy fruit seeds is apparent. As a group, the Late Archaic through Late Woodland periods produce low maypops percentages compared to the Mississippian/ Protohistoric and Historic periods, although these values do not increase steadily over time. The Late Woodland percentage is lower than either the Late Archaic or Early and Middle Woodland. The relatively small number of sites used in calculations for these earlier time periods are likely to be responsible for this deviation. Nonetheless, there seems to be a dichotomy between pre-Mississippian and post-Mississippian representation of maypops seeds in archaeological deposits that correlates with the beginnings of the preeminence of maize as a crop plant in the East.

An even clearer pattern is obtained by comparing quantities of seeds recovered from different time periods within a more restricted geographical area. Data from Chapman and Shea (1981) from sites in the Tellico Reservoir were used for this purpose. Quantities obtained for each time period and representation of maypops as percentage of fleshy fruit seeds for the Tellico Reservoir are given in Table 3. In this case, there is clearly an increase in the representation of maypops

TABLE 2.—*Maypops seed counts and percentages.*

Period	Site	No. of Maypops Seeds	No. of Fleshy Fruit Seeds	% Maypops Seeds
Late Archaic	40LD38	1	284	0.5
	1FR310	5	5	100.0
Total		6	289	2.1
Early/Middle Woodland	9CK(DOT)7	1	3	33.3
	1FR310	5	6	83.3
	40MR23	4	46	8.7
	40CF32	2	146	1.4
Total		12	201	6.0
Late Woodland	40FR8	3	105	2.9
	1Gr1x1	1	6	16.7
	16WC5	1	69	1.4
	1JE31	1	50	2.0
	1JE33	2	332	0.6
Total		8	562	1.4
Miss./Protoh.	Moundville	44	1304	11.0
	40MR20	13	82	15.9
	Lubbub Creek	7	37	18.9
	9EB85	166	234	70.9
	22JE501	1	2	50.0
	9Cla62	2	261	0.8
	38AN8	12	50	24.0
	44HA22	3	40	7.5
	22Cl814	21	139	15.1
	31OR11	10	39	25.6
	40MR6	53	266	19.9
Total		332	2454	13.5
Historic	9MU102	11	511	2.2
	40MR62	6	29	20.7
	40MR2	53	103	51.5
	GP-HK-08	28	29	96.6
	40MR3	3	7	42.9
	31SKla	15	249	6.0
	31CH452	5	20	25.0
31OR231		64	271	23.6
Total		185	1219	15.2

TABLE 3.—*Tellico Reservoir sites, maypops percentages by period.*

	No. Maypops Seeds[1]	No. Fleshy Fruit Seeds[1]	% Maypops Seeds
Late Archaic	1	284	0.4
Middle Woodland	4	39	10.3
Early Miss.	20	57	35.1
Late Miss.	43	87[2]	49.4
Historic	118	359	32.9

[1]From Chapman and Shea (1981); estimates based on number of whole seeds + number of fragments/2.

[2]Excludes the ~2752 persimmon seeds reported, most of which were recovered from a single structure.

seeds from the Archaic to the Early Mississippian. Percentages are similar for the Early Mississippian, Late Mississippian, and Historic periods. A general pattern of increasing relative quantities from Archaic to Woodland and from Woodland to Mississippian and Historic periods is evident.

For the Southeast as a whole, calculation of ubiquity of maypops as percentage of sites from which it was recovered per time period produces stronger evidence of increasing use. These ubiquity values are displayed graphically in Figure 2. These data show a clear and steady increase in the likelihood of maypops being recovered from a site. The time periods can be roughly grouped into classes according to these ubiquity values. The first class (0%) includes the Early and Middle Archaic. The second (Late Archaic, Terminal Archaic and Early Woodland) has values near 7%. The third class includes the Middle and Late Woodland, both with values of 16.7%. The fourth and fifth classes include the Mississippian/Protohistoric and Historic periods, respectively. There is a strong positive correlation between lateness in the temporal sequence (and, presumably, the extent and intensity of anthropogenic disturbance) and the representation of maypops in the archaeological record as determined by ubiquity.

