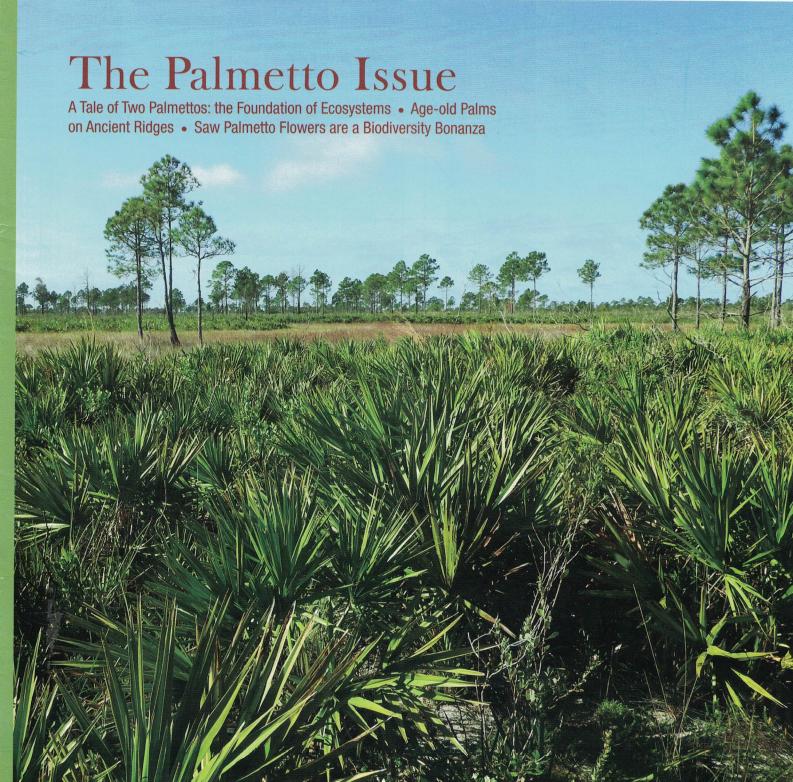
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Palmetto



A Tale of Two Palmettos: The Foundation of Ecosystems



Figure 1: Ripe (black) and unripe (orange) fruits of saw palmetto 10 months after a prescribed fire at the Archbold Biological Station. Photo by Dr. Warren Abrahamson.

"...The wilderness country looked very dismal, having no trees, but on sand-hills covered with shrubby palmetto, the stalks of which were prickly, so there was no walking amongst them..."

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The Quaker merchant Jonathan Dickinson was describing the foreboding coastal saw palmetto (Serenoa repens) landscape following his 1696 shipwreck near his namesake state park on Florida's Atlantic coast. Held for nearly a month by the native Jobe people, Dickinson and his companions did not enjoy some foods in their keepers' diet particularly the fruits of saw palmettos. "...the Cassekey [Jobe king] ordered Master Joseph Kirle, Solomon Corsson, my wife and me, to sit upon their cabbin to eat our fish, and they gave us some of their berries to eat; we tasted them, but not one amongst us could suffer them to stay in our mouths, for we could compare the taste of them to nothing else but rotten cheese steep'd in tobacco juice" (Small 1926).

After dissecting hundreds of saw palmetto fruits to determine their energy, mineral element, nutrient, and water contents, my wife Chris and I can empathize with Dickinson and his companions' inability to eat the repugnant saw palmetto fruits. Yet, these fruits so repulsive to humans are favorites among raccoons, opossums, foxes, whitetail deer, black bears, feral hogs, gopher tortoises and others (Halls 1977, Bennett and Hicklin 1998, Tanner et al. 1999, Dobey et al. 2005). There's a good reason they are favorites. Fruits of the widespread saw palmetto are a high-quality wildlife resource with an energy content (per dry mass) and level of total digestible nutrients (i.e., digestible proteins, fats, carbohydrates and fiber) comparable to turkey oak acorns (Abrahamson and Abrahamson 1989, Layne and Abrahamson 2010). Compared to saw palmetto, the fruits of the co-occurring but narrow Florida-endemic scrub palmetto (Sabal etonia) contain less energy and total digestible nutrients but more fiber. Given their taste, I'll never replace the blueberries or bananas on my breakfast cereal with palmetto drupes!

