ANALYSES OF NATURAL POPULATIONS OF PECAN, WATER HICKORY, AND THEIR HYBRID, BITTER PECAN

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Abstract.--Morphological leaf analyses were effective in studying Carya populations in southern Louisiana. Hybrid indices and scatter diagrams constructed from a composite of leaf and leaflet traits separated the parent species, pecan and water hickory, and characterized the intermediacy of the hybrid, bitter pecan. Water hickory had more individual tree variation than pecan, and it also displayed greater modification due to site differences. The large number of hybrid types encountered on several sites suggests that disturbed bottomland sites may support complex pecan-water hickory-bitter pecan populations.

Additional keywords: Multivariate analyses, hybrid viability, introgression, growth rate, Carya illinoensis, C. aquatica, C. x lecontei.

The ranges of pecan (Carya illinoensis (Wangenh.) Koch) and water hickory (C. aquatica (Michx. f.)Nutt.) are sympatric from southern Illinois down the Mississippi River Valley through Arkansas, Louisiana and East Texas. Within this area of overlap, however, the two species are normally found on somewhat different sites. Pecan is usually found on well drained loam soils, while water hickory is found on poorer sites such as imperfectly drained, heavy clay flats. In bottomland areas, different soil and drainage types are in close proximity, often represented by parallel flats, sloughs, and ridges. Therefore, while there is a spatial site preference barrier between the two species, they frequently occur together within effective pollination range. The species do hybridize in natural stands, but reports of the hybrid, bitter pecan (C. x lecontei), have been rather limited and it is generally considered a rather rare tree.

Bitter pecan may have first been described by Major John C. LeConte (for whom it is named) in 1853, but he classified the tree as a new species rather than the hybrid of pecan and water hickory. In 1889 Mohr observed that pecan hybridized with water hickory both in cultivation and in forest stands, and he also reported that these hybrids were frequently found. It was not until 1937, however, that Palmer described bitter pecan

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as a hybrid of pecan and water hickory. More recently, Stone et al. (1964) presented evidence that C. x lecontei possesses morphological and chemical traits that are intermediate to the parent species. Their work was done on herbarium specimens, however, and no population data were included.

Our studies indicate that contrary to earlier reports, the hybrid C. x lecontei may be found much more frequently on disturbed bottomland sites within the area of parental sympatry as part of complex Carya populations. The lack of field or population studies and the inability to identify hybrid individuals in the absence of seed were formidable barriers to early work. The seed, or nut, is the most easily distinguishable feature of the mature hybrid. Without the nut, the hybrid is very difficult to identify.

Population studies were made in the Baton Rouge, Louisiana area during the fall of 1975. These studies yielded a large number of putative hybrids from several locations and also identified a more extensive area which appears to support a hybrid swarm of Carya. This paper reports the development of an identification technique incorporating leaf traits into multivariate indices and the application of these to population analyses.

METHODS

Leaf samples were obtained from two Carya populations in southeastern Louisiana. Both populations are situated along the Mississippi River; the Baton Rouge population is located in East Baton Rouge Parish while the Raccourci Island population is in West Feliciana Parish, about 60 miles north of Baton Rouge.

The major difference between these two populations is that the Baton Rouge location is an urban area characterized by open-grown pasture trees, while the Raccourci Island location is still heavily forested with very little disturbance by man. Another difference, related to the habit of the trees, was in sampling procedure. A 30 ft. pruning pole was used to sample the trees in the Baton Rouge population, whereas a .22 caliber scope-mounted rifle had to be used to obtain samples from the crowns of trees at Raccourci Island. These disparate procedures resulted in the collection of shade leaves at Baton Rouge and sun leaves at Raccourci Island, and this affected the data analysis, as discussed later.

Leaf samples were obtained from five pecan and five water hickory trees at each location, while only three putative hybrids from Baton Rouge and two from Raccourci Island were collected. Putative hybrids were selected on the basis of nut characteristics. From each tree, eight individual leaves were collected, and data on the number of leaflets, rachis length, rachis diameter, leaflet length, leaflet width, number of serrations per two centimeters of leaflet margin, and amount of pubescence were collected.