The geographical range of maypops during different time periods might also be used to assess its importance as a food plant in the Southeast. A range extension would be an expected consequence of husbandry of the species or simply of an increasingly close relationship with human populations. Figure 3 presents archaeological occurrences of maypops seeds constructed using sources listed in Table 1. Unfortunately, the archaeological record of the distribution of maypops is heavily biased by the nonrandom geographical clustering of research efforts. More importantly, the archaeological record is not extensive enough to provide a realistic depiction of the entire range of the species during different time periods. However, some aspects of the premodern range of maypops seem not to be merely products of sampling bias. In contrast to the modern range of the species (Fig. 1), there is so far no archaeological evidence of maypops from Kentucky, Illinois, or Arkansas. West-central Illinois has yielded a particularly large and well-researched body of paleoethnobotanical data (e.g. Asch and Asch 1985) and paleoethnobotanical research has been actively undertaken in both

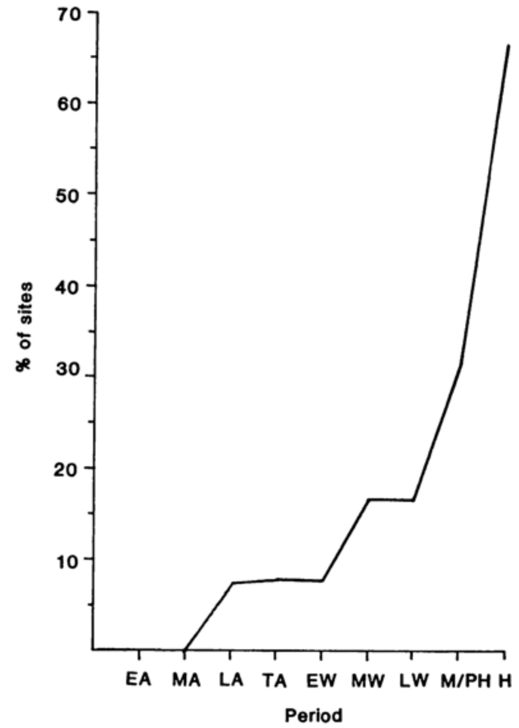

FIG. 2.—Archaeological ubiquity of maypops. The vertical axis indicates the percentage of total sites reporting plant remains that also reported maypops seeds. E = Early, M = Middle, L = Late, A = Archaic, W = Woodland, M/PH = Mississippian Protohistoric, H = Historic. Total numbers of sites for each time period are: EA, 8; MA, 4; LA, 14; TA, 13; EW, 13; MW, 18; LW, 30; M/PH, 32; H, 12.

Arkansas (Fritz 1986) and Kentucky (Watson 1985). Thus it is apparent that maypops either did not occur in these states in the prehistoric and early Historic periods or that it was not manipulated by people in such a way as to ensure its incorporation into the archaeological record.

IMPLICATIONS OF DISTRIBUTION AND USE PATTERNS

Having established a temporal pattern of increasing use of maypops in the archaeological record, it remains to be seen what hypotheses can be formulated to explain this pattern. Examination of evidence for the development of human-plant mutualism can help to define the ecological relationships between aboriginal populations and this species and how it may have changed over long periods of time. The hypotheses generated must be consistent with the observation that a general trend to increased use (and presumably abundance) of maypops in