My fascination with palmettos began in 1972 during my first visit to south-central Florida's Archbold Biological Station (ABS). The ubiquity of palmettos across the landscape made me wonder what attributes enabled their tremendous success. Palmettos appeared to provide a matrix for their ecosystems. They are what ecologists refer to as "foundation species," that is, species that play major roles in structuring a community. So what features of palmettos facilitate their success in environments with nutrient-impoverished soils, frequent fires, and seasonal droughts? The answers lie in their growth forms, patterns of growth, and reproductive responses.

The thick, evergreen, heavily cutinized leaves of palmettos are well designed to conserve water and nutrients (Tomlinson



Figure 2: A dense understory of saw palmetto in a recently burned cutthroat grass flatwoods at the Archbold Biological Station. The cluster of scrub palmettos left of the arrow are surrounded by a sea of saw palmettos. Photo by Dr. Warren Abrahamson.

1961), two resources often in short supply in sandy soils and during Florida's dry seasons. Moreover, the long-lived leaves of palmettos provide an advantage over plants with short-lived leaves under nutrient-poor and low-light conditions. On a global level, plants of nutrient-impoverished and/or low-light habitats have longer living leaves than plants of nutrient-rich or high-light environments. This is because harsh environments force inherently slow rates of photosynthesis and high leaf construction costs (Kikuzawa and Ackerly 1999, Wright et al. 2002, Wright et al. 2005, Poorter and Bongers 2006). Simply put, longer leaf life spans allow time to recoup leaf construction costs.

Palmetto leaf life spans can be as long as 3½ years but life spans vary across regions, habitats, and even within habitats. Saw palmettos growing on seasonally xeric, nutrient-impoverished sands at ABS exhibit longer leaf life spans [mean = 2.4 years (Abrahamson 2007)] than those growing in more mesic, coastalplain flatwoods [1.5-2.0 years (Hilmon 1969)]. Likewise, the leaves of ABS scrub palmettos have longer life spans [mean = 2.5 years (Abrahamson 2007)] than those of dwarf palmetto (*Sabal minor*) growing in rich alluvial soils [just over 1 year (Hesse and Conner 1996)]. Scrub palmetto's longer leaf life span likely compensates for construction costs of its thicker and presumably more costly leaves relative to dwarf palmetto leaves (Zona 1990).

Leaf life spans of palmettos are inversely related to light availability. Palmetto leaves survive longer in shaded environments compared to high-light environments at ABS. Average leaf life spans for palmettos of open-overstory flatwoods, for example, are 2.2 years, whereas life spans average 2.8 years in long-unburned, shaded sand pine scrub (Abrahamson 2007).

In addition, palmettos modify their leaf sizes according to light availability. We found that palmettos growing in nearly

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closed-canopy sand pine scrub have the largest leaf blades, longest petioles, and greatest total leaf area, whereas the smallest leaf blades, shortest petioles, and least total leaf area are associated with palmettos in open-canopy scrubby flatwoods. Palmettos compensate for reduced light availability with increased leaf areas which intercept more light. Moreover, saw and scrub palmetto leaves differ in size within the same habitat. Scrub palmetto leaves are larger; they survive longer; but have fewer leaves compared to saw palmettos. Depending on the habitat and plant size, saw palmettos maintain 7-9 leaves while scrub palmettos retain only 3-5 leaves (Abrahamson and Abrahamson 2006, Abrahamson 2007).

