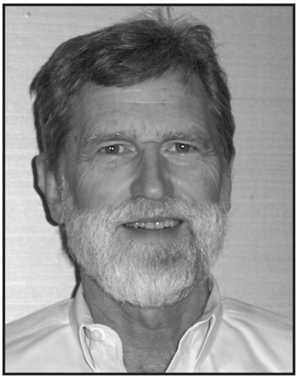

PECAN SEED STOCK SELECTION — REGIONAL IMPLICATIONS

L. J. Grauke
USDA-ARS Pecan Breeding and Genetics
Somerville TX

Grafted pecan trees are large, long-lived organisms whose growth shows the integrated, cumulative effects of a compound genetic system (both the rootstock and scion have an effect), operating within the constraints of the environment (climate, soils and associated biotic factors), under the influence of the cultural practices (irrigation, fertility and pest control) provided by the manager. Managers face complex choices in selecting the scion cultivars for their orchards. Often, rootstock selection is invisible to the manager and may not be an active choice. The choice was made by the nurseryman who planted a seed stock, grew the rootstocks, propagated the scion cultivars, and from whom trees were purchased. Understanding rootstock differences is crucial for the nurseryman, since increased seedling vigor reduces time from planting to sale, reducing management costs and increasing profit. Understanding rootstock differences can also be crucial for the pecan grower, since appropriate rootstocks adapted to the specific constraints of the orchard site can improve tree performance and increase profits while poor choices can result in devastating loss. For researchers, controlling the variable of rootstock is a question of degree and increases resolution in tests. The purpose of this paper is to review seed stock selection within regional constraints as they apply to nurserymen, growers and researchers.

Pecan is distributed in relatively contiguous populations from Illinois and Iowa in the north, to the Gulf Coast of Louisiana in the south, and from Indiana in the east to the Edwards Plateau of Texas in the west. Disjunct populations of (supposedly) native pecans are found east into Ohio and Alabama, west to the Allende Valley of Chihuahua, Mexico, and south to Oaxaca, Mexico (Fig. 1). To appreciate the adaptability of pecan, consider the range of climatic variation from north (with an average minimum winter temperatures of -10.8 C at Moline, IL) to south (where freezing temperatures do not occur in Oaxaca, MX). Consider the variation in the range of seasonal rainfall from east [with 1431.2 cm (56.3 inches) of rain/year in West Feliciana Parish, Louisiana] to west [452.7 cm (17.8 inches) of rain/year in Val Verde County TX). Consider the soil variation in the native range (Fig. 2), from the acidic Ultisols of the east to the calcareous