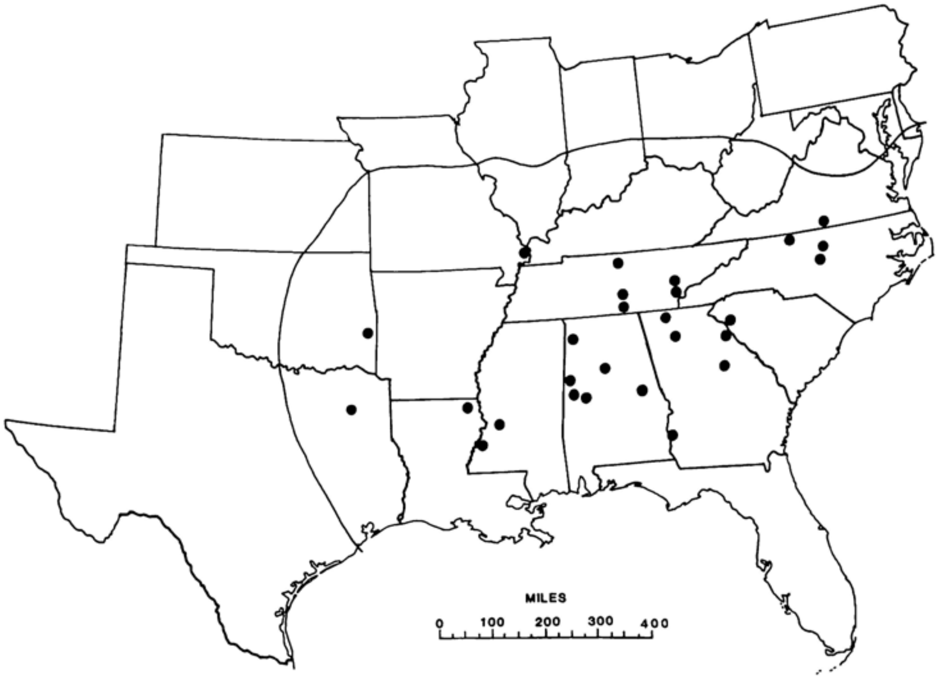

FIG. 3.—Archaeological occurrences of maypops. Each dot represents one pre-AD 1800 aboriginal site. The line indicates the approximate limits of maypops' modern range.

aboriginal contexts seems to have been followed by an extension of range in more recent times that coincides with its decline in importance as a food plant.

Rindos (1984:143) has developed a model of domestication as a "coevolutionary process in which any given taxon diverges from an original gene pool and establishes a symbiotic protection and dispersal relationship with the animal feeding upon it." Domestication is seen as a process in which both human and plant populations undergo change as a consequence of the increased fitness brought about by this relationship. If natural selection is the mechanism by which such a symbiotic relationship develops, an increase in the fitness of both symbionts is expected. Human populations benefit from these relationships through the energetic contributions of the plants involved, usually via their consumption. Two important components of human-plant relationships that enhance the fitness of the plant species involved and thus contribute to the development of mutualism are dispersal of propagules and environmental modification that increases the potential range of the plant.

Dispersal.—Animals may act as either generalized or specialized dispersal agents for plants. Generalized dispersal relationships are opportunistic whereas specialized dispersal usually results in obligate symbiosis and the evolution of morphological traits in the plant that attract the dispersal agent and prevent effective dispersal by other animal species. Both kinds of dispersal relationship may act to stimulate the development of human/plant mutualism, but in general it is specialized dispersal relationships that characterize the more fully developed phases of the domestication process (Rindos 1984:112-120).

Based upon its presumed dispersal relationship with humans, several characteristics of maypops indicate the likelihood of a mutualistic relationship between these two species. The maypops fruit is fleshy and edible, and its seeds have a durable woody wall. In fact, germination of seeds of some *Passiflora* species is thought to be enhanced by passage through the human digestive tract (Hladik and Hladik 1967, cited in Rindos 1984:135). Presumably maypops seeds, which are small enough to be comfortably ingested by a human being, also retain viability thereafter. These characteristics argue for a general pattern of animal dispersal in the species and provide weak evidence in favor of the assertion that a dispersal relationship between maypops and humans existed in the aboriginal Southeast, whether or not the seeds were intentionally planted. Stronger evidence for human dispersal of maypops seeds is provided by the presence of 80 seeds found in association with a human burial in a context suggesting ingestion at the Windover site in Florida, dating to around 7200 BP (Newsom 1988). Ingestion of the seeds prehistorically can safely be assumed, if not the viability of the seeds after consumption or the precise role of humans as dispersal agents.

