

From Forest Nursery Notes, Winter 2013

**33. Growth of cane (*Arundinaria sensu stricto*), the mysterious native bamboo of North America.** Campbell, J. J. N. International Plant Propagators' Society, combined proceedings 2011, 61:334-345. 2012.

## Growth of Cane (*Arundinaria sensu stricto*), the Mysterious Native Bamboo of North America<sup>©</sup>

**Julian J.N. Campbell**

Bluegrass Woodland Restoration Center, 3525 Willowood Road, Lexington, Kentucky 40517, U.S.A.

Email: julian.campbell@insightbb.com

### INTRODUCTION

In recent years, the generic name *Arundinaria* has become restricted in usage to the native “cane” species of eastern North America: *gigantea* (= *macrosperma*), *gigantea* subsp. *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 hundreds or thousands of acres or even whole regions, after nonflowering 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 partly on literature, meetings, and conversations with growers. It also draws on 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. (in Hart County, Kentucky), John and Randy Seymour, have also become much involved, and they are also working with Mark Smith at Auburn University in Alabama. I do not deal here with tissue culture and micropropagation, which is being studied by Baldwin et al. (2009), Margaret Cirtain (University of South Carolina, pers. commun.), Sharon Kester (University 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 from propagators (e.g., Betty Shor, American Bamboo Society, pers. commun.; B. Baldwin et al., 2009; and pers. commun.) and ecologists [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 hundreds or thousands 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.

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 (pers. comm.)]. Long-term observations of particular cane patches in the wild suggest that the lifecycle is usually at least several decades. In an early account, Neisler (1860) indicated that ca. 25 years was typical in *A. gigantea*, but longer periods are generally suspected today. There are only two flowering records for *A. 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 (pers. commun.) has reported recovery of *A. gigantea* without producing seed at Tripple Brook Farm in Massachusetts.

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. commun.) 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.

Seed of bamboos 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 generally considered 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 and 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 pretreatment, such as stratification or refrigeration at 5 °C [41 °F].”

Recent research on seed of *Arundinaria* by myself at the University of Kentucky (in the lab of Carol and Jerry Baskin) and Mississippi State University (Baldwin et al., 2009; Neal et al., 2011) 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. Zero germination is observed after seeds drop below ca. 6%–8% moisture content. 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. commun.) 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 failed to produce any mature seed within the past decade, before they die (R. Seymour, pers. commun.). However, an initial flowering patch in 2000 did produce much seed, 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 (Klyn Nurseries, 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 100–1,000 m or more during its sexual life cycle. Brian Baldwin (pers. commun.) has evidence from DNA markers that one clone of *A. 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 *A. gigantea* subsp. *tecta* (and sometimes *A. 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*, *P.*

*heteroclada*, *P. 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 *A. gigantea* subsp. *tecta* is more tolerant (Baldwin et al., 2009; Milles et al., 2011). 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 *A. gigantea* seedlings on well-watered but well-drained soil had more 1-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 and Sue Turtle (pers. commun.) 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. (2009) showed that the vascular system of *A. gigantea* is sensitive to embolism (cavitation) when rhizomes are 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.

If care is taken, at least 50% success rate is expected with transplants of *A. gigantea* from existing stands. The best season for transplanting is probably Feb. – March, 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 in. 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™ 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 being actively sought in several studies (Sexton et al., 2003; Zaczek et al., 2003, 2009; Hartleb and Zaczek, 2007; Brendecke and Zaczek, 2008; Baldwin et al., 2009; Schoonover et al., 2011). Based on these studies (especially Baldwin et al., 2009 and pers. commun.), 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. Bill Hendricks (pers. commun.) has suc-

cessfully grown many rhizome sections in the spring by enclosing them in a humid polyhouse. Chuck Rhodes (pers. commun.) has observed reliable rooting by floating rhizome sections in full sunlight. Paul Capiello (pers. commun.) is currently comparing rhizome cuttings in fall versus spring, since other bamboos have shown more successful rooting in the fall. In the field, 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. Schoonover et al. (2011) have shown that in-leaf 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 containerized stock.

