

### INTRODUCTION

In recent years, the generic name *Arundinaria* has become restricted in usage to the three native 'cane' species of eastern North America: *gigantea* (= *macrosperma*), *tecta* and *appalachiana* (Triplett et al. 2006, 2009, 2010). The closest living relatives of these bamboos are in East Asia, where they are now classified into several distinct genera (Li et al. 2006, Triplett and Clark 2010). The purpose of this paper is to summarize what is known, superficially, about the biology of *Arundinaria*, as applied to problems in horticulture, restoration and ecology.

Arundinaria has several unusual or unique characters, when compared to other native plants of eastern North America. These characters are also typical of many bamboos in temperate regions of East Asia. In flowering behavior, however, species of Arundinaria differ from most of their long-lost East Asian cousins, which generally exhibit gregarious flowering over many 100s or 1000s of acres or even whole regions, after non-flowering periods of several decades. Flowering is generally rare and sporadic in Arundinaria, with no evidence of such widespread gregarious events.

The following review is based on literature, meetings and conversations with growers, plus 20 years of personal experience in Kentucky trying to grow and establish cane, especially transplants into restoration sites and, more recently, seedlings. My associates at Roundstone Native Seed Inc. (Bonnieville, Kentucky), John and Randy Seymour, have also become much involved, and they are also working with Jeremy Hamlington and Mark Smith of Auburn University in Alabama (School of Forestry and Wildlife Sciences). I do not deal here with tissue culture and micro-propagation, which is being studied by Baldwin et al. (2009), Margaret

**Figure 1**. Mason Brock helping the author to collect cane seed (*Arundinaria gigantea*) in June 2009. This is the only patch of cane known in Harrison County, Kentucky, growing along Wornall Lane about 4 miles north of Griffith Woods. During 2009-2012, there have been several flowerings of cane in central Kentucky.



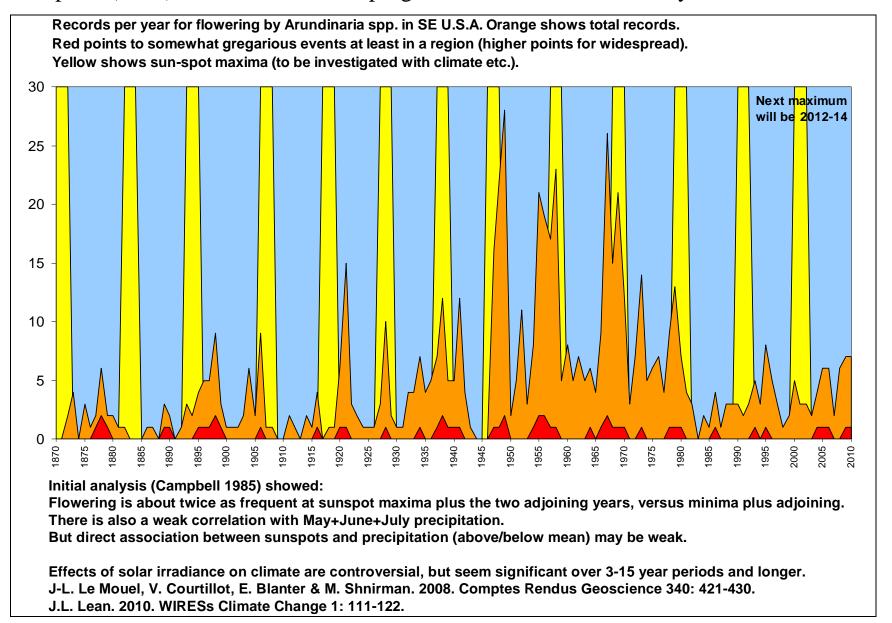
Cirtain (Dept. of Biological Sciences, Univ. of South Carolina, pers. comm.), Sharon Kester (Dept. of Horticulture, Univ. of Kentucky, pers. comm.) and others. Moreover, Susanne Lucas (Pioneer Plants LLC, Plymouth, Massachusetts), in partnership with Oprins Plant NV in Belgium, is developing the market for mass-production of selected bamboo clones.

### FLOWERING, SEEDING AND GERMINATION

Essential sources of information on flowering of *Arundinaria* are the many herbaria, with dried specimens dating back to the earliest periods of botanical exploration (Campbell 1985). In recent decades, there has also been some useful accumulation of records by the American Bamboo Society (Betty Shor, La Jolla, California, pers. comm.), Brian Baldwin at Missississipi State Univ. (Dept. of Plant and Soil Sciences, pers. comm.; Baldwin et al. 2009), and other researchers (e.g. Marsh 1977, Gagnon and Platt 2008, Mathews et al. 2009). There appears to be some tendency for more frequent flowering in some years in some regions, with clusters of records covering 100s or 1000s of square miles. But even this clustering generally includes no more than 1-10% of the plants within those regions. There may be weak association between flowering frequency and years with sun-spot maxima and wetter periods, but deeper analysis is needed (Figures 1 and 2).