The few, but large leaves of palmettos are an anomaly among their neighbors that have numerous small leaves — the typical arrangement for plants of nutrient-impoverished and/or low-light habitats (Ackerly et al. 2002). Palmetto leaves are roughly 10 times longer and have two to three orders of magnitude more area than the leaves of sympatric plants (Abrahamson 2007). Why are the leaves of palmettos so large? The most likely explanation is the constraint imposed by their evolutionary past (Ackerly 2004). Palms possess some of the largest leaves known, yet among palms, saw and scrub palmettos bear diminutive and few leaves (Tomlinson 1990, Zona 1990, Henderson 2002) — a probable adaptation to the nutrient-poor, seasonally xeric conditions.

How can palmettos prosper in fire-prone environments? When burned, palmettos grow new leaves with added urgency to quickly restore their leaf canopies (Hough 1965, Abrahamson 1984, Abrahamson and Abrahamson 2006). As a consequence of their long leaf life spans and hence limited leaf turnover, recently burned palmettos have elevated numbers of leaves and greater total leaf areas compared to pre-burn levels. Canopies with additional leaves boost photoassimilate gains, which aid recovery of the resources expended to regenerate leaves following fire (Abrahamson and Abrahamson 2006).

Furthermore, fire stimulates palmetto reproduction. We observed strong flowering by palmettos in an ABS sandhill following each of three successive fires during an 8-year period (Abrahamson 1999) but saw only limited flowering during the intervals between fires. What is it about fire that produces these episodic reproductive events and why do some, but not all, palmettos flower?

We non-destructively estimated the mass of individual palmettos using a measure of crown size and the number of living leaves (Abrahamson 1995, 1999) and we tested experimentally whether increased nutrient availability, enhanced light availability, leaf loss, or a combination of these factors affects palmetto reproduction (Abrahamson 1999). The study results were unmistakable. Mass (hence the amount of stored resources) determines whether a palmetto flowers and how much it flowers, a pattern similar to that of other plants (Clark and

Clark 1987, Thompson et al. 1991, Chazdon 1992, Kettenring et al. 2009). As expected, palmettos that flower occur under more open canopies than those that don't flower. Clearly both size and light availability are factors influencing flowering. But most telling was the finding that leaf loss is a powerful flowering stimulant if the palmetto is sufficiently large. Even though the soils in palmetto habitats have increased nutrient availability following fire (Schafer and Mack 2010) fertilization did not encourage palmetto flowering. The trigger that turns on reproduction in both saw and scrub palmetto is leaf loss (Abrahamson 1999).

Clearly saw and scrub palmettos share many fundamental adaptations to their environment but there are differences. For example, in spite of saw palmetto's ability to have net photosynthetic gains under low light and relatively high gains under high light (DeMoraes 1980), saw palmettos require more light than do scrub palmettos to initiate flowering (Abrahamson 1999). In addition, saw palmettos produce higher quality fruits and they produce far greater quantities of fruits than do scrub palmettos in large part because scrub palmettos are considerably smaller on average than saw palmettos (Abrahamson 1995, 1999).

Plants of fire-prone Florida ecosystems evolved with summer, wet-season fires. Yet today anthropogenic fires occur during any season, often in the winter, dry season. When burned during the dry season, saw and scrub palmettos break dormancy to produce new leaves but the two palmettos differ markedly in their reproductive responses to winter fires. Saw palmettos produce flowers that are asynchronous with flowers of summer-burned or unburned saw palmettos, which results in reduced fruit set. In contrast, winter-burned scrub palmettos remain vegetative through the first growing season following fire and initiate flowers that are synchronous with unburned scrub palms in the second growing season (Abrahamson 1999).

Growth rates of palmettos are markedly slowed by the nutrient-impoverished, droughty, fire-prone environments in which they grow. Adult saw palmettos grow very slowly (~2 cm/year) in their native habitats (Hilmon 1969, Abrahamson 1995) and their seedlings require many decades to a century just to reach modest size (Abrahamson and Abrahamson 2009). But fortunately for ecological restoration saw palmettos can grow considerably faster in disturbed sites such as former citrus groves (Foster and Schmalzer 2012).