Was this dispersal relationship opportunistic or obligate? The characteristics of the maypops fruit today do not point to an obligate dispersal relationship with humans. The fruits, although relatively large, are small enough for other mammals to consume, and the seeds themselves are small enough and sturdy enough to pass through other types of mammalian digestive systems and retain viability. In contrast, fleshy fruit-bearing species that rely on a more or less obligate dispersal relationship with humans often have unusually large seeds that prevent effective dispersal by smaller, non-human animals (Rindos 1984:117). Other correlates of this type of dispersal relationship include nutritional content and fruiting season. Species relying on specialized dispersal tend to be high in energetically expensive lipids and proteins, whereas opportunistically dispersed species contain the more common (and ''cheaper'') carbohydrates and water (Rindos 1984:116). Since the maypops fruit is high in water (89.6%) and carbohydrates (7.9%) (Paul Gardner, pers. comm., 1987), its characteristics more closely approximate those of the typical opportunistically dispersed fruit. The fruiting seasons of plants with obligate dispersal agents tend to be long thus ensuring that the dispersal agent will find and consume sufficient quantities of the fruit (Rindos 1984:118); by this criterion maypops, which fruits in late summer and early fall in the Southeast, seems to be opportunistically dispersed. In general, maypops fits the general pattern of temperate-zone angiosperms in lacking a specialized dispersal agent (Rindos 1984).

There is also no evidence that human populations had come to depend upon maypops as a food source, in contrast to what seems to have been the case with many starchy grain crops worldwide. Reliance on domesticates (i.e., obligate symbiosis) to maintain population densities at newly-established levels is not likely to occur when only fleshy fruit-producing species are involved, since these are dietary supplements rather than staples (although such supplements may be important nutritionally, if not calorically). The coevolutionary relationship is more likely to have been opportunistic than obligate for both symbionts.

Environmental modifications.—Another aspect of the domestication process, namely the creation and maintenance of disturbed habitats, can also be applied to the development of a mutualistic relationship between humans and maypops. The role of anthropogenic disturbance in the development of plant husbandry has long been recognized (Anderson 1952) and recently reconsidered in light of new archaeological evidence (B. Smith 1987). Development of anthropogenic habitats is an important component of human/plant mutualism since it benefits certain species by increasing their reproductive potential near human habitations (Rindos 1984:140). Dumpheaps and middens are examples of such anthropogenic habitats (Anderson 1952, Dewar 1982) as are old fields and abandoned gardens. The latter are parts of an already existing agricultural ecosystem. Maypops is today well-adapted to such disturbed habitats and in fact seems to require them in order to establish large populations.

A case study.—Perhaps it is more profitable to assess the roles of dispersal and disturbance in the development of mutualism between humans and maypops in the wider context of human/plant relationships. If domesticatory systems are considered, a temporal sequence of increasing interdependence of humans and certain plants can be proposed for the Southeast. Although full discussion of such a hypothesis exceeds the scope of this paper, Chapman *et al.*'s (1982) study of environmental disturbance and plant husbandry in the Tellico Reservoir can be used to summarize the changes involved and how they might be related to the development of symbiosis between humans and maypops.

The domesticates *Lagenaria* and *Curcurbita* are present by the Late Archaic (although *Cucurbita* at this time may have been only a protodomesticate). Maygrass (*Phalaris caroliniana* Walter), a small grain best classified as a quasi-cultigen (Yarnell and Black 1985), is also relatively abundant (Chapman and Shea 1981). The relative representation of taxa classified as "disturbance-favored" in the wood charcoal spectrum changed little from the Middle Archaic to the Late Archaic. Judging by the presence of the incipient cultigens during this period, initial processes of domestication were in place. The Late Archaic is also when maypops first appears in the archaeological record of the Tellico Reservoir.