There is virtually no definitive documentation of life-span for individual clones of *Arundinaria*. A few horticultural observations indicate that as little as 3-15 years can sometimes elapse between seed germination and flowering, but these plants are probably aberrant individuals within seed lots (observations of myself, G. Cooper, G. Lundquist, and others compiled by Betty Shor). Long-term observations of particular cane patches in the wild suggest that the life-cycle is usually at least several decades. In an early account, Neisler (1860)

**Figure 2**. Numbers of flowering records for *Arundinaria* spp. from the southeastern U.S.A., in relation to date and the sun-spot cycle. This is an updated version of the presentation in Campbell (1985), but still a 'work in progress' that needs further analysis.

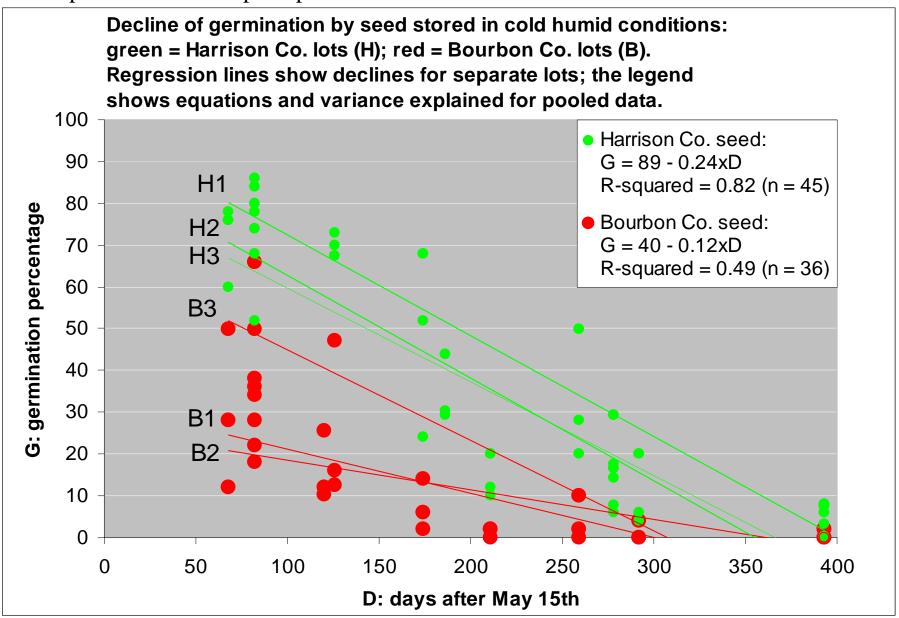


indicated that ca. 25 years was typical in *gigantea*, but longer periods are generally suspected today. There are only two flowering records for *appalachiana* (1956 and 2006). Whole clones of *Arundinaria* usually die after flowering and seeding but sometimes death is delayed for 1-3 years. Stephen Breyer (Tripple Brook Farm, Southampton, Mass., pers. comm.) has reported recovery of *gigantea* without producing seed at a site well north of its native range.

Potential problems from inbreeding might occur if flowering is somehow decoupled from regular gregarious behavior. Research of Franklin (2004) on a bamboo species in northern Australia has shown much higher rates of cross-pollination, seed-set, and regeneration among plants in peak flowering years, versus precocious or straggling plants. Baldwin et al. (2009, and pers. comm.) suspect similar problems based on initial observations of low seed set in Mississippi, with much more viability after artificial cross-pollination. However, I have got good germination (ca. 80-100% of sound fresh seed) with several batches of seed that were probably self-pollinated in Kentucky.

Bamboo seed generally dies after drying out at ca. 60-80°F (15-25°C) for 2-4 months, and is thus considered 'recalcitrant' (McClure 1966, Stapleton 1987, 1994, Bellairs et al. 2008). Drying in some sun for one day is often useful, in order to slow immediate germination and reduce microbial attack, but several days may be damaging. Germination usually occurs within a few days if seed are kept in a continually moist state after shedding. However, a few reports indicate that germination by some East Asian species of colder zones may occur after 1-5 years of 'dormancy' on the forest floor or similar storage (Qin 1985, Taylor & Qin 1988, Stapleton 1994, Wang et al. 2007). Stapleton stated: "Seed of the smaller subtropical and temperate bamboos may have substantial dormancy, and it might germinate more quickly after a period of cold pre-treatment, such as stratification or refrigeration at 5°C [41°F]."

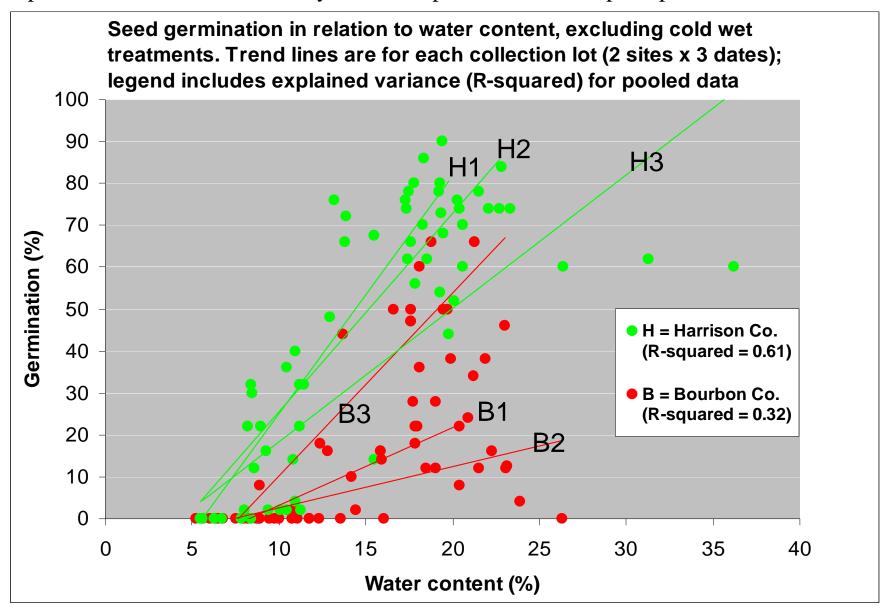
**Figure 3**. Decline of germination by seed stored under cold humid conditions. Six seeds lots (3 dates at 2 sites) were stored under various conditions; full explanation of methods and analysis will be provided in a complete publication.