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 *A. 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 pers. commun.) grew *A. gigantea* with a shaded pot-in-pot system, regular watering, and NPK amendments; they found that total growth increased in full sun, but above-ground growth alone was maximal under 60% shade. Smith (2011) has shown that *A. 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 *A. gigantea* is relatively sensitive to moderate drought, displaying signs of wilting or cavitation before any of the Asian species that were compared.

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.

Bamboos are generally considered to be relatively 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 *A. gigantea* seedlings until after their first year. With transplants of *A. gigantea* into an old field, Datillo and 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 *A. 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) *A. 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 *A. 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 *A. gigantea* in 2 × 2 × 5-in. cells on acid soils with unusually low Ca level, using 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™ 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 obviously 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 *A. gigantea* transplants, Dattilo and Rhoades (2005) found that mulch (with or without extra nutrients) increased culm numbers by ca. 40%–60% after 2 years, but there was less effect on height. Using various manipulations, Certain (2009), Hartleb and Zaczek (2007), Osland et al. (2009), and Schoonover et al. (2011) found that *A. gigantea* transplants were not much reduced by dense competition in the ground vegetation, such as Japanese grass (*Microstegium vimineum*). However, Baldwin (pers. commun.) found that after 1 year of experiments, transplanted rhizomes of *A. 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 *A. 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).

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 *A. 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, *A. 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 ft across in a decade then gradually declined in the subsequent decade without any flowering, and 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 *A. gigantia* subsp. *tecta* in Alabama (Olive, 1945); see also Hyde et al. (2002). Rabbits caused repeated significant damage to my planting of 7-year-old *A. 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

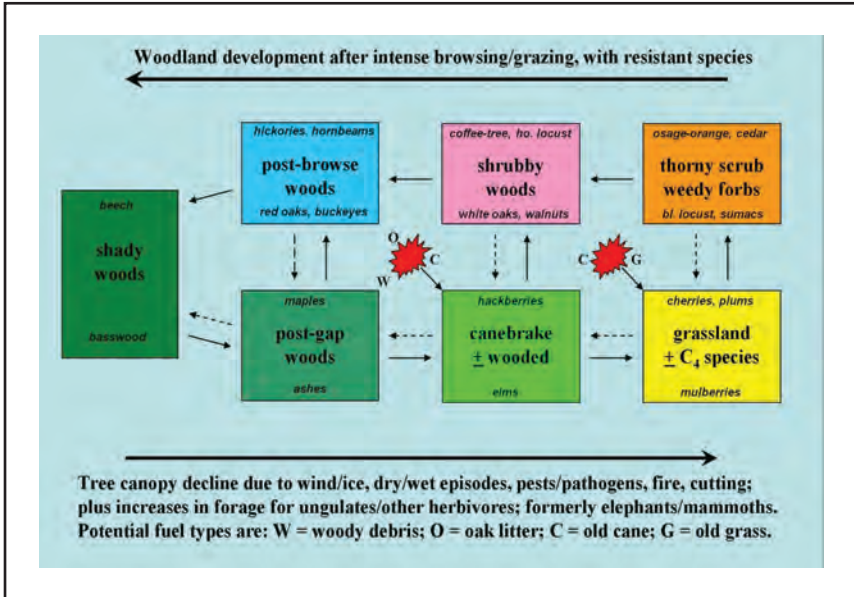
As outlined above, *Arundinaria* is generally typical of edges and other transitions from deep woods to full sun, probably with repeated disturbance rather than a simple “successional” niche after catastrophic disturbance. Within this broad zone, the three species have somewhat distinct habitats along the gradient in moisture conditions: from subhydric (*A. gigantea* subsp. *tecta*) to submesic (*A. gigantea*) to subxeric (*A. appalachiana*). In addition, *A. gigantea* tends to occur on more base-rich soils, especially alluvial soils in the Mississippi Valley. The spread of *A. 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 *A. gigantea* from the Mississippi Valley does appear somewhat distinct in DNA from *A. gigantea* of Atlantic states. Hybridization does appear to occur between *A. gigantea* and *A. gigantea* subsp. *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 *A. gigantea* subsp. *tecta*, and that the cane could be successfully browsed by cattle in alternate years, especially during the winter. Gagnon and Platt (2008a; Gagnon 2009) found that *A. gigantea* grew more in a blow-down area, compared to deeper woods, and much more ( $\times 2$ ) with fire as well as blow-down; but growth was less with fire alone. They also found (Gagnon and Platt 2008b) that sown seed did less well on bare burned ground than with regular leafy litter. Zaczek et al. (2010) planted rows of *A. gigantea* rhizomes then observed effects of prescribed fire, which increased culm density and rhizomatous spread 2 years later but with reduced culm sizes and reduced overall leafy cover.

