



Variation in fiber cables in the lacunae of leaves in hybrid swarms of *Typha* × *glauca*



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ABSTRACT

The presence or absence of fiber cables in the lacunae of the last formed leaf blades of flowering *Typha* plants is a diagnostic character. The fiber cables are present in all leaves of *Typha angustifolia* L., but are absent in the last formed leaves of *Typha latifolia* L. We find great variation in the presence of fiber cables in the last formed leaves of individuals in stands of *Typha* × *glauca* Godr. (pro sp.). We find that individuals that comprise the hybrid swarms that are closer to *T. angustifolia* in terms of standard characters have fiber cables in most or all of the last formed leaf blades before the inflorescence. By contrast, those individuals closer to *T. latifolia* in terms of standard characters do not have fiber cables in the last formed leaves before the inflorescence. The lengths of the longest fiber cables are correlated with the lengths of the leaves in *T. angustifolia* and the “angustifoliod” *T.* × *glauca*, but not in *T. latifolia* and the “latifoliod” *T.* × *glauca*. The variability in the taxonomically, morphologically and biomechanically-significant fiber cables in the lacunae in reproductive plants may be useful in characterizing and understanding the composition of a *Typha* stand.

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1. Introduction

Typha is a cosmopolitan genus found in marshes, ponds, drainage ditches and other fresh water or slightly brackish habitats (Comstock, 1922). The one-to-three meter tall photosynthetic green leaves act as a sink for carbon dioxide, a means for removing pollutants, provide habitat for red-winged blackbirds, marsh wrens and waterfowl, and have been used by humans for roof thatch, chairs and barrel caulking (Wiegand and Eames, 1925; Marsh, 1955; Smith, 2000). We studied the fiber cables in the air lacunae of the leaves of *Typha* that may contribute to the stability of the wind-resilient leaves (Witztum and Wayne, 2014). The occurrence or absence of these fiber cables in the last leaves produced before the fertile spike is diagnostic for some species. Fiber cables are present in the last formed leaves of *Typha angustifolia* L. and *Typha dominicensis* Pers., but absent in the last formed leaves of *Typha latifolia* L. produced before the fertile spike. Here, we show that in hybrid swarms of *Typha* × *glauca* Godr. (pro sp.) (1844; fide Mason, 1957; Smith, 2000), the fiber cables may or may not be present in the last leaf produced before the fertile spike. The presence or absence of the fiber cables in the last leaf produced before the fertile spike in

individual plants of *T.* × *glauca* can be used as a character to help define the relationship between the individuals that comprise a hybrid swarm of *T.* × *glauca* and pure populations of *T. angustifolia* and *T. latifolia*. Knowledge of the diversity in the biomechanical structures of *Typha* may be useful in understanding the function and distribution of these wetland plants.

2. Methods

2.1. *Typha* populations

We studied stands of *Typha* in Ithaca, New York growing at Beebe Lake, Flat Rocks, Newman Arboretum, Bluegrass Lane, and Ringwood Preserve, all of which are part of the Cornell Plantations (see descriptions, images and maps at <http://www.cornellplantations.org/our-gardens/natural-areas/profiles>). We studied stands growing along the side of the road in Ithaca, New York near the corner of Maple Avenue and Pine Tree Road, near the corner of Arrowwood Drive and Warren Road, along Pleasant Grove Road, along Hanshaw Road, and along Neimi Road. We sampled stands growing in these habitats for three months. While the sample area was limited, the habitats and the *Typha* growing in them were diverse. We also studied a stand growing in a marsh in Michigan Hollow in Spencer, New York.

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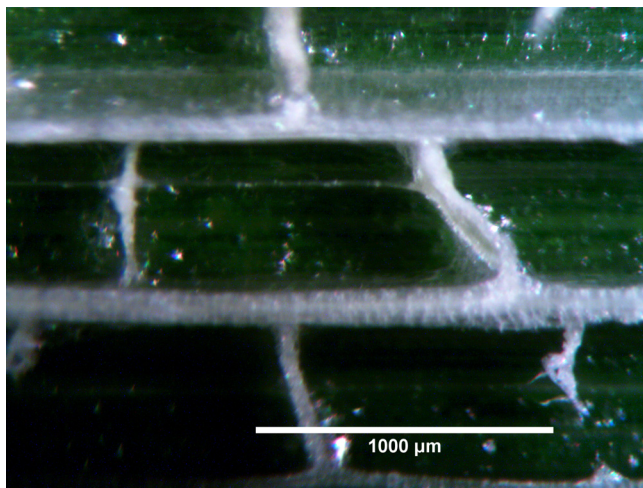


Fig. 1. The end of the longest fiber cable in a leaf of *T. x glauca* observed with a stereo microscope.