Rachis diameter was measured with a vernier caliper to the nearest .01 mm at three places: below the first leaflet pair, midpoint of rachis, and below the last leaflet pair. The length of the rachis was measured to the nearest millimeter. The width and length of the leaflets, amount

of pubescence, and the number of serrations were measured on six of the main leaflets per leaf. Amount of pubescence was visually rated on a scale of 0 (no pubescence) to 4 (heavy pubescence).

Analyses of variance for unequal numbers of observations were run on each of the seven morphological variables. Correlations among each variable and their levels of significance were determined, along with variance components.

A hybrid index was constructed by assigning a relative value to each trait, based upon its diagnostic value as determined by variance component analyses (Table 1). The value of 0 designates the "typical" condition of *C. aquatica*, and the highest value describes the "typical" condition of *C. illinoensis*. Thus, in applying the index to population samples, intermediate types (putative hybrids and introgressants) should be characterized by intermediate index scores. When applied to the population of 25 trees in this study, the index generated total scores ranging from 3 to 32.

Table 1.--Characters and index values for Carya illinoensis and C. aquatica used to construct a hybrid index

Characters	*C. aquatica* index value	*C. illinoensis* index value
Nut (visible obs.)	0	6
Number of leaflets	0	4
Rachis length	0	6
Rachis diameter	0	4
Leaflet length	0	3
Leaflet width	0	3
Pubescence	0	6
Number of serrations	0	6
Total	0	34

RESULTS

The putative hybrids were found to be intermediate for all seven morphological characteristics when overall means were computed. However, there were differences between locations. The Baton Rouge population was characterized by larger and more numerous leaflets than the Raccourci Island population. This was due to the sampling procedure, which biased the type of leaf collected (i.e., shade leaves from the inner, lower crowns of open-grown Baton Rouge trees and sun leaves from the outer, upper crowns of forest-grown Raccourci Island trees). Nevertheless, when the means for each location were examined separately, putative hybrids were again intermediate for most leaf traits; six of seven in the Baton Rouge population and five of seven in the Raccourci Island population.

Analysis of variance determined that, for all seven traits, there was a great degree of individual tree variation in all taxa. Although this variation was large, it was not strong enough to mask the statistically significant taxa and location differences. Therefore, it appears that all seven of the morphological variables are under relatively strong genetic control, and may serve as useful criteria for analyzing natural populations. This is particularly true of the number of serrations and degree of pubescence, which seem to be under very strong genetic control and are independent of the other leaf traits.

The intermediacy of the putative hybrid samples indicates that the mature trees are indeed hybrids between pecan and water hickory and that they may be distinguished by means other than nut characteristics. One such method is the hybrid index first developed and used on Tradescantia herbarium specimens by Anderson (1936). The hybrid index is based upon the principle that there is a characteristic correlation between traits which are genetically independent of each other but which, collectively, lead to the type and range of natural variation caused by hybridization and subsequent introgression.

The frequency distribution of the total index values of the 25 trees (Figure 1) shows some typical parental types, and a large range of variation for both parental species. This variation suggests both environmental differences and, possibly, some degree of hybridity or introgression. However, the index values are somewhat biased because of the developmental correlations between some of the leaf characteristics, and also by the inclusion of nut characteristics as an a priori selection criterion. Nevertheless, the separation of typical parental types and intermediates by the index supports the conclusion that morphological leaf characteristics may be used to determine hybridity, and to characterize populations.

A graphic representation of the genetic structure of the population is available through the use of a scatter diagram. When properly designed and presented, the diagram represents a pictorial presentation of not only each individual but of the overall makeup of the population. The x and y axes are represented by two characteristics which have high diagnostic values, and individual trees are plotted at their absolute mean values. Secondary traits are quantified and are added to these initial points.