Recent research on seed of *Arundinaria* by myself at the Univ. of Kentucky (in the lab of Carol & Jerry Baskin) and Mississippi State University (Baldwin et al. 2009; D. Neal et al., in prep.) has confirmed that even in cold storage at ca. 32-35°F [0-2°C], germination of seed (when warmed-up and wetted for 14 days) gradually declines to zero after 1-2 years, with considerable variation between seed lots (Figure 3). Zero germination is observed after seeds drop below ca. 6-8% moisture content (Figure 4). To date, no freezing treatment has been found to preserve viability for longer periods. But after cold damp storage, with or without slight freezing, there was faster germination in some seed from Kentucky, as compared to cold dry storage. After wetting and maintaining sound seed at ca. 70-80°F [25-30°C], germination generally starts within a few days, and the first leaves appear at 1-4 weeks. Older seed tends to be slower, with leaves sometimes not appearing until 2 or even 3 months. If seed does not start to germinate within a few weeks, it is almost certainly dead—or perhaps fatally infected by microbial growth.

Like other bamboos (Janzen 1976), cane seed is consumed by a wide range of pathogens, pests and herbivores. For example, much fungus and other microbial growth often occurred in petri dishes used for 14-day germination tests by myself. However, there was significantly less microbial growth after seed had been stored in cold damp versus cold dry treatment; seeds lost weight during cold damp storage, presumably exuding anti-microbial compounds. Sharon Kester (pers. comm.) has had great difficulty extracting sterile material from seeds for tissue culture. It is likely that cane seed in the wild is generally threatened with excessive drying and microbial attack. Cane seed often does not mature due to attack of flowers by weevils, which need to be identified. Due to such insects, several patches of flowering cane in Hart County have generally failed to produce any mature seed within the past decade, before they die (R. Seymour, pers. comm.). However, an initial flowering patch in 2000 did produce much seed,

**Figure 4**. Relationship of germination to moisture content of seed, dried slowly in varied types of storage. Data from cold damp treatments and frozen treatments are excluded. Full explanation of methods and analysis will be provided in a complete publication.



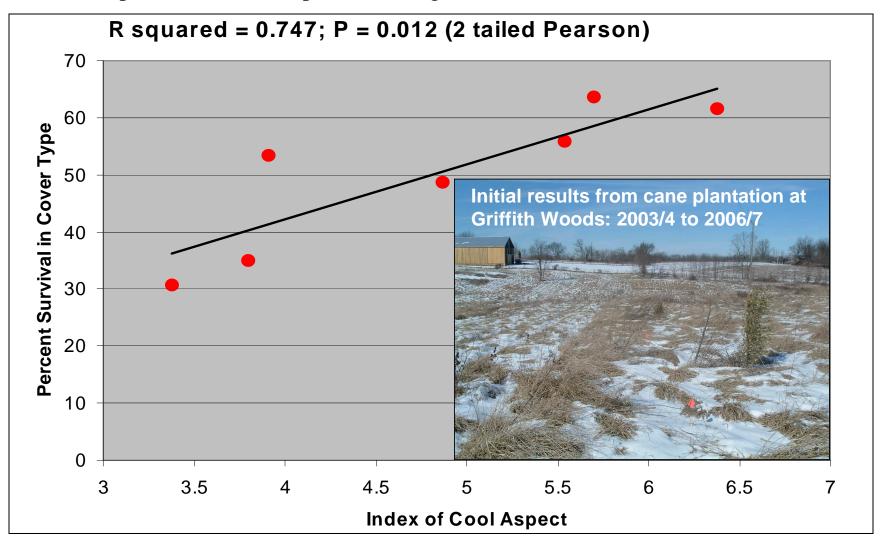
which was used by Cirtain et al. (2004, 2009) to grow seedlings for their experiments. Small mammals are avid eaters of cane seed—it is usually essential to protect flats of germinating seeds using wire mesh or other means.

### GROWTH, PROPAGATION AND ENVIRONMENTAL FACTORS

`Based on general horticultural experience, bamboos in general are known to be particularly sensitive to interruptions in moisture supply, poor aeration of roots, and other physical stresses. For example, Stapleton (1987) found that division and repotting in hot dry nurseries was risky, "thus it seems division of seedlings is only suited to cooler or more humid nursery locations." Thanks especially to experienced growers like Bill Hendricks (Kline Nursery, Perry, Ohio), Ned Jacquith (Bamboo Garden, North Plains, Oregon) and Nevin Smith (Suncrest Nurseries, Watsonville, California), it is possible to gain some general insights into the best physical conditions for growing temperate species. From varied successes and failures, it appears to me that stresses often cause plants to go into physiological 'shock'—presumably involving growth-suppressing hormones, and sometimes aggravated by microbial problems. With return of good conditions, it can take up to a year for plants to resume rapid growth. In containers, much more stress can occur with smaller sizes, especially if exposed to extremes of temperature and moisture during daily or seasonal cycles. Study of hormones in bamboos is a promising field that will eventually help in understanding of how these plants deal with stress (e.g. Zhang et al. 2011).