Observation of characters and determination of the ratio (B/A) of the length of the longest fiber cable (B) to the length of the leaf blade (A). Leaves of *Typha* were sliced open with a razor blade along the length of the leaf blade close to the abaxial surface and observed with an Olympus SZH stereo microscope. The length of the longest fiber cable (B) that traversed the longitudinal air chambers of the leaf blade was noted. The end of the cable is shown in Fig. 1. Leaf blade measurements were from the point of highest attachment of the basal leaf sheath to the tip of leaf blade (A). Analysis of variance and analysis of covariance using the ANOVA and ANCOVA functions were performed on non-zero log transformed data with XLSTAT. Stigmas and pistils were also observed with the stereo microscope. Lengths of leaf blades, fiber cables, female part of the inflorescences and sterile zone between the female and male parts of the inflorescences were measured with a ruler. An Olympus BH-2 microscope was used to observe pollen and isolated fiber cables. When viewed with polarizing optics and a full wave plate, the fibers in the fiber cables isolated from the lacunae are seen to be enveloped by a monolayer of cells, each containing a single prismatic calcium oxalate crystal (Fig. 2). These fiber cables were shown by McManus et al. (2002) in their Fig. 1H and by Ni et al. (2014) in their Fig. 1E and Fig. 2J. However, the fiber cables, which contain no tracheary elements (tracheids or vessel elements) or sieve elements (sieve cells or sieve-tube elements) and which are not hollow, have been wrongly referred to as “vascular bundles” by Ni et al. (2014) or “vertical ducts” by Kaul (1974). The evidence

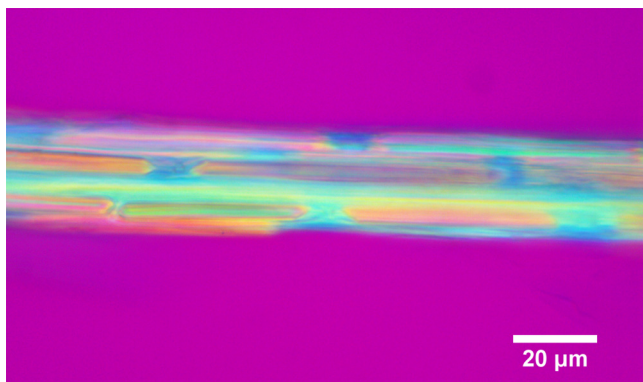


Fig. 2. An isolated fiber cable of *T. x glauca* observed with polarized light microscopy and a full wave plate compensator.

for the construction and physical properties of the fiber cables has been presented in Witztum and Wayne (2014).

Digital images of the fiber cables in the lacunae were captured with a 5 MP digital camera (AmScope, Irvine, CA) using the TouPView (Ver. $\times 86$, 3.7.939) image processing program and calibrated scale bars were inserted using ImageJ (<http://rsb.info.nih.gov/ij/>).

In a previous paper (Witztum and Wayne, 2014), we numbered leaves from the oldest to the youngest. Since the emphasis in this paper is on the youngest leaves, here we have numbered the leaves from the youngest to the oldest.

3. Results

Individuals in hybrid swarms of *T. x glauca* may look more like either *T. angustifolia* or *T. latifolia* (Fig. 3). An individual plant of *Typha* collected from the pond in the Newman Arboretum of Cornell Plantations had the morphological characters (Table 1) of *T. angustifolia* and serves as an example. There are fiber cables present in the lacunae of all the leaves produced before the flowering spike (Table 2). An individual plant of *Typha* collected from the pond in Ringwood Preserve of Cornell Plantations had the morphological characters (Table 1) of *T. latifolia* and serves as an example. There are no fiber cables present in the lacunae of the last five leaves produced before the flowering spike (Table 3). Statistical analysis with ANOVA and ANCOVA indicates that the lengths of the longest fiber cables are significantly correlated with the lengths of the leaves in *T. angustifolia* but not in *T. latifolia*.

We measured the total length of the longest fiber cable that traverses the lacunae of each leaf blade of flowering individuals in various stands of *T. x glauca*. In hybrid individuals that were most like *T. angustifolia* (narrower and more semicylindrical leaf blades, more auriculate sheath, longer sterile axis between the female and male parts of the inflorescence, chestnut color of female part of the inflorescence, single pollen grains (monads), sterile pistils more truncate, stigmas linear-lanceolate (more filiform and less spatulate)), the last formed leaves bore fiber cables (Table 4; Fig. 4). In



Fig. 3. *T. x glauca* from a stand on the corner of Maple Avenue and Pine Tree Road in Ithaca, New York. None of the specimens were pure *T. angustifolia* or *T. latifolia* but contained various combinations of characters from each species. A meter stick is included for scale.