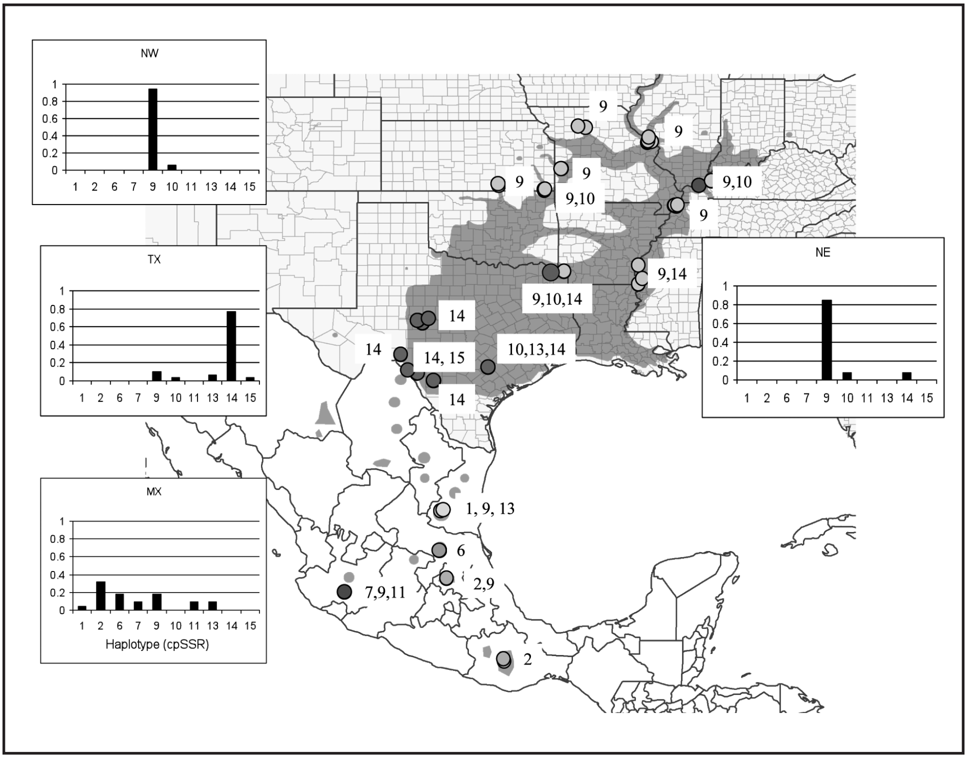

Figure 1. Distribution of plastid haplotypes in pecan populations, with frequencies by region (MX= Mexican populations, TX=all Texas populations, NE= populations along the Mississippi River, NW=populations from Illinois west to Kansas. Haplotype numbers represented in each population are shown to the right, or slightly below the location. Native distribution of pecan shaded. Population collection sites shown as circles. (See Grauke et al., 2010)

Mollisols of the west. Now consider that the cultivated area of pecan culture extends over an even greater range, from the Atlantic coastal states of Georgia, Florida, North and South Carolina, through the Mesilla Valley of New Mexico, the deserts of Arizona, to the Central Valley of California (Fig. 3).

To understand the genetic contribution of rootstocks, it is helpful to consider the flowering system of pecan, which contributes to the patterns of tree variation across the species range and must be controlled to optimize seed production. Pecan flowering is heterodichogamous: male and female flowers produced on the same tree mature at different times (Thompson and Romberg, 1985; Grauke and Thompson, 1996). Protandrous trees mature their male flowers first and shed pollen prior to pistillate receptivity. Protogynous trees mature female flowers first, with stigmas receptive before their catkins shed pollen. Some trees typically have complete separation of male and female bloom (complete dichogamy), while others have overlapping of female receptivity with pollen shed within the tree (incomplete dichogamy). When pollen from

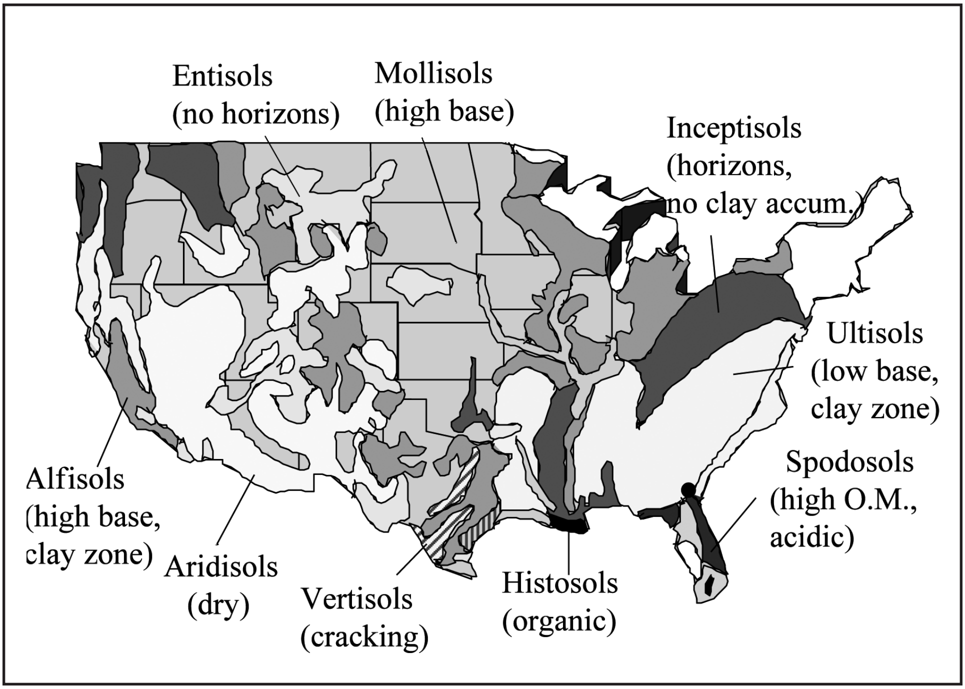

Figure 2. Soil orders of the United States. Adapted from Brady (1974).