The obvious unusual feature of *Arundinaria*, compared to associated plants in North America, is its long spreading rhizome system, allowing clonal growth for 100-1000 meters or more during its sexual life cycle. Brian Baldwin (pers. comm.) has evidence from DNA

**Figure 5**. Survival of cane plantings at the 'front-central' field of Silver Lake Farm (Griffith Woods), in relation to an index of cool aspect. Data from ca. 300 plants (mostly 10 year old seedlings) are grouped here into seven vegetation types as the plotted observations, each the mean of many plants. The index of cool aspect = [[difference of site aspect from 200° azimuth (SSW)] × [slope in degrees] / 90]. Ongoing research indicates that growth (instead of survival), shows a weak positive relationship with drainage.



markers that one clone of *gigantea* has spread over 1-2 km at Dahomey National Wildlife Refuge in Mississippi. Another unusual feature is the concentration of extension growth by new culms during just 1-2 months in the summer, usually when soils are still damp after spring rains. It is likely that the extensive rhizome system allows rapid supply of moisture for such growth. Moreover, on less well-drained ground, the air-canals in rhizomes of *tecta* (and sometimes *appalachiana*) are presumed to enhance oxygen delivery for the rapid extension of culms (McClure 1963, Triplett et al., 2006). Similar air-canals are known in some East Asian species (e.g. *Phyllostachys atrovaginata*, *heteroclada*, *nidularia*). New culms are protected by leathery sheaths, which are shed within a year or so, especially when upper nodes develop branches. There is one dominant branch per node, like most temperate bamboos of eastern China and Japan, but in marked contrast to most Sino-Himalayan and tropical bamboos.

Arundinaria is sometimes assumed to be a plant of wetlands—the USDA has misleadingly listed it a "facultative wetland" species (Griffith et al. 2009). Although sometimes flooded for short periods in the wild, these bamboos do not have optimal growth on saturated soils, but tecta is more tolerant (Baldwin et al. 2009; with R. Jolley, M.C. Mills, and D. Russell, in prep.). Like most bamboos, Arundinaria is moderately 'mesophytic'—easily stressed by droughts or floods during the growing season, especially if the rhizome system is reduced or cut. Cirtain et al. (2004) found that gigantea seedlings on well-watered but well-drained soil had more one-year growth (ca. 28 cm shoots) than periodically dried or periodically flooded (ca. 20 cm shoots). However, transplants or cut rhizome sections do best when humidity is maintained at high levels. Adam & Sue Turtle (Summertown, Tenn., pers. comm.) recommend that during the growing season, transplanted bamboos in general should be regularly soaked and kept in shade for a month or so before planting out. Baldwin et al. showed that the vascular system of gigantea is sensitive to embolism (cavitation) when rhizomes cut. These researchers

also recommend soaking root-rhizome systems of larger plants for a month or more, or enclosing plants with leafy tops in plastic bags, before they are set out in the field.

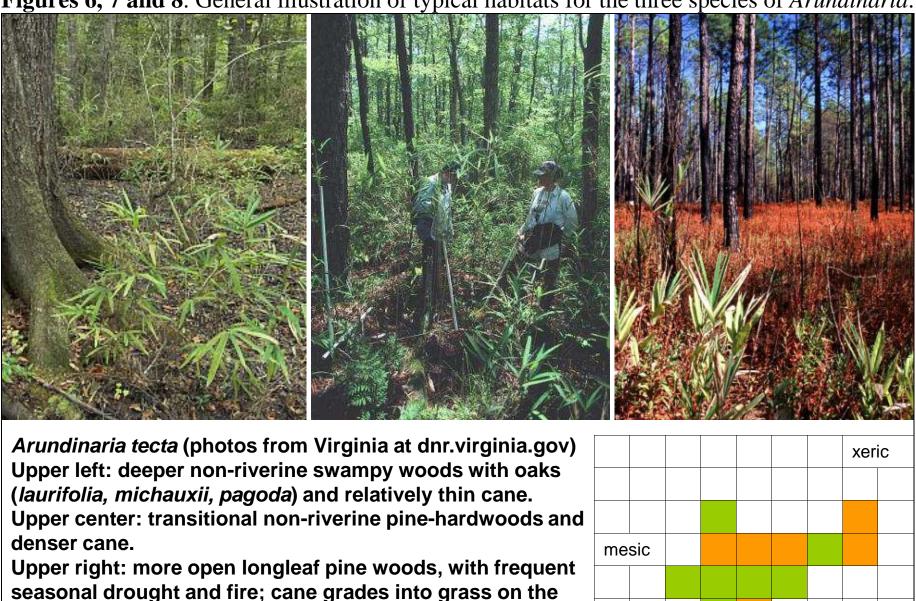
With care, at least 50% success rate is expected with transplants of *gigantea* from existing stands. The best season for transplanting is probably Feb-Mar, based on much experience in Kentucky. When digging plugs from the wild, it is important to select 1-3 good culms for each unit and to retain an approximate cylinder of at least 6-9 inches of soil—in depth and width—together with the rhizome and root system. It is important to dig straight down with a long heavy sharp spade (e.g. the King of Spades<sup>TM</sup> made by W.W. Manufacturing, Bridgeton, New Jersey)—and to dig all around the culms, not angling down into the plug or otherwise reducing or damaging the transplanted rhizome sections. However, even with much care, loose soil often falls off roots, and tying plants up with burlap (or similar material) could be useful in some contexts. To reduce transpiration, it is often important to cut off the top 30-70% of leafy material when digging transplants, especially if plants are large and soil falls off. It is also important to keep transplants cool and cover them with wet blankets (or similar material) when transporting them, then settle them gently into their new homes within a day or so. And pray for as much rain as possible, but without severe floods or winds, for the next few months.