By the Woodland period, the percentage of disturbance-favored taxa had increased to about 35%-45% from the 20%-30% of the Late Archaic. Cultigen sumpweed *Iva annua* var. *macrocarpa*), as well as large quantities of chenopod (*Chenopodium* sp.) first appear in the Early Woodland at Tellico. Knotweed (*Polygonum* sp.) was an important small grain crop in some parts of the East, but seems to have been of only minor importance in the Tellico Reservoir, occurring in small numbers during the Early Archaic and Middle Woodland. The earliest maize is from a Middle Woodland component (Chapman and Crites 1987), although it apparently did not become important until the Mississippian (Champman and Shea 1981).

Thus, the crop plants bottle gourd, pepo, maygrass, sumpweed, chenopod, knotweed and maize were all present by the Middle Woodland in the Tellico

Reservoir. Although archaeological evidence of Middle Woodland maypops is sparse for the Tellico Reservoir, the relative percentage of maypops seeds increased from the Late Archaic (Table 3). Presumably by this time domestication had become well-established and associated behaviors such as planting, cultivating, and other forms of management had come to characterize human relationships with the abovementioned plant species. Thus, maypops was one species participating in a network of domesticatory relationships evolving between plants and local human populations during the Woodland period. The wood charcoal evidence for increased environmental disturbance probably reflects both intentional disruption associated with clearing and planting as well as unintentional modification that allowed for the increase of populations of weeds and weed crops or quasi-domesticates, including maypops.

Elsewhere in the Southeast, as well as in the Tellico Reservoir, the Mississippian period saw the florescence of fully developed agricultural systems. In the late Mississippian "disturbance-favored" taxa make up roughly half of the wood charcoal analyzed, compared to about 25% for the early Mississippian. Early and late Mississippian periods produced similar percentages of maypops seeds, although late Mississippian values are somewhat lower. The Historic period shows a definite increase both in disturbance (as reflected in wood charcoal evidence) and in representation of maypops.

In general, the sequence presented in Chapman *et al.* (1982) supports the proposed relationship between maypops and anthropogenic disturbance. Maypops occupies a niche in various kinds of anthropogenic habitats ranging from slightly disturbed to agricultural (that is, dominated by human management of plant life cycles). Although itself not involved in an obligate dispersal relationship with humans, this species seems to have become dependant on anthropogenic disturbance for maintenance of large populations. In fact, development of truly agricultural ecosystems seems to have been accompanied by an increase in human consumption of fruits of this species (and presumably its abundance near settlements as well). These generalizations hold whether or not maypops was intentionally planted at any time during this chronological sequence.

Maypops, then, developed a mutualistic relationship with people that was facilitated by anthropogenic disturbance and dispersal, both processes that frequently provide a foundation for plant domestication. It may have been planted as well as harvested, but it is equally likely that maypops increased in abundance by invading gardens and was encouraged because of its usefulness. Because there is evidence that maypops developed a mutualistic, non-obligate relationship with humans and their agricultural and proto-agricultural ecosystems, should maypops be considered a domesticate?

The relationship between humans and maypops certainly fits the definition of domestication used by Rindos (1984). However, this definition is broad enough to encompass virtually all human-plant feeding relationships and is therefore of little use in differentiating between types of mutualism of varying intensity. Rindos (1984) divides the continuum of domesticatory relationships into categories according to the human behaviors (such as planting, storage and protection) and characteristics of plant populations associated with each. The sequence from incidental to specialized to agricultural domestication reflects the increasingly obligate nature of human-plant mutualism and the greater importance of environmental modification, dispersal relationships, and human management in fueling coevolution. Whether maypops should be considered as characteristically participating in incidental, specialized, or agricultural domestication cannot be satisfactorily resolved because its relationship with people is opportunistic. Although it is well adapted to agricultural systems, maypops is also at home in protoagricultural and non-agricultural systems.

Rindos' model is useful in identifying ecological processes that contribute to the development of mutualistic relationships between human groups and useful weedy opportunists such as maypops. The notion that domestication is a process rather than an event also makes intelligible the seemingly ambiguous status of species that do not fall into "wild" or "domesticated" categories but rather between these extremes of the continuum. On the other hand, application of the subcategories of domestication does meet with problems when faced with a species that seems to fit almost equally well into systems that might be characterized as incidental, specialized or agricultural. Perhaps for the time being, a term such as Yarnell's "weed crop" or "quasi-cultigen" (1987) is best for species that seem to be intermediate between cultigens and "wild" (i.e., utilized but not managed) plant resources.