a tree fertilizes a female flower on the same tree, the nut is “self pollinated” or “selfed”. Pollen from a different tree results in “cross-pollination”. Although a tree will be consistent in dichogamy from year to year, seasonal differences in temperature result in seasonal differences in bloom overlap between different neighboring trees. Seasonal differences also effect the extent of bloom separation within the tree (Worley et al., 1992; Grauke and Thompson, 1996), effecting the amount of selfing. This flowering system encourages cross pollination, increases heterozygosity and maintains genetic diversity in populations. Cross-pollinated nuts have higher percent kernel than self-pollinated nuts from the same tree (Romberg and Smith, 1946). Cross-pollinated nuts produce more vigorous seedlings than self-pollinated nuts, giving those seedlings a selective advantage in either a native population or in a nursery row.

Pecan pollen is distributed by the wind. The distance pollen travels has been studied in commercial pecan orchards due to its relevance for nut set and nut quality improvement provided by cross pollination (Wood, 1997: Wood and Marquard, 1992). Wood (1997) estimated that successful pollinations decrease if pollen donors are separated by more than 80 m. However, pollen may travel long distances in low frequencies, making the genetic contribution of the male parent very mobile. At the population level, it is hard to measure exactly how far pollen can travel and still be effective. In comparison to pollen, pecan nuts are large and heavy. Although dispersed to some extent by birds and mammals, the genetic contribution of the female parent is relatively sedentary. The mating system of migratory pollen and sedentary seed strongly encourages genetic diversity while allowing for local adaptation by natural selection (Namkoong and Gregorius, 1985).

It is important to note that the provenance of pollen origin influences the performance of the pollinated nut. If pollen comes from northern cultivars, nuts will germinate later than seed of the same tree pollinated with southern pollen (Hanna, 1972; Ou et al., 1994; Grauke, 1999;). Seedling size is also reduced by the northern pollen (Hanna, 1972; Grauke, 1999). This might offer a competitive advantage via increased vigor of seedlings pollinated by pollen coming from southern populations, if they establish in seasons when late freezes are not limiting. However, in seasons with late freezes, seedlings pollinated by northern pollen could have an advantage. This also has implications for nurserymen trying to increase seedling size and uniformity within the constraints of their nursery location.

There are native pecan populations that have been growing at their present locations for thousands of years. Pecan was used by the people living at Modoc rock shelter, Randolph County Illinois over 10,000 years ago (Styles et al., 1983). Pecans have been recovered in association with human artifacts from Baker's Cave in the Devil's River area of Val Verde Co., Texas, from strata dated to over 8,000 years ago (Dering, 1977; Hester, 1981). One of the easternmost populations of "native" pecans is the disjunct population in west central Alabama on the Black Warrior River, near Moundville, an important site of the Mississippian culture of west central Alabama (Welch and Scarry, 1995). Archeological excavations at Moundville confirm that pecan was present in those locations at least as early as the Moundville I phase (1050-1250 AD). The longer a population has been in a location, the greater the opportunity to develop local adaptation. Thousands of years is long enough time to develop local adaptation in each pecan growing region (east, west and north).

We have recently used microsatellite markers to characterize both the plastid profiles (inherited from the female parent) and the nuclear genome (distributed in the pollen) from native pecan populations from southern Mexico to the northern US (Grauke et al., 2010). Patterns indicate that local populations are very diverse across the range, with maternal markers showing different patterns than nuclear markers between populations (Fig. 1). We know that the "youngest" populations are in the northern part of the range, since they were dispersed or migrated there after the last glacial maximum, about 15,000 years ago (Delcourt and Delcourt, 1987). Northern populations have the fewest maternal profiles, with one type being very common. The greatest number of maternal profiles was found among Mexican populations. Although data are still being interpreted, patterns of haplotype diversity suggest that the populations in Mexico may be old, isolated and unique, raising possibilities of valuable local genetic adaptation. Although this does not mean we can make recommendations for seedstocks based on plastid haplotypes, it does reinforce that regional genetic differences carried in seed are present.