Propagation from rhizome sections is somewhat erratic, but reliable methods can probably be developed and have been actively sought in several studies (Sexton et al. 2003, Zaczek et al. 2003, 2009, Hartleb & Zaczek 2007, Brendecke and Zaczek 2008, Baldwin et al. 2009, Schoonover et al. 2011). Based especially on Baldwin et al. (2009 and pers, comm.), the source and initial condition of material can be a significant factor. Larger containers or trays with at least 2-3 nodes are recommended, especially sections closer to culms of origin (proximal); diameter of rhizomes appears to have little or no effect on success. A misting system can

probably enhance success rates, but rooting hormones may not be particularly useful. Zaczek et al. (2003) achieved more success when rhizomes were planted shallow, exposed to sunlight. Jane Harrod (Jane's Native Plants, Lawrenceburg, Ky., pers. comm.) and Bill Hendricks (pers. comm.) have successfully grown many rhizome sections in early spring to summer by enclosing them in humid poly-houses with root temperatures ca. 40-70° F and regular watering. Chuck Rhodes (when at Dept. of Forestry, Univ. of Ky., pers. comm.) has observed reliable rooting by floating rhizome sections in full sunlight. Paul Capiello (Yew Dell Garden, Crestwood, Ky., pers. comm.) is currently comparing rhizome cuttings in fall versus spring, since other bamboos have show more successful rooting in the fall. Rhizomes simply cut and transplanted during the growing season tend to die much more readily than if some leafy tops are retained, even if watered regularly. Containerized stock is clearly superior for field plantings than just rhizome sections—but there is much potential for mortality of rhizomes in the greenhouse while developing that stock (Schoonover et al. 2001).

Like many bamboos, *Arundinaria* can grow well in full sun, if soil conditions are suitable, but some shade is tolerated well and may be beneficial for reducing temperatures and resulting moisture stresses. Cirtain et al. (2009) found that *gigantea*—in growth chamber and woods—did best in full sun, and there was a positive interaction with N level in their growth chamber. Baldwin et al. (2009; and in prep.) grew *gigantea* with a shaded pot-in-pot system, regular watering and NPK amendments; they found that total growth increased in full sun, but aboveground growth alone was maximal under 60% shade. Smith (2011) has shown that *gigantea* is a relatively light-demanding bamboo, compared to some of its East Asian relatives, including smaller bamboos like *Sasa* species which did not increase photosynthetic rates when grown in less shade. But she also showed that *gigantea* is relatively sensitive to moderate drought, displaying signs of wilting or cavitation before any of the Asian species that were compared.

Figures 6, 7 and 8. General illustration of typical habitats for the three species of *Arundinaria*.



Lower right: soils, red = strongly acid; green = average

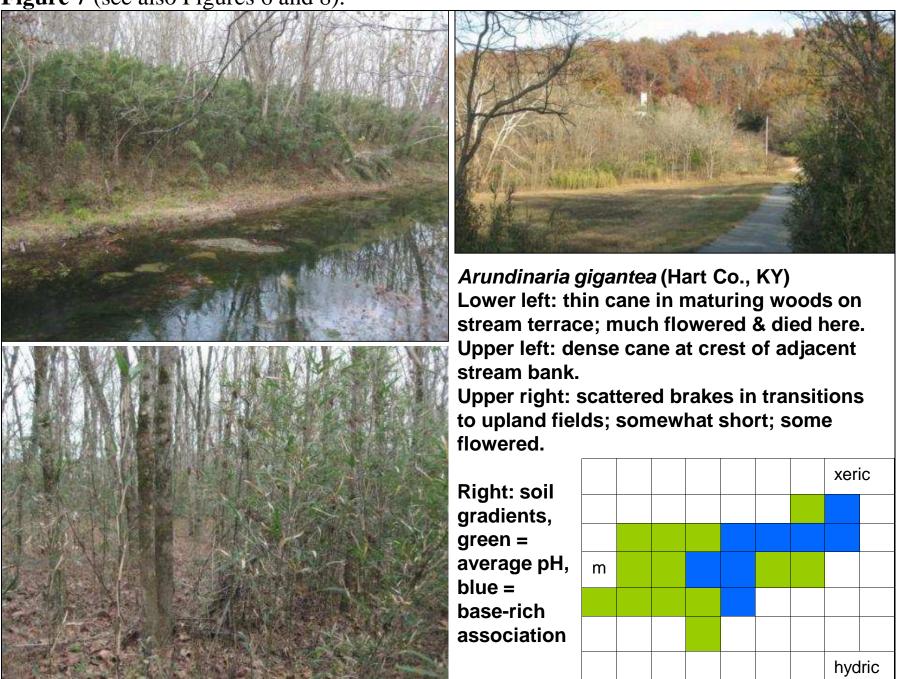
ground.