On relatively uniform base-rich soils, Fig. 1 presents a conceptual model for the original “niche” of *A. 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; Brand, 2010), 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).





**Figure 1.** Diagram of ecological concept for dynamic variation in woodland of the central Bluegrass (assuming uniform eutrophic soil).

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.

## 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, when repeated at intervals of ca. 5–25 years, probably 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 millennia, 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 discussed previously (Campbell, 1985), their “monocarpny” (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.

**Acknowledgements.** Many people have directly or indirectly helped me to grow and study cane—or other bamboos—over the past 30 years. These include Carol and Jerry Baskin, Frank and Melinda Boyer, Adam Datillo, Ned Jacquith, Li De-zhu, Susanne Lucas, Will Overbeck, Tim Phillips, Layton Register, Chuck Rhoades, Qin Ze-sheng, John and Randy Seymour, Nevin Smith, Chris Stapleton, Adam and Sue Turtle, and Josh Wysor. Four other special people also provided initial inspiration at local and global levels, but are now, sadly, deceased: Peter Addington, David McClintock, Willem Meijer, Tom Soderstrom, and Xiao Xue (son of Xue J.R.).

## LITERATURE CITED

- Baldwin, B.** 2009. Pers. commun. Dept. of Plant and Soil Sciences, Mississippi State University.
- Baldwin, B.S., M. Cirtain, D.S. Horton, J. Ouellette, S.B. Franklin, and J.E. Preece.** 2009. Propagation methods for rivercane [*Arundinaria gigantea* L. (Walter Muhl.)]. *Castanea* 74:300–316.
- Biswell, H.H.** 1951. Studies of rotation grazing in the southeast. *J. Range Mgmt.* 4:52–55.
- Brand, D.** 2010. Disturbance, growth and non-native invasibility of river cane (*Arundinaria gigantea*). Abstract, Natural Science Seminars, Warren Wilson College, North Carolina.
- Blattel, C.R., K. Williard, S. Baer, J. Schoonover, and J. Zaczek.** 2009. Ground water dynamics in giant cane and forest riparian buffers. *Castanea* 74:259–270.