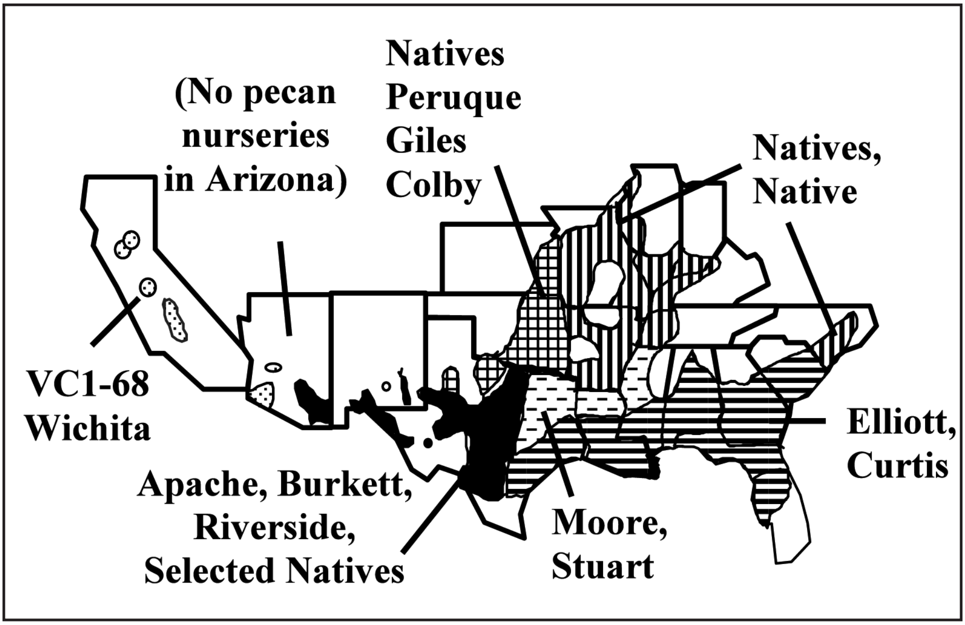

Figure 3. Seed stocks preferred by pecan nurserymen within regions.

Some patterns of growth in native populations are consistent across areas, indicate adaptation and influence selection. Trees originating from southern seed begin growth first in spring, with Mexican populations beginning growth as early as February. As a result, trees may be damaged by late freezes (Grauke, 1999; Volk et al., 2009). Trees originating from southern seed continue growth later in the fall (Dec.) and may be damaged by early freezes (Grauke 1999). Seedling size varies with seed origin, with decreases to the far north and far south of orchard location (Grauke 1999). Scion growth has been shown to vary as a function of rootstock, with early budding rootstocks forcing early growth in scions (Grauke and Pratt, 1992). Nutrient uptake by scions has been shown to vary as a function of rootstock (Grauke et al., 2003).

There are many genetic traits associated with seed from particular regions. The challenge is to understand which of them is adaptive, then select for improved performance in a target area. Although we are actively involved in that process and are succeeding in developing informative techniques, there is much work to be done. Over the short history of the commercial pecan nursery industry, there has always been regional variation in the use of seedstocks (Fig. 3). The driving force of selection has historically been vigor. By selecting for vigor, nurserymen reduce the time between planting, propagation and sale. When the diameter growth of seedstocks used by nurserymen is compared to the growth of unselected native pecans, the nursery selected seed produced the largest seedlings (Grauke 1999). Since southern seed stocks make the largest seedlings, there is an incentive to use that seed. If moved too far north, problems occur due to freezes.

Pecan rootstock recommendations for pecan growers: If you already have trees planted and do not know what your rootstock is, don't worry: there is nothing you can do about it. When planting a new orchard, pay attention to rootstock. The safest path for a pecan grower is to use rootstocks that worked successfully in the area in the past, that are currently being propagated in local nurseries. Improved methods of communication and transportation make it possible to purchase trees from distant sources. The farther a pecan grower goes from a local nursery supplier, the more important it is to confirm that the seedling rootstocks are appropriate for the intended orchard site. Catastrophic failure due to rootstocks has primarily been due to moving non-hardy materials too far north. Buy vigorous, well grown trees from a trusted nursery producer. The greatest vulnerability is apparently in the establishment phase of the orchard.