hydric

At Roundstone Native Seed, we suspect that hot summer temperatures can be highly detrimental, especially when black pots are exposed to full sun or within trays on greenhouse benches. In several cases, we have observed much better survival and growth, above ground at least, where containers remain below ca. 75-85° F (25-30°C)—experimental work is needed to determine the exact response. For example, large freshly transplanted, potted plants did much better when placed along the north side of a barn but still receiving skylight from above. Even with drip-fed irrigation and a sunken pot-in-pot system, similar plants in full sun mostly died above ground during 2011. In an experimental planting of 150 cane seedlings at Griffith Woods (Harrison Co., Kentucky), survival after 3 years was correlated with an index of cool (N/NE-facing) aspect (Figure 5).

Bamboos are generally considered nutrient-demanding plants (Lawson 1968, Lucas 2008). Relationships of nutrient levels to *Arundinaria*—especially nitrogen (N)—have been studied in a few, varied contexts. Cirtain et al. (2004, 2009) found that N amendment did not improve growth of *gigantea* seedlings until after their first year. With transplants of *gigantea* into an old field, Datillo & Rhoades (2005) found that fertilizer and manure both increased culm numbers by ca. 10-40% after 2 years, but there was less effect on height. With transplanted rhizomes of *gigantea*, Zaczek et al. (2010) found that NPK increased survival after 2 years, but it did not offset short-term reductions of above-ground growth due to fire. Blattel et al. (2009) surveyed soils across riparian buffers with native (unplanted) *gigantea* at three sites, and found 80-95% decreases in nitrate from field to interior (downslope) soils at one site, in ammonium at another site, and no significant trends at the third sites. Griffith et al. (2009) found that *gigantea* in western North Carolina is associated with well-drained sandy soils, relatively low nutrient levels, but low C:N ratios and pH of 5-6.6. A partner of Roundstone Native Seed grew seedlings of *gigantea* in 2 × 2 × 5 inch cells on acid soils with unusually low Ca level, using

**Figure 7** (see also Figures 6 and 8).

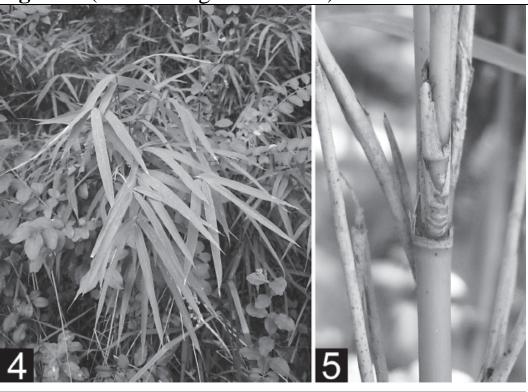


standard medium for loblolly pine seedlings. These developed much less rhizome growth after 6 months, with virtually none escaping the containers. In better soil with the same cell size (PRO-MIX<sup>TM</sup> plus clay and nutrient amendments), leafy shoot growth was similar after the same period but several rhizomes usually appeared out of the bottom of each cell. There is a need for broader experimental studies of growth under a range of nutrient conditions.

### **COMPETITORS AND CONSUMERS**

Some observations, including mulching studies, may indicate effects of competing plants with similar or shorter stature. In their field of gigantea transplants, Datillo & Rhoades (2005) found that mulch (with or without extra nutrients) increased culm numbers by ca. 40-60% after two years, but there was less effect on height. Using various manipulations, Cirtain (2009), Hartleb and Zaczek (2007), Osland et al. (2009) and Schoonover et al. (2011) found that gigantea transplants were not much reduced by dense competition in the ground vegetation, such as Japanese grass (Microstegium vimineum). However, Baldwin et al. (in prep.) found that after one year of experiments, transplanted rhizomes of gigantea grew much less among rhizomatous alien grasses (Johnson grass and Bermuda grass) than among native deep-rooted clumpers (big blue-stem and Indian grass). Reduction of this competition by tilling or herbiciding increased cane growth among the alien grasses, but reduced it among the natives might these grasses have protected the cane from hot dry air? I found that establishment of gigantea transplants was virtually all prevented by the densely rhizomatous quackgrass (Elymus repens) at Griffith Woods, in Harrison County, Kentucky, but it was often partially successful with much taller but thinner competition including ironweed (Vernonia gigantea) and even poison hemlock (Conium maculatum). Tall associates may be beneficial in some cases, by reducing hot sun and drying out of the soil surface (see previous section).

**Figure 8** (see also Figures 6 and 7).



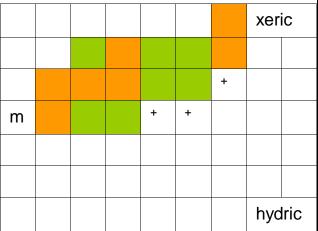


Figs. 4—5. Arundinaria appalachiana. 4. Habit, in Rhea Co., Tennessee. 5. Close-up of primary branch with compressed basal internodes, Dekalb Co., Alabama. (Photos by J. Triplett)

## Arundinaria appalachiana

Upper left: typical habit, from Triplett et al. (2006, Sida). Upper right: denser growth along upland roadsides, Rt. 76 in northern GA (photo from Paul Schneider).