Given slow rates of growth, persistence is essential if palmettos are to reach reproductive size. But is persistence an option for palmettos in the face of repeated fire and drought? Palmetto adults and seedlings show astonishing persistence and tolerance. We began following marked adults of saw and scrub palmettos in 1980 and by 1991 we were annually evaluating growth and survival in 940 adults and 178 seedlings. The severe and prolonged drought of 1999-2001 that affected Florida and the southeastern USA provided a unique opportunity to measure the impacts of drought on palmettos. Then, an intense,

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dry-season wildfire at the height of the drought allowed us to witness the combined effects of severe drought and an extremely hot wildfire on all marked seedlings and a subset of our marked adults (Abrahamson and Abrahamson 2002, 2009).

All marked populations of adult palmettos lost mass during the drought but remarkably, the survivorship of adult palmettos was little affected by drought or by the combination of drought and fire (Abrahamson and Abrahamson 2002). No adult saw palmettos died and only two smaller-than-average adult scrub palmettos died, one of which was impacted by the wildfire. Seedlings fared less well during the drought and fire, yet astoundingly 70% of the 1989 flatwoods cohort and 55% of the 1989 scrubby flatwoods cohort survived through the preceding 13 years, drought, and wildfire. As of 2008 (after 19 years), 57% of the flatwoods cohort and 35% of the scrubby flatwoods cohort continued to survive. But after 19 years, the flatwoods seedling cohort averaged only 17 cm in height and the scrubby flatwoods cohort only 14 cm. (Abrahamson and Abrahamson 2009).

Slow plant growth and plant longevity (persistence) are often linked (Johnson and Abrams 2009), which raises the question of just how long slow-growing palmettos can live. Saw palmettos, which are highly clonal, have amazing longevity, living literally thousands of years (Takahashi et al. 2011, 2012). The accompanying article in this issue "Age-old Palms on Florida's Ancient Ridges" tells the fascinating story of how we aged several clones of saw palmettos by coupling genetic fingerprinting technology and mathematical modeling with field studies (Abrahamson 2016). We suspect that the non-clonal scrub palmetto also has impressive longevity given its slow growth but this needs study.

Saw and scrub palmettos share many essential attributes, so it's no surprise that they co-occur in many Florida habitats. Yet, their fine differences should generate divergence in how they use those habitats. Indeed, sampling of their abundances across ABS habitats documented that saw palmetto reaches its highest and lowest abundance in flatwoods and sandhills, respectively. Scrub palmetto, on the other hand, is infrequent in flatwoods but abundant in sand pine scrub and sandhills (Abrahamson 1995). When we examined the distribution of individual palmettos, we discovered in flatwoods, for example, that saw palmetto is tolerant of both poorly drained and betterdrained microsites while scrub palmetto is clumped in betterdrained microsites. Furthermore, neighboring plants differed for the two palmettos. Scrub palmettos had nearly twice as many fetterbush (Lyonia lucida) plants and other scrub palmettos as neighbors and an order of magnitude more sand live oaks (Quercus geminata) as neighbors than did saw palmetto. The competitive interactions of the two palmettos are at least partially ameliorated by microsite and neighborhood differences.

Palmettos are beautifully adapted to the rigors of the environment in which they evolved. But today's world is different than the evolutionary past due to anthropogenic influences.

The evolutionary fire regimes of palmettos included late-spring and summer fires, but today they are often burned by winter, dry-season fires. Fire-return intervals, including an absence of fire, are unlike those of their evolutionary past. Palmettos are experiencing altered hydroperiods due to drainage and water use. Climate change with alteration of temperatures and precipitation is likely to challenge species, including palmettos, unable to redistribute in a highly fragmented landscape. Even the uncontrolled harvesting of saw palmetto fruits from natural communities for pharmaceutical products has consequences. The strong market for saw palmetto fruits has generated poaching from federal, state, and private lands, reducing fruit availability for wildlife and plant recruitment. The long-term persistence of palmettos is threatened by human influences.