RANGE EXTENSIONS

The present-day distribution of maypops reflects an apparent extension compared to its early Historic range (Fig. 3). At first glance this situation seems to be incompatible with the hypotheses generated about the roles of dispersal and anthropogenic disturbance in the development of human/maypops relationships in the Southeast. With the demographic decline of aboriginal population and subsequent replacement by European populations with different dietary and agricultural traditions, the species might be expected to experience a decline in abundance along with its symbiont. Its range also should be expected to contract. But the apparent extension is a sign of the ecological flexibility of maypops and its lack of an obligate relationship with specific types of anthropogenic disturbance.

The most likely explanations for this range extension are in fact compatible with Rindos' model and the hypotheses presented above. Although the feeding practices that are often crucial components of dispersal relationships were lost with the substitution of Euroamerican for Native American populations (and cultural systems), they have been replaced by the cultural practice of raising ornamentals. Extension of the range of maypops into Indiana, Ohio, Kentucky, and Illinois may be a result of the attempts of horticulturalists to raise maypops near their homes because of their showy flowers. The second component of this model of developing mutualism, anthropogenic disturbance, has increased since Euroamerican settlement. An extension of the range of any colonizing species should be expected under such conditions.

SUMMARY

I have presented archaeological evidence indicating that mutualism between maypops and human groups developed along with plant husbandry based chiefly upon other plant species. I hypothesize that the symbiotic relationship between maypops and human groups (or maypops and human cultural systems) reached a stable level in which a mutually beneficial (i.e., fitness-enhancing) relationship was maintained without the application of intentional behaviors such as planting, seed storage, and cultivation. In any case, I have shown that the patterns of aboriginal use of maypops can be explained in part by examining the evidence with reference to two important aspects of human-plant mutualism, seed dispersal and environmental modification. A modern extension of the geographic range of the species can also be explained simply with reference to these processes.

This study has illustrated the applicability of theoretical models of plant domestication (e.g. Rindos 1984) to paleoethnobotanical data and has also explored some of the problems encountered therein. Further study of species like maypops that fall outside of traditionally accepted categories such as "wild" and "domesticated" will be a necessary prerequisite to an adequate understanding of the full range of human-plant relationships.

APPENDIX

The following sources were consulted for information used in constructing the modern distribution map for maypops (Fig. 1): Allen *et al.* 1975; Avery and Loope 1980; Braun 1943; Brown 1972; Brown and Brown 1984; Clewell 1985; Deam 1940; Great Plains Flora Association 1977; Harvill *et al.* 1977; Kellerman and Werner 1894; Lakela 1965; Mellenger and Whipple 1981; Mohlenbrock and Ladd 1978; Radford *et al.* 1968; Sharp *et al.* 1960; Small 1913; E. Smith 1978; Steyermark 1962; Strausbaugh and Core 1978; Wherry *et al.* 1979. In addition to the Herbarium of the University of North Carolina at Chapel Hill, the Herbarium of the University of Alabama provided range information used in constructing Fig. 1.

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NOTES

[1]A vernacular name for the genus, passionflower, derives from the Italian *fior della passione,* applied to the flower because of its symbolic representation of objects, persons and events associated with the crucifixion (Fernald 1950:1042). The term maypops, often applied to the species, refers to its fruit.

[2]In addition to *Passiflora incarnata,* the following taxa reported in the sources consulted have been included in the fleshy fruit category: *Amelanchier, Celtis, Crataegus, Diospyros virginiana, Fragaria, Gaylussacia, Gleditsia triacanthos, Passiflora lutea, Physalis, Prunus, Rhus, Rubus, Sambucus canadensis, Solanum, Vaccinium, Viburnum, Vitis.*

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