Lower right: typical position along soil gradients; red = associated species of strongly acid soils; green = associated species of average soil pH.



There has been virtually no systematic study of consumer relations—herbivores, pests and pathogens—but there have been varied initial anecdotal observations. In petri dishes used for my germination tests with gigantea seed, fungal growth became severe in several cases, but was much less after cold moist storage of seeds (unpublished data). In the greenhouse at Roundstone Native Seed, gigantea seedlings suffered greatly from fungal infection of leaves during the hot humid conditions of summer 2010. In my garden, a patch of cane grew to 10-20 feet across in a decade then gradually declined in the subsequent decade without any flowering, and with no obvious reduction in light or other resources—I suspect fungal accumulation in the plants, as evidenced by blackened twigs and leaves. A new genus of rust-like fungus has been discovered on "tecta" in Alabama (Olive 1945); see also Hyde et al. (2002). Rabbits caused repeated significant damage to my planting of 7-year old gigantea seedlings at Cane Run (Fayette County) during 2000-2002, but the plants finally prospered. Mammalian herbivores in general can have significant effects on cane. Cattle have often browsed it back in Kentucky, and continuous grazing appears to kill the plants after a decade or so. On the uplands of central Kentucky, most remaining cane has survived in old fencerows, wherefrom it locally recovers into rights-of-way (especially along interstate highways) and other abandoned land that is no longer grazed or mowed.

# ECOLOGICAL NICHES, HABITATS AND RESTORATION

As outlined above, *Arundinaria* is generally typical of edges and other transitions from deep woods to full sun, probably with repeated disturbance rather than a simple 'successional' niche after catastrophic disturbance. Within this broad zone, the three species have somewhat distinct habitats along the gradient in moisture conditions (Figures 6, 7, 8): from subhydric (*tecta*) to submesic (*gigantea*) to subxeric (*appalachiana*). In addition, *gigantea* tends to occur

on more base-rich soils, especially alluvial soils in the Mississippi Valley. The spread of *gigantea* onto some calcareous uplands, such as the Bluegrass region of Kentucky, may be a relatively recent phenomenon. Triplett et al. (2010) have not yet detected consistent genetic differences between upland and lowland plants, but *gigantea* from the Mississippi Valley does appears somewhat distinct in DNA from *gigantea* of Atlantic states. Hybridization does appear to occur between *gigantea* and *tecta*—the geographic and ecological context of any intergradation will deserve deeper study.

In nature, there has been little experimental work into what disturbance regimes are optimal. Hughes et al. (1960, Hughes 1966) showed that burning or other intense disturbance at intervals of about 10 years was probably optimal for *tecta*, and that the cane could be successfully browsed by cattle in alternate years, especially during the winter. Gagnon & Platt (2008a; Gagnon 2009) found that *gigantea* grew more in a blow-down area, compared to deeper woods, and much more (× 2) with fire as well as blow-down; but growth was less with fire alone. They also found (Gagnon & Platt 2008b) that sown seed did less well on bare burned ground than with regular leafy litter. Zaczek et al. (2010) planted rows of *gigantea* rhizomes then observed effects of prescribed fire, which increased culm density and rhizomatous spread two years later but with reduced culm sizes and reduced overall leafy cover.

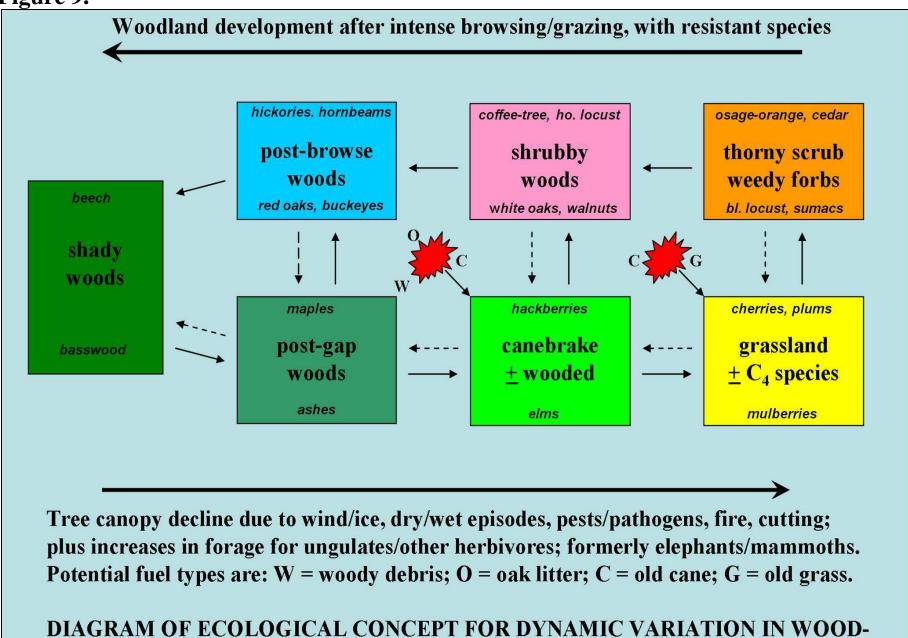
On relatively uniform base-rich soils, Figure 9 presents a conceptual model for the original 'niche' of *gigantea* within the dynamics of native woodland, based on much general observation and historical data from the Bluegrass region of Kentucky. In addition to the general gradient from deep shade to full sun (left to right), one can envisage an independent gradient related to browsing by generalist herbivores. Before excessive human influence, large animals such as giant bison and mastodons probably were significant browsers in woodland