The statistical analyses again supplied the basis for the construction of the diagram (Figure 2). The degree of pubescence and number of serrations were used as the x and y axes, respectively. These two traits were negatively correlated (r^2=-.36), and best separated the parent species. Other traits, such as number of leaflets, leaflet length, rachis length, rachis diameter, and leaflet width were used as "secondary characteristics", which further helped distinguish the amount of variation. In the diagram, nut characteristics are indicated by different symbols merely to put the previous classification into perspective and to compare variation in nut characteristics with the separation based on leaf morphology.

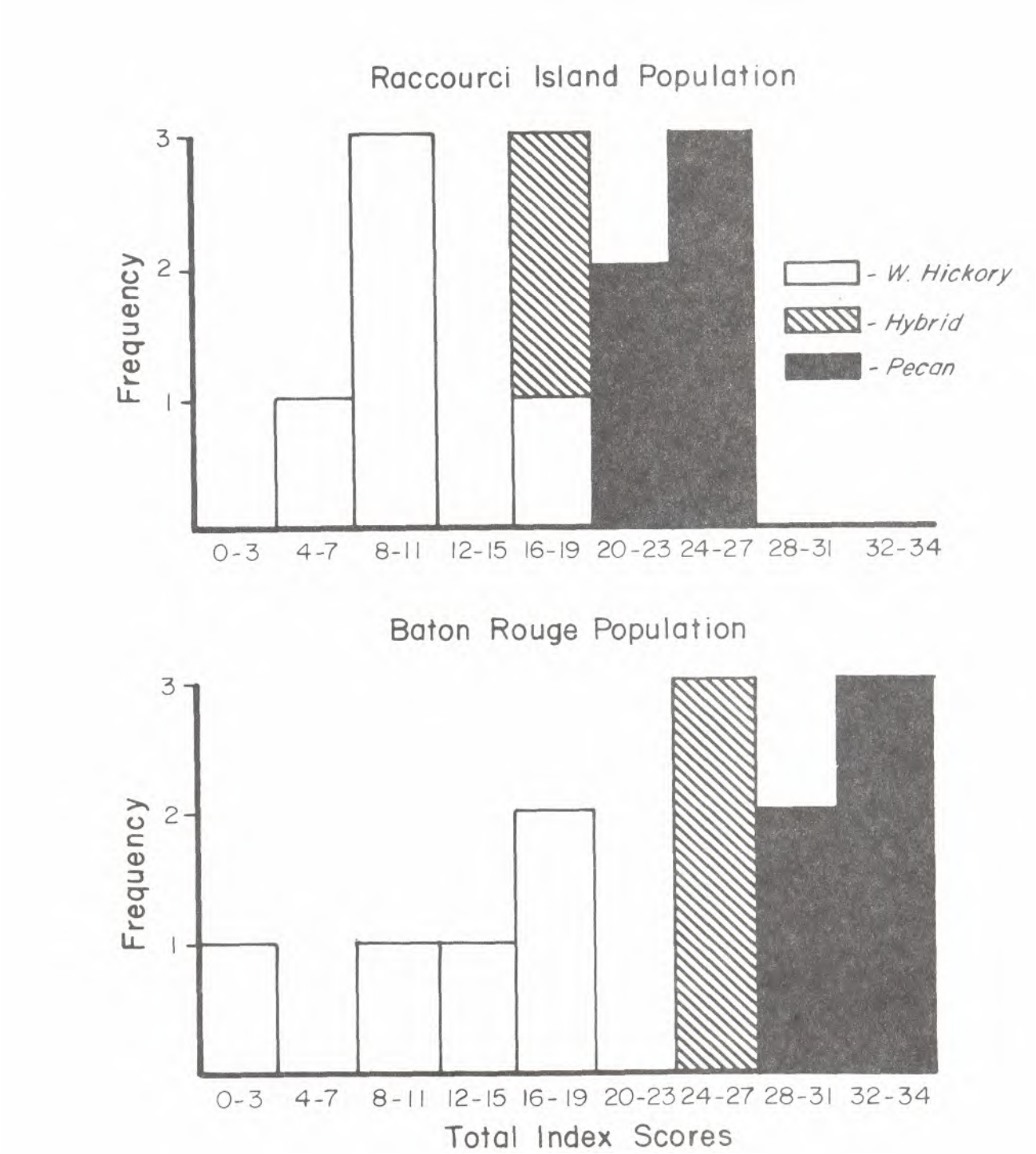

Figure 1.--Frequency distribution of individual index scores for Carya trees sampled at Raccouri Island and Baton Rouge, Louisiana.