Pecan rootstock recommendations for nursery producers: Selected seed stocks can contribute increased vigor, reducing the time from planting to propagation, increasing profit. Cross pollinated seed will be more vigorous than selfed seed. Cultivars with complete dichogamy (no pollen shed during pistillate receptivity) will have less chance of self pollination than cultivars with increasing levels of incomplete dichogamy (pollen shed overlapping pistillate receptivity). The greater the diversity in parents, the greater will be the diversity of the progeny, so for increased uniformity, ensure limited pollen parents. For maximum uniformity, ensure that a single, selected cultivar with complimentary bloom is interplanted with seedstock cultivars. Pollen from northern sources will delay germination time of seed and reduce vigor in seedlings. Cull poor quality seed to improve stand uniformity. Since self pollinated seed has lower fill, culling seed further reduces selfed seed, increasing the vigor of the stand. Rogue out the smaller seedlings from nursery rows. Since self pollinated seedlings have lower vigor, culling smaller seedlings is the final step to ensure maximum heterosis and vigor due to outcrossed seed.

Pecan rootstock recommendations for researchers: Rootstocks grown from different open pollinated seed stocks influence patterns of nutrient uptake and growth of grafted trees throughout the life of the orchard. Control the variable of rootstock in field tests. To distinguish rootstock effects, careful control of site variation is required.

Following is a description of each of the major seed stocks currently used in the pecan nursery industry.

'Apache' is a controlled cross (Burkett X Schley) released by the USDA in 1962. It typically has about 50 nuts per pound, with around 60 percent kernel. Trees are protogynous, with mid- to late-season pollen shed and mid-season receptivity. Trees usually yield well and nuts are well filled, making seed abundant. Seed usually stores well and has acceptable germination and vigor. Initiation of growth in spring is not as early as 'Elliott' and 'Curtis'. 'Apache' and its ungrafted seedlings are very susceptible to pecan scab disease (*Fusicladium effusum* Winter).

‘Burkett’ is a native selection from Callahan County, Texas, from Battle Creek (which flows to the Brazos River). Trees are protogynous, with mid-season pollen shed and receptivity. The nuts are typically large (43 nuts per pound), very round, and may have 55 percent kernel. Poor filling is often associated with these nuts, as with Riverside. As a result, germination percentages may be low, but seedlings tend to be vigorous. ‘Burkett’ seedlings are very susceptible to pecan scab disease. Increased availability as well as improved performance of its progeny ‘Apache’ has resulted in reduced use of ‘Burkett’.

‘Colby’ is a native seedling selection made from Wash Orrell farm, Clinton County, IL, by Wm. W. and J. W. Lawrence, Fayette County, IL in the early 1940’s. Selected by A. S. Colby and J. C. McDaniel, Univ. Illinois, and tested as Illinois 1-19A. Released in 1957, named in honor of A.S. Colby. Protogynous, with mid- to late-season pollen shed and early pistillate receptivity. Medium precocity and prolificacy, with regular production. Matures in 160 day growing season; grown as far north as Niagara on Lake, Ontario, Canada. Used as a seed stock in KS and north.

‘Curtis’ is a seedling selection which grew from a nut of ‘Turkey Egg’ in Alachua County, Florida. The nut was planted 1886, bore first in 1893 and was introduced in 1896. ‘Turkey Egg’ was a seedling selection from John Hunt’s orchard in Bagdad, FL, established with seed brought from Mexico (Blackmon, 1929). ‘Curtis’ trees are protogynous, with late-season pollen and mid-season pistillate receptivity. Nuts are small (89 nuts per pound), but are usually well-filled (57 percent kernel). Seedlings tend to be uniform. ‘Curtis’ is used as a rootstock in the southeastern U.S. Seedlings were more damaged by freeze in Shreveport, Louisiana, than ‘Moore’ seedlings (Grauke and Pratt, 1992). ‘Curtis’ seedlings tend to be quite resistant to pecan scab disease.

‘Elliott’ is a seedling selection from Florida’s Santa Rosa County. Since pecans are not native to Florida, the parents of ‘Elliott’ were introduced. ‘Elliott’ was selected within the area where John Hunt established orchards using nuts brought from Mexico (Blackmon, 1929). Trees are protogynous, with mid-season pollen shed and early pistillate receptivity. Slow to bear, and not a heavy producer, but known for excellent quality nuts. Excellent scab resistance. Very susceptible to black aphid. Nuts are medium-¬sized (68 nuts per pound), round, and have about 54 percent kernel. Well-filled nuts germinate very well and produce uniform, vigorous seedlings that have good lateral root formation. Seedlings make early spring growth, making them more susceptible to freeze damage than ‘Moore’ in Shreveport, Louisiana (Grauke and Pratt, 1992). ‘Elliott’ seedlings tend to be very resistant to pecan scab disease.