- Brendecke, W.W., and J.J. Zaczek.** 2008. Greenhouse and field performance of giant cane propagules from natural and planted stands, pp 8–19. In: Proc. 16th Central Hardwoods Forest Conference GTR-NRS-P-24. General Tech. Rpt. SRS-101. U.S. Dept. Agric., Forest Service, Southern Research Station.
- Breyer, S.** 2011. Tripple Brook Farm, Southampton, Mass., pers. commun.
- Campbell, J.J.N.** 1985. Bamboo flowering patterns: A global view with special reference to East Asia. *J. Amer. Bamboo Soc.* 6:17–35.
- Cirtain, M.** 2011. pers. commun. Dept. of Biological Sciences, Univ. of South Carolina.
- Cirtain, M.C.** 2009. Reintroduction of the *Arundinaria gigantea* (Walt.) Muhl. canebrakes through improved propagation and establishment. Ph.D. dissertation, University of Memphis, Tennessee.
- Cirtain, M.C., S.B. Franklin, and S.R. Pezeshki.** 2004. Effects of nitrogen and moisture regimes on *Arundinaria gigantea* (Walt.) Muhl. seedling growth. *Natural Areas J.* 24:251–257.
- Cirtain, M.C., S.B. Franklin, and S.R. Pezeshki.** 2009. Effect of light intensity on *Arundinaria gigantea* growth and physiology. *Castanea* 74:236–246.
- Datillo, A.J., and C.C. Rhoades.** 2005. Establishment of the woody grass *Arundinaria gigantea* for riparian restoration. *Restoration Ecol.* 13:616–622.
- Li, D.Z., Z.P. Wang, Z.W. Guo, G.Y. Yang, and C. Stapleton.** 2006. Bambuseae. In: Z. Wu, P. Raven et al. (eds). *Flora of China*, Vol. 22. Science Press and Missouri Botanical Garden, St. Louis, Missouri (see also <<http://hua.huh.harvard.edu/china/>>).
- Gagnon, P.R., and W.J. Platt.** 2008. Reproductive and seedling ecology of a semelparous native bamboo (*Arundinaria gigantea*, Poaceae). *J. Torrey Bot. Soc.* 135:309–316.
- Gagnon, P.R.** 2009. Fire in floodplain forests in the southeastern USA: insights from disturbance ecology of native bamboo. *Wetlands* 29:520–526.
- Griffith, A.D., D.A. Kinner, B.R. Tanner, A. Moore, K.G. Mathews, and R.S. Young.** 2009. Nutrient and physical soil characteristics of river cane stands, western North Carolina. *Castanea* 74:224–235.
- Halvorson, J.J., K.A. Cassida, K.E. Turner, and D.P. Belesky.** 2010. Nutritive value of bamboo as browse for livestock. *Renewable Agriculture and Food Systems* 26:161–170.
- Hartleb, J.L., and J.J. Zaczek.** 2007. Culm production and morphology of fresh and stored rhizomes from field-planted and wild giant cane, pp. 652–657. In: D.S. Buckley, and W.K. Clatterbuck (eds). Proc. 15th Central Hardwood Forest Conference. General Tech. Rept. SRS-101. U.S. Department of Agriculture, Forest Service, Southern Research Station.
- Hughes, R.H.** 1951. Observations of cane (*Arundinaria*) flowers, seed and seedlings in the North Carolina coastal plain. *Bull. Torrey Bot. Club.* 78:113–121.
- Hughes, R.H.** 1966. Fire ecology of canebrakes. *Proc. Tall Timbers Fire Ecol. Conf.* 5:149–158.
- Hughes, R.H., E.U. Dillard, and J.B. Hilmon.** 1960. Vegetation and cattle response under two systems of grazing cane range in North Carolina. *North Carolina Agricultural Experiment Station Bulletin* 412.
- Hyde, K.D., D.Q. Zhou, and T. Dalisay.** 2002. Bambusicolous fungi: A review. *Fungal Diversity* 9:1–14.
- Janzen, D.H.** 1976. Why bamboos wait so long to flower. *Ann. Rev. Ecol. Systematics* 7:347–391.
- Keeley, J.E., and W.J. Bond.** 1999. Mast flowering and semelparity in bamboos: The bamboo fire cycle hypothesis. *American Naturalist* 154:383–391.
- Kester, S.** 2011. Pers. commun. Dept. of Horticulture, Univ. of Kentucky.
- Lawson, A.H.** 1968. *Bamboos: A Gardener's Guide to their Cultivation in Temperate Climates.* Faber and Faber, London, U.K.
- Lucas, S.** 2008. Graceful grass or jungle giant: Growing bamboos indoors. In: *Landscaping Indoors, Bringing the Garden Inside.* Brooklyn Botanical Garden Publ. 165.
- Marsh, D.L.** 1977. The taxonomy and ecology of cane, *Arundinaria gigantea* (Walter) Muhlenberg. Ph.D. dissertation, University of Arkansas, Little Rock.
- Mathews, K.G., J. Huguelet, M. Lanning, T. Wilson, and R.S. Young.** 2009. Clonal diversity of *Arundinaria gigantea* (Poaceae; Bambusoideae) in western North Carolina and its relationship to sexual reproduction: An assessment using AFLP fingerprints. *Castanea* 74(3):213–223.