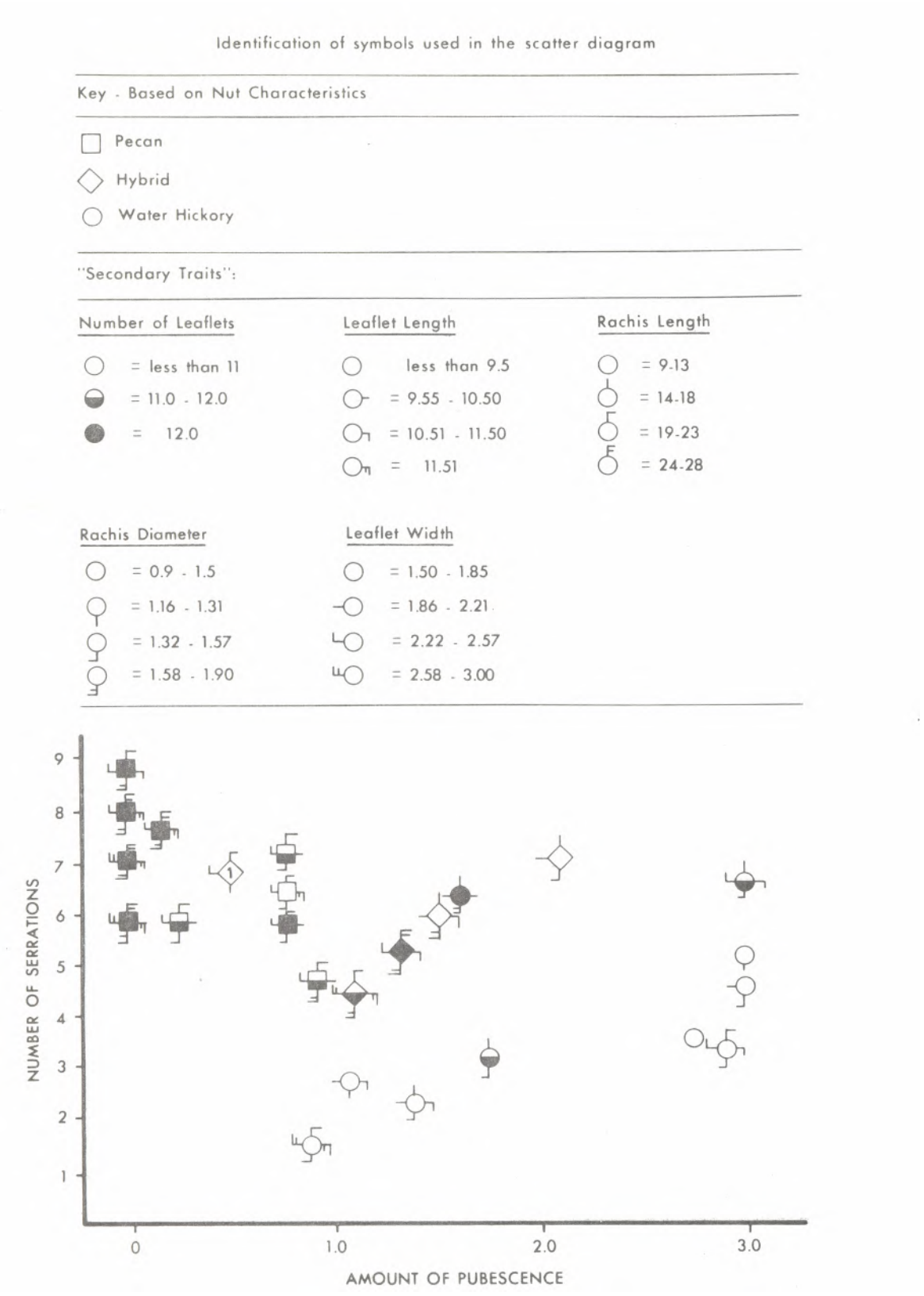

Figure 2.--Diagram of relationships among 25 Cara trees based on leaf morphology.

The diagram effectively separates the parental species, with the putative hybrids being more or less intermediate, However, there is some overlap with the parental species, especially in the secondary traits. It is interesting to note that the hybrid labeled "1", which is positioned near a typical pecan in number of serrations and degree of pubescence, is also very much like water hickory in secondary traits. Water hickory exhibits a much wider range of variation than pecan in both pubescence and number of serrations, but is relatively uniform in secondary traits. These results emphasize the importance of including an adequate number of diagnostic traits in the analysis, and sampling a large number of trees.

The multivariate analysis techniques, especially the scatter diagram, are useful to determine the population structure of Carya complexes and to validate hybridity on the basis of leaf morphology. In application, these methods are important because they provide an objective procedure to determine if the population includes mature hybrid trees. Studies have shown that natural hybrids produce viable seeds, representing a milieu of F2 or backcross progeny (Rousseau 1976), and the methods may prove useful in determining the extent and pattern of introgression.

Despite reduced viability of hybrid seed (Rousseau 1976) and other possible barriers to hybridization such as non-synchronization of flowering time or genetic incomparability, our study has shown that hybrid trees are encountered in natural stands at a much higher frequency than previously reported. It is quite probable that severely disturbed bottomland sites provide the environment for hybridization and introgression that favors the development of hybrid swarms. One such area has been