‘Giles’ is a native selection from Cherokee County, Kansas, and is used as a seed stock in parts of Kansas, Oklahoma, and far north Texas. Trees are protandrous, with mid-season pollen shed and pistillate receptivity. Nuts are small (74 nuts per pound), with 53 percent kernel. The primary advantage of this seedstock is its hardiness, although it evidently does not have sufficient hardiness for Illinois, Indiana and parts of Missouri.

'Moore' is another seedling selection from Florida, originating in Jefferson County, near the town of Waukeenah. Pecans in Florida were introduced, but the source of seed from which 'Moore' grew is not known. 'Moore' carries the maternal haplotype most common in northern pecans (shown as 9 in Figure 1), but also found in populations from Mexico and Texas (Grauke et al., 2010). 'Moore' is a sib of the pecan cultivar 'Waukeenah', which was also used as a rootstock in the southeastern U.S. Trees are protandrous, with early pollen and mid-season pistillate receptivity. Moore was the most productive rootstock used in a test at Shreveport, Louisiana, in the 1930's (Sitton and Dodge, 1938) and has produced the largest seedlings in tests begun in the 1980's (Grauke and Sanderlin-----). It produces vigorous, uniform seedlings that have some scab resistance.

'Riverside' is a seedling selection from Big Valley, Mills County, Texas, that grew near the confluence of Pecan Bayou and the Colorado River. It is thought to have originated from the rootstock of a grafted tree on which the scion died. The rootstock may be a product of E. E. Risien's early rootstock development program. Our SSR analysis indicates that it is probably a cross between 'Longfellow' and either 'San Saba' or 'Family Use', all of which are Risien's selections. Trees are protandrous, with early pollen shed and mid-late season receptivity. 'Riverside' is commonly used as a rootstock for the western pecan growing region, due to demonstrated salt tolerance (Miyamoto, et al., 1985). Although it also has the reputation of having strong taproots, 'Riverside' seedlings form good lateral roots. Nut germination is limited by poor quality and can be a problem, since 'Riverside' trees often overbear. Seedlings tend to be very susceptible to pecan scab.

'Stuart' is a seedling selection from the orchard of J. R. Lassabe at Pascagoula, Jackson County, MS. Lassabe planted the orchard about 1874 using nuts of unknown parentage obtained from Mobile, AL. Trees are protogynous with late pollen shed and mid-season pistillate receptivity. Although once considered quite resistant to scab, now susceptible. Seedlings tend to be late to begin growth in spring, offering some protection from spring freezes.

'VC1-68' is a seedling selection that originated near Phoenix, Arizona, and is used as a rootstock in the west, especially California. The tree is protandrous with early pollen shed and mid-season pistillate receptivity. Nuts are very large (41 nuts per pound) but are thick-shelled, resulting in low kernel percentage (43 percent kernel). Nuts germinate well and seedlings are uniform and vigorous, with excellent lateral root formation. The parent is very susceptible to scab, but observations of progeny have not shown a particular liability. Freeze susceptibility may limit use of this rootstock to the southern part of the southeast and southwest.

'Wichita' is from a controlled cross ('Halbert' X 'Mahan') made in 1940 by L. D. Romberg, USDA-ARS, Brownwood, TX. The scion was budded into a bearing tree in 1941, first fruited in 1947, and was tested as 40-9-193. 'Wichita' was released in 1959 and has been widely planted in the western pecan region. Scab susceptibility limits use of Wichita in the southeast. Nuts tend to be well filled, germinate well, and seedlings grow vigorously, but typically share the seed parent's susceptibility to scab (Thompson and Grauke, 1994).

There are many pecan rootstock questions still to be answered. We need to understand more about regional adaptation in order to develop improved methods of selection. Regional differences in soils and climates, coupled with long-term adaptation in native populations, reinforces the recognition of regional boundaries of seed stock deployment. Resolution of rootstock effects will increase as we refine methods of evaluation and use them in critically structured test systems that control the variable of seedling rootstock.

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