About the Author

Dr. Warren G. Abrahamson is an evolutionary ecologist whose research interests include Florida vegetation ecology, conservation biology, and plant-animal interactions of goldenrods, gall insects, and natural enemies as well as of oaks and gall wasps. He is a Research Associate at the Archbold Biological Station, Venus, FL, and is the David Burpee Professor of Plant Genetics Emeritus at Bucknell University, Lewisburg, PA.

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References Cited

Abrahamson, W. G. 1984. Species responses to fire on the Florida Lake Waies Ridge. American Journal of Botany 71: 35-43.

Abrahamson, W. G. 1995. Habitat distribution and competitive neighborhoods of two Florida palmettos. Bulletin of the Torrey Botanical Club 122: 1-12.

Abrahamson, W. G. 1999. Episodic reproduction in two fire-prone palms, *Serenoa repens* and *Sabal etonia* (Palmae). Ecology 80: 100-115.

Abrahamson, W. G. 2007. Leaf traits and leaf life spans of two xeric-adapted palmettos. American Journal of Botany 94: 1297-1308.

Abrahamson, W.G. 2016. Age-old palms on Florida's ancient ridges. The Palmetto 33: 4-7, 15.

Abrahamson, W. G., and C. R. Abrahamson. 1989. Nutritional quality of animal-dispersed fruits in Florida sandridge habitats. Bulletin of the Torrey Botanical Club 116: 215-228.

Abrahamson, W. G., and C. R. Abrahamson. 2002. Persistent palmettos: effects of the 2000-2001 drought on *Serenoa repens* and *Sabal etonia*. Florida Scientist 65: 281-292.

Abrahamson, W. G., and C. R. Abrahamson. 2006. Post-fire canopy recovery in two fire-adapted palms, *Serenoa repens* and *Sabal etonia* (Arecaceae). Florida Scientist 69: 69-79.

Abrahamson, W. G., and C. R. Abrahamson. 2009. Life in the slow lane: Palmetto seedlings exhibit remarkable survival but slow growth in Florida's nutrient-poor uplands. Castanea 74: 123-132.

Ackerly, D. D. 2004. Adaptation, niche conservatism, and convergence: comparative studies of leaf evolution in the California chaparral. The American Naturalist 163: 654-671.

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Age-old Palms on Florida's Ancient Ridges

The dwarf palm known as saw palmetto (Serenoa repens) occurs in most of Florida's natural upland plant communities. With horizontal stems that look something like an alligator's back (Figure 1) because of persistent leaf bases and large, palmate leaves (Henderson et al. 1995, Henderson 2002), the saw palmetto is among the Southeast's most recognized plants. Yet few who recognize saw palmetto appreciate its ecological importance to plant communities or realize that saw palmettos can survive to become thousands of years old!

The individuals of saw palmetto that we see are most often a small fraction of a much larger palmetto clone composed of genetically identical saw palmettos. As saw palmettos spread along the ground via their horizontal stems, their stems often fork in response to multiple sprouts, damage from fire, or mechanical

injury to form additional stems (Figure 2). This clonal trait facilitates the remarkable longevity of saw palmettos that can attain 5,000 and more years of age (Takahashi et al. 2011, Takahashi et al. 2012).

But you should wonder: "How can we determine the age of palms given both their lack of wood and absence of annual growth rings?" While it's relatively straightforward to age woody trees such as oaks, hickories, and maples that lay down annual growth rings, estimating longevity of plants that lack annual growth rings and those that live in aseasonal tropical environments presents an appreciable challenge. My laboratory group at Bucknell University took up the challenge to estimate ages of saw palmettos and to address additional questions about saw palmetto as well as the scrub palmetto (Sabal etonia) because of the importance of palmettos to the ecology and conservation of vegetation associations throughout Florida and the southeastern USA coastal plain.



Figure 1: The "alligator backs" of saw palmetto rhizomes reveal the wandering growth patterns of saw palmetto following an April 2014 fire at the Avon Park Air Force Range. Photo by Dr. Steve Orzell.