located south of Baton Rouge, containing at least 14 putative hybrids in several age classes. This population is currently under study, using the techniques reported herein. Since the natural hybrid produces viable seed representing at least F2 or backcross generations, it might also be productive to institute a program of artificial hybridization. These F1, F2 and backcross hybrids could be used to establish parameters for studying natural populations.

Although the nut of the bitter pecan has no commercial value, the hybrid shows promise as a timber tree. Adams (1976) evaluated the early height growth of hybrid seedlings and found that the hybrids grew 60 percent taller than pecan for the first two years. Mature hybrid trees have excellent form, and attain heights of greater than 100 feet in forest stands. As a potential timber tree with the added attraction of a mast producer, the bitter pecan hybrid should be further investigated to evaluate its potential for reforestation of bottomland sites.

LITERATURE CITED

Adams, J. C. 1976. A study of genetic variability in wild populations of pecan (*Carya illinoensis* (Wangenh.) K. Koch). Ph.D. Dissertation, Louisiana State Univ., Baton Rouge. 111 p.

Anderson, E. 1936. Hybridization in American *Tradescantia*. Ann. Mo. Bot. Gard. 23:511-525.

LeConte, J. 1853. Description of a new species of pacane nut. Proc. Acad. Sci. Phil. 6:402.

Mohr, D. 1889. The pecan tree. Garden and Forests 2569-570.

Palmer, E. J. 1937. Notes on North American Trees and Shrubs. J. Arnold Arbor. 18:133-140.

Rousseau, R. J. 1976. A taxonomic and genetic study of *Carya illinoensis*, *C. aquatica* and their hybrid, *C.* x *lecontei*, M.S. Thesis, Louisiana State Univ., Baton Rouge. 83 p.

Stone, D. E., G. A. Adrouny and S. Adrouny. 1964. Morphological and chemical evidence on the hybrid nature of bitter pecan, *Carya* x *lecontei*. Brittonia 17:97-106.