with cane. Similar patterns do occur in modern vegetation, though they have been fragmented and any ancient migrations are now of course lost. In the original woods, it is suggested that there was a messy (highly stochastic) cyclical tendency, counterclockwise on the diagram. This concept is allied with Vera's (2000) hypothesis concerning the ancient role of herbivores in the woodlands of central Europe.

Focus on cane in conservation deserves much more effort, given this plant's historical abundance in some regions, its potential role to counter invasive alien shrubs (Osland et al. 2009; David Brand, Warren Wilson College, 2010 abstract), its potential role in nutrient uptake and reducing erosion, especially along riparian zones and headwater streams (Schoonover et al. 2005, 2011), and its potential role as a perennial forage for wildlife (McHargue 1941, Platt et al. 2001) or even livestock in some contexts (Biswell 1941, Hughes et al. 1960, Smart et al. 1960, Halvorson et al. 2010).

Griffith Woods (Silver Lake Farm), covering 750 acres in Harrison County, provides an excellent site for deeper study of cane in the Bluegrass region of Kentucky. In addition to patches of ancient woodland, including the world champion chinquapin oak, there are many old fields where cane can be established. Several general goals can be set: (1) genetic collection, with varied uses; (2) comparative study of growth rates and responses to site types; (3) experimental management—browsing, burning, cutting, chemical, competition, other consumers; (4) studying effects of cane (compared to other vegetation) on soil, plants, animals, etc. Now transferred from The Nature Conservancy and University of Kentucky to the Kentucky Department of Fish and Wildlife Resources, this old farm should become the center for restoration of Bluegrass woodlands, their canebrakes and their wildlife, together with associated research and education.

Figure 9.



LAND OF THE CENTRAL BLUEGRASS (ASSUMING UNIFORM EUTROPHIC SOIL)

### **DISCUSSION**

So what generally characterizes the growth form, life cycle and ecology of temperate bamboos, and does *Arundinaria* have any special distinction? Bamboos in general have a unique 'punching and branching' ability to send up rapidly growing culms through brush and vines in transitions from shady woodland to more open vegetation. After escaping herbivory in tender young stages, and growing through any competing thickets, culms then branch out into spaces above. In species with running rhizomes, large areas can be colonized, especially on gentle uniform slopes and plains without excessive droughts or floods. Disturbances of varied kind—from tree-falls to wild fires, when repeated at intervals of ca. 5-25 years, generally provide the optimal habitat for bamboos.

Arundinaria is similar in these respects to its East Asian cousins, with a somewhat similar range of habitats from low, seasonally damp plains to drier, broad ridges in the mountains. The loss of large canebrakes from more fertile lowland plains and some calcareous uplands presents a significant problem for conservation and restoration, since the plant has not yet been propagated in large numbers (Platt and Brantley 1997, Stewart 2007). East Asian people have cultivated many species of temperate bamboo for millenia, but the many Native American uses of cane were interrupted (Platt et al. 2009). There was little initial adoption of these plants by the settlers from Europe or even by their slaves from Africa, except for some local uses as fishing-poles, bean-stalks and the like.

Bamboos in general, especially running temperate species, tend to develop dense competitive stands that can generally prevent seedling survival except after parental death. As previously discussed (Campbell 1985), their 'monocarpy' (death after flowering) could have

been selected partly by such need for parental death, assuming that occasional sexual reproduction is essential. Other evolutionary forces favoring infrequent or gregarious flowering could include selection for 'satiation' of seed consumers when large seed crops are produced (Janzen 1976), and selection for association with particular phases of environmental cycles—perhaps allowing seedlings to renew the population in rainy periods after parents decline in drier periods, or after fire (Keeley and Bond 1999). The rare flowering, poor dispersal, and frequent self-pollination of bamboos pose special problems for maintaining genetic diversity.

The much reduced extent of observed gregarious flowering in *Arundinaria*, compared to its East Asian cousins, suggests possible decoupling of a more regular ancestral life-cycle from environmental cues. Such decoupling might have developed as climatic patterns became less predictable during the Quaternary era, including severe disruptions during glacial periods. Problems for cross-pollination and genetic conservation may be particularly acute in these bamboos. Nevertheless, I am confident that more concentrated attention by horticulturalists and biologists can refocus North American effort on this worthy cause (Figure 10).

### **ACKNOWLEDGEMENTS**

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**Figure 10** (next page). The cane planting along Cane Run on north side of Lexington. In the winter of 1999/2000, 100-150 seven-year old seedlings were planted here on the old university farm, part of the first 'Reforest the Bluegrass' event of Lexington Fayette Urban Couinty Government. Plants were mulched and manured initially, suffered much from rabbits in 2002-2003, then exploded in growth during 2005-2010.