- McClure, F.A. 1963. A new feature in bamboo rhizome anatomy. *Rhodora* 65:134–136.
- McClure, F.A. 1966. The bamboos: A fresh perspective. Harvard Univ. Press.
- McHargue, J.S. 1941. Canebrakes in prehistoric and pioneer times in Kentucky. *Annals of Kentucky Natural History* 1:1–13.
- Mills, M.C., B.S. Baldwin, and G.N. Ervin. 2011. Evaluating physiological and growth responses of *Arundinaria* species to inundation. *Castanea* 76:395–409.
- Neal, D.M., B.S. Baldwin, G.N. Ervin, R.L. Jolley, J.J.N. Campbell, M. Cirtain, J. Seymour, and J.W. Neal. 2011. Assessment of seed storage alternatives for river-cane [*Arundinaria gigantea* L. (Walter) Muhl.]. *Seed Technology*, in press.
- Neisler, H.M. 1860. Notes on the habits of the common cane (*Arundinaria macrosperma* Michx.). *Amer. J. Sci. Arts* 30:14–16.
- Olive, L.S. 1945. A new *Dacrymyces*-like parasite of *Arundinaria*. *Mycologia* 37:543–552.
- Osland, M.J., J.W. Pahl, and C.J. Richardson. 2009. Native bamboo [*Arundinaria gigantea* (Walter) Muhl., Poaceae] establishment and growth after the removal of an invasive non-native shrub [*Ligustrum sinense* Lour., Oleaceae]: Implications for research. *Castanea* 74:247–258.
- Platt, S.G., and C.G. Brantley. 1997. Canebrakes: An ecological and historical perspective. *Castanea*. 62:8–21.
- Platt, S.G., C.G. Brantley, and T.R. Rainwater. 2001. Canebrake fauna: Wildlife diversity in a critically endangered ecosystem. *Journal of the Elisha Mitchell Scientific Society*. 117:1–19.
- Platt, S.G., C.G. Brantley, and T.R. Rainwater. 2009. Native American ethnobotany of cane (*Arundinaria* spp.) in the southeastern United States: A review. *Castanea* 74(3):271–285.
- Qin, Z.S. 1985. Giant panda's food resources in Sichuan, China, and the regeneration of the bamboo groves. *Journal of Bamboo Research (Nanjing)* 4:1–10.
- Rhoades, C. Pers. commun. U.S. Forest Service, Fort Collins, Colorado.
- Schoonover, J.E., K.W.J. Williard, J.J. Zaczek, J.C. Mangun, and A.D. Carver. 2005. Nutrient attenuation in agricultural surface runoff by riparian zones in Southern Illinois. *Agroforestry Systems*. 64(2):169–180.
- Schoonover, J.E., K.W.J. Williard, J.J. Zaczek, J.C. Mangun, and A.D. Carver. 2006. Agricultural sediment reduction by giant cane and forest riparian buffers. *Water, Air, and Soil Pollution* 169:303–315.
- Schoonover, J.E., J.L. Hartleb, J.J. Zaczek, and J.W. Groninger. 2011. Growing giant cane (*Arundinaria gigantea*) for canebrake restoration: Greenhouse propagation and field trials. *Ecol. Restoration* 29:232–242.
- Sexton, R.L., J.J. Zaczek, J.W. Groninger, S.D. Fillmore, and K.W.J. Williard. 2003. Giant cane propagation techniques for use in restoration of riparian forest ecosystems, pp. 421–424. In: J.W. Van Sambeek, J.O. Dawson, and F. Ponder (eds). *Proceedings 13th Central Hardwood Forest Conference*. General Tech. Rept. NC-234. U.S. Dept. Agric., Forest Service, North Central Research Station.
- Seymour, R. 2011. Pers. commun. Roundstone Native Seed, Bonnieville, Kentucky.
- Shor, B. 2011. Pers. commun. American Bamboo Society, La Jolla, California.
- Smart, W.W.G., G. Matrone, W.O. Shepard, R.H. Hughes, and F.E. Knox. 1960. The study of the comparative composition and digestibility of cane forage (*Arundinaria* sp.). *North Carolina Agric. Expt. Station Tech. Bull.* 140.
- Smith, M.C. 2011. Predicting plant naturalizations in the Pacific Northwest: The fate of bamboos in the understory of coniferous forests. Ph.D. dissertation, Washington State University.
- Stewart, M.A. 2007. From king cane to king cotton: Razing cane. *Environmental History*. 12(1):59–79.
- Stapleton, C.M.A. 1987. Bamboo (Gramineae), pp. 199–214. In: Jackson, J.K. (ed.) *Manual of Afforestation in Nepal*. Nepal-UK Forestry Research Project. Forest Survey and Research Office, Dept. of Forestry, Kathmandu, Nepal.
- Stapleton, C.M.A. 1994. Bamboos of Nepal. An Illustrated Guide. Royal Botanic Gardens, Kew.
- Taylor, A.H., and Z-S Qin. 1988. Regeneration from seed of *Sinarundinaria fangiana*, a bamboo, in the Wolong Giant Panda Reserve, Sichian, China. *Amer. J. Bot.* 75:1065–1073.