Our quest to understand palmetto ecology and survivorship began in 1980 when my wife Chris and I tagged 120 saw palmettos and 120 scrub palmettos that grew at the Archbold Biological Station (ABS) near the southern end of the Lake Wales Ridge (LWR). In subsequent years, my Bucknell University students and I tagged an additional 700 saw and scrub palmettos and marked 178 palmetto seedlings. Through the years, our censuses and measurements of these palmettos generated insights into the distribution of palmettos across vegetation associations (Abrahamson 1995), the episodic flowering of palmettos following fire (Abrahamson 1999), their remarkable ability to withstand drought and fire (Abrahamson and Abrahamson 2002, Abrahamson and Abrahamson 2006), the longevity of their leaves (Abrahamson 2007), the incredible survivorship and slow growth of palmetto seedlings (Abrahamson and Abrahamson 2009), as well as the data necessary to estimate the ages of saw palmetto clones (Takahashi et al. 2011, Takahashi et al. 2012).

Estimating the ages of saw palmetto required data from three separate approaches. (1) Long-term field studies of tagged saw palmettos allowed us to determine their stem growth rates, which told us how fast their horizontal stems move through space (Abrahamson 1995). (2) Laboratory studies using Amplified Fragment Length Polymorphisms (AFLP), a

genetic "fingerprinting" method that could accurately distinguish saw and scrub palmettos (including their seedlings) and importantly could differentiate the individuals that belonged to different clones. Finally, we used (3) Minimum Branching Trees (MBT), a mathematical model that enabled us to calculate the time necessary to produce the arrangement of the saw palmettos that were parts of an identified clone (Abrahamson 1995, Takahashi et al. 2011, Takahashi et al. 2012).

With a goal of estimating longevity of plants that potentially live a very long time, we needed a location with sufficient long-term stability that plants with the potential to live a long time could realize their potential. ABS on Florida's Lake Wales Ridge was an ideal location given its elevation above sea level and the relatively stable long-term climate of the Florida peninsula. For most of the Earth's geological history, ocean levels have been considerably higher than current sea level (Muller et al. 2008). For example, during the late Pliocene and early Pleistocene ocean shorelines were 50 meters higher than today's shorelines – a level that inundated substantial portions of the Florida peninsula (Webb 1990). Florida's sand ridges, including the Lake Wales and Brooksville Ridges, offered refugia for terrestrial plants and animals. As a consequence, the LWR exhibits remarkable endemism today (Deyrup and Eisner 1993, Stap 1994). While northern glaciated and near-glaciated regions experienced dramatic plant community changes during the

past 50,000 years (Jacobson, Jr. et al. 1987), Florida had more limited climatic fluctuations during the same time period (Watts and Hansen 1994). Times of higher precipitation produced pinedominated forests on the LWR while during more arid times, oak savannas and grasslands were common. The modern vegetation of the LWR has been in place for 5,000 years. This climatic history



Figure 2: The branching and interactions of saw palmetto ramets are apparent in a flatwoods at the Archbold Biological Station. Photo by Dr. Reed Bowman.

set a stage that has been conductive to the survival of long-lived plants (Grimm et al. 1993).

Our ABS-based field studies established a number of attributes shared by saw and scrub palmetto, but we also identified important differences in the two palmettos. The patterns of stem growth in saw palmettos produce considerable clonal propagation. Plant ecologists have a specific term, "genet," to refer to clonal plant colonies. A genet is a group of genetically identical plants growing in a given location that have originated vegetatively from a single ancestor. The genet is composed of individuals that plant ecologists refer to as "ramets." A ramet is a physiologically distinct organism that may or may not be connected physically to other members of a genet. Thus, most often the plants of saw palmetto that we see are ramets that are part of a clonal colony or genet. In sharp contrast to saw palmetto, scrub palmetto with its corkscrew, S-shaped subterranean stem is non-clonal and does not grow horizontally in space (Corner 1966, Abrahamson 1995, Takahashi et al. 2011). While the clonal growth of saw palmetto coupled with its horizontal stem growth allow us to estimate its longevity, the longevity of non-clonal scrub palmetto cannot be estimated with the methods that work so conveniently with saw palmetto.

Saw palmetto ramets grow very slowly (ranging from 0.6 to 2.2 cm/year) in the nutrient-poor sands of the LWR but their growth rates differ across years and among vegetation associations (Abrahamson 1995). For example, saw palmettos in ABS flatwoods grew faster than those growing in scrubby flatwoods (i.e., oak scrub). Because the saw palmettos that we sampled for clonal spread and longevity lived in scrubby flatwoods, we used the 4-year mean stem growth rate of 0.88 cm/year that was based on 60 saw palmettos that occurred at three ABS scrubby flatwoods sites (Abrahamson 1995, Takahashi et al. 2011). Using mean stem growth rate, we could approximate the age of a saw palmetto ramet by multiplying the length of its living stem by the site-appropriate growth rate. Doing so produced age estimates that suggested 500-year-old saw palmetto ramets were common. However, our field observations told us that saw palmettos were clonal and that the palmetto ramets composing a clone (=genet) do not remain permanently connected to one another. As saw palmetto ramets grow, the "tail" end of their stem dies, eventually causing physical separation of ramets. Hence, we needed a means to identify separate ramets of a given clone. The age of a saw palmetto clone depends on the distances that separate its component ramets and on the number of palmetto ramets that compose a clone. Large clones will be older than the estimated ages of the individual palmetto ramets that compose it.

In order to genetically identify palmettos that occurred within a 20×20 m scrubby flatwoods grid, we collected and froze small leaf fragments from 218 saw palmetto ramets, 55 scrub palmetto ramets, and 139 field-unidentifiable small individuals noting the 1×1 m cell in which the palmetto occurred (Takahashi et al. 2011, Takahashi et al. 2012). The field-unidentifiable indi-

viduals could be seedlings of either saw or scrub palmettos or saw palmetto vegetative sprouts. Back at our Bucknell laboratory, we used AFLP genetic analyses which identified 263 saw palmetto (9 of which were seedlings and 44 vegetative sprouts) and 134 scrub palmettos (79 of which were seedlings and 0 vegetative sprouts). Our results confirmed our field observations that scrub palmetto is non-clonal. However, as expected, the résults showed that saw palmetto was highly clonal, frequently occurring as clonal networks (Takahashi et al. 2011, Takahashi et al. 2012). Among the sampled saw palmettos, we distinguished five clones (=genets) of varying size and shape (Figure 3).

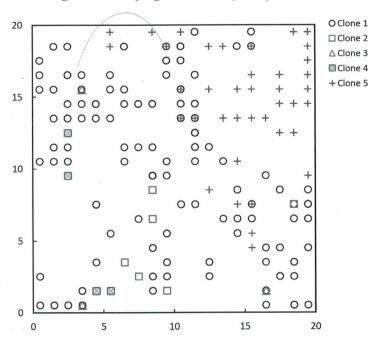


Figure 3: Clonal distribution of ramets of five clones of saw palmettos within our 20 x 20 m study plot in scrubby flatwoods at Archbold Biological Station (from Takahashi et al. 2011). Used with permission of John Wiley & Sons, Inc.

Our genetic analyses showed us the locations of saw palmetto clonemates, but it was impossible to know how the distribution of clonemates that we saw developed through time because the physical connections among clonemates are lost over time. To overcome this hurdle, we repeatedly constructed Minimum Branching Trees (MBT) by successively designating each adult ramet as a starting point for the clone's development and using the sprouts as the endpoints. The MBT analyses generated a series of the most parsimonious (i.e., the simplest explanation) pattern of clone development for each clone. Finally, we calculated a series of maximum distances from each ramet to its clonemates. From these distances, we could calculate the maximum, minimum, and average estimated age for each clone (Figure 4). Amazingly, the estimated ages for the five saw palmetto clones within our scrubby flatwoods grid ranged from 1,227 to 5,215 years (Table 1).