- Triplett, J.K., and L.G. Clark.** 2009. Towards a stable nomenclature for the North American temperate bamboos: Epitypification of *Arundo gigantea* Walt. and *Arundinaria macrosperma* Michx. (Poaceae). *Castanea* 74:207–212.
- Triplett, J.K., and L.G. Clark.** 2010. Phylogeny of the temperate bamboos (Poaceae: Bambusoideae: Bambuseae) with an emphasis on *Arundinaria* and allies. *Syst. Bot.* 35:102–120.
- Triplett, J.K., L.G. Clark, and A.S. Weakley.** 2006. Hill cane (*Arundinaria appalachiana*), a new species of bamboo (Poaceae: Bambusoideae) from the Southern Appalachian Mountains. *Sida* 22:79–95.
- Triplett, J.K., K.A. Oltrogge, and L.G. Clark.** 2010. Phylogenetic relationships and natural hybridization among the North American woody bamboos (Poaceae: Bambusoideae: *Arundinaria*). *American Journal of Botany* 97:471–492.
- Turtle, A. & S.** 2011. Pers. commun. Summertown, Tennessee.
- Vera, F.W.M.** 2000. Grazing ecology and forest history. CABI, Wallingford, U.K.
- Wang, W., S.B. Franklin, and M.C. Cirtain.** 2007. Seed germination and seedling growth in the arrow bamboo *Fargesia qinlingensis*. *Ecological Research* 22:467–474.
- Zaczek, J.J., R.L. Sexton, K.W.J. Williard, and J.W. Groninger.** 2003. Propagation of Giant Cane (*Arundinaria gigantea*) for Riparian Habitat Restoration, pp. 103–106. In: Riley, L. E., Dumroese, R. K., and Landis, T. D. (eds.). National Proc. Forest and Conservation Nursery Associations — 2003. Proc. RMRS-P-33. Fort Collins, Colorado: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Zaczek, J.J., S.G. Baer, and D.J. Dalzotto.** 2010. Fire and fertilization effects on the growth and spread of rhizome-transplanted giant cane (*Arundinaria gigantea*). *Restoration Ecol.* 18:462–468.
- Zhang, F., X.Q. Wan, H.Q. Zhang, G.L. Liu, M.Y. Jiang, Y.Z. Pan, and Q.B. Chen.** 2011. The effect of cold stress on endogenous hormones and *CBF<sub>1</sub>* homolog in four contrasting bamboo species. *J. For. Res.* DOI 10.1007/s10310–011–0253-x.