So how accurate are these estimates? Our estimates are likely conservative for several reasons. Foremost, our samples

Configuration with Minimum-Maximum Distance root=874 (11.50, 10.50), max=22.993 to 702 (0.50, 2.50)

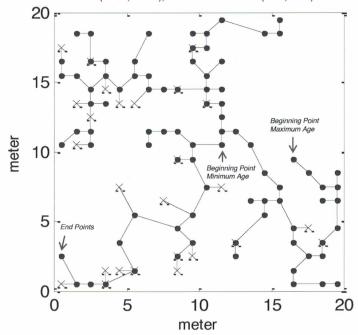


Figure 4: Minimum branching tree (MBT) for minimum and maximum age estimations for Clone 1. Filled circles are adult ramets and Xs are sprouts. Beginning and end points for the maximum age and minimum age estimation are indicated with arrows (from Takahashi et al. 2011). Used with permission of John Wiley & Sons, Inc.

most likely did not include all the ramets of a given clone. The distributions of ramets composing clones 1 and 5 suggest that there were additional ramets that went unsampled outside of our grid (see Figure 4). Our 20 x 20 m sample grid was embedded within a hugely larger saw palmetto population and it is quite possible that the origins of clones were outside the sampled grid. In addition, estimation of clone ages using MBTs is conservative because clones likely developed much less parsimoniously. Furthermore, we assumed constant stem growth rates based on adult saw palmettos. Yet, we know from nearly 20 years of

seedling measurements that palmetto seedling growth rates in ABS scrubby flatwoods (Abrahamson and Abrahamson 2009) are about one-third (0.3 cm/year) that of nearby adult palmettos. Our MBT models do not account for the decades to centuries needed for seedlings or sprouts to extend their stems spatially and to grow to reproductive size (Abrahamson 1995, Abrahamson 1999, Abrahamson and Abrahamson 2009). For instance, if we use the conservative estimate of 100 years for a sprout to become an adult, the estimated maximum age of clone 1 increases to 8,000 years. As a consequence, we suspect that 10,000-year-old saw palmetto clones are common in LWR scrubby flatwoods (Takahashi et al. 2011).

The remarkable longevity of saw palmetto is not unique among clonal plants. A Pennsylvania clone of box huckleberry (Gaylussacia brachycera) has an estimated age of 8,000 years, a Mojave Desert clone of creosote bush (Larrea tridentata) is thought to be 11,700 years old, and a Utah clone of quaking aspen (Populus tremuloides) may be 80,000 years old (Sussman 2014). Nonetheless saw palmetto's slow growth and longevity offers insight into land preservation and conservation. Saw palmetto has been part of Florida ecosystems for a remarkably long time. But human changes and disturbances to those ecosystems are adversely impacting plants like saw palmetto as well as the numerous species that are dependent on palmettos ((Maehr and Layne 1996). If scrub plants such as saw palmetto are extirpated at a site, reestablishment is extremely difficult and very slow (Schmalzer et al. 2002).

The next time you look at a saw palmetto, consider its potential age relative to your own age. Our short human lifetimes most often cause us to think short term – particularly relative to conservation of nature and nature's resources. But if we were to think on the scale of saw palmetto lifetimes, we would make far better decisions about our environment and on behalf of future humans.

	Clone 1	Clone 2	Clone 3	Clone 4	Clone 5
Number of ramets	148	8	3	4	48
Number of sprouts	36	2	0	3	3
Estimated age (years)					
Maximum	5,215	2,253	3,181	1,294	3,774
Minimum	2,609	1,227	1,702	1,294	1,710
Average	3,920	1,552	2,689	1,294	2,483

Table 1: Number of ramets, sprouts, and estimated ages for five saw palmetto clones identified from a 20 x 20 m grid (Takahashi et al. 2011).

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