Table 1

Some morphological diagnostic characters of *T. angustifolia* and *T. latifolia* compiled from Gray (1859, 1870), Hotchkiss and Dozier (1949), Fernald (1950), Smith (1967, 2000), Cronquist et al. (1977), Grace and Harrison (1986) and Kuehn and White (1999).

Character	<i>Typha angustifolia</i>	<i>Typha latifolia</i>
Leaf blade	Narrow and semicylindrical	Wide and planar
Leaf sheath	Auriculate	Tapering
Sterile gap between female and male parts of the inflorescence	Present	Absent
Color of female part of the inflorescence	Chestnut	Dark brown
Pollen grains	Monads	Tetrads
Sterile pistils	Truncate	Oval-shaped
Stigmas	Linear (filiform)	Lance-ovate (spathulate)
Fiber cables in last formed leaf blades of flowering plants	Present	Absent

Table 2

Length and width of leaf blades and longest fiber cable length and B/A ratio of an individual of *T. angustifolia* collected from the Newman Arboretum.

Leaf number	Leaf length (A) (cm)	Fiber cable length (B) (cm)	B/A	Leaf width (mm)
1	56.2	20.9	0.37	7.5
2	73.7	36.8	0.50	8.0
3	87.1	43.4	0.50	8.0
4	84.9	49.5	0.58	7.0
5	91.2	45.3	0.50	7.0

Sterile zone, 4 cm; leaf sheaths, auriculate; pollen, monads; female part of the inflorescence, 14 cm × 1.7 cm, chestnut; stigmas, filiform; abortive pistil, truncate. Analysis of variance shows that the longest fiber cable length is significantly correlated with the leaf length ($p=0.007$) and not significantly correlated with leaf width ($p=0.212$). The correlation coefficient (r) is 0.967 for the longest fiber cable length and leaf length and $r=-0.788$ for the longest fiber cable length and leaf width. Analysis of covariance shows that the longest fiber cable length is not significantly correlated with the leaf length and width together ($p=0.066$) and width alone ($p=0.935$), but is significantly correlated with length alone ($p=0.036$).

hybrid individuals that were more like *T. latifolia* (wider and more planar leaf blades, more tapering leaf sheath, shorter or no sterile axis between female and male parts of the inflorescences, darker brown color of female part of the inflorescence, pollen grains in tetrads, sterile pistils more oval shaped, stigmas linear-lanceolate (less filiform and more spatulate)), the last formed leaves lacked fiber cables as was the case in *T. latifolia* (Table 5; Fig. 5). Statistical analysis with ANOVA and ANCOVA indicates that the lengths of the longest fiber cables are significantly correlated with the lengths of the leaves in the “angustifoloid” *T. × glauca* but not in the “latafoloid” *T. × glauca*.

Table 3

Length and width of leaf blades and longest fiber cable length and B/A ratio of an individual of *T. latifolia* collected from Ringwood Preserve.

Leaf number	Leaf length (A) (cm)	Fiber cable length (B) (cm)	B/A	Leaf width (mm)
1	47.3	0	0	15.5
2	65.8	0	0	18.0
3	77.5	0	0	20.0
4	87.6	0	0	21.0
5	98.6	0	0	22.0
6	116.9	21.9	0.19	22.5
7	115.4	47.9	0.42	23.0
8	115.5	59.1	0.51	23.0
9	119.4	64.5	0.54	23.0
10	117.9	64.7	0.55	21.0
11	110.5	66.5	0.60	20.0

Sterile zone, none; leaf sheaths, tapering; pollen, tetrads; female part of the inflorescence, 13.5 cm × 2.8 cm, dark brown; stigmas, spatulate; abortive pistil, oval-shaped. Analysis of variance shows that the longest fiber cable length is not significantly correlated with the leaf length ($p=0.764$) and not significantly correlated with leaf width ($p=0.533$). The correlation coefficient (r) is -0.322 for the longest fiber cable length and leaf length and $r=-0.159$ for the longest fiber cable length and leaf width. Analysis of covariance also shows that the longest fiber cable length is not significantly correlated with the leaf length and width together ($p=0.845$), width alone ($p=0.638$) or length alone ($p=0.929$).

Table 4

Length and width of leaf blades and longest fiber cable length and B/A ratio of an individual of an “angustifoloid” *T. × glauca* collected from Newman Arboretum.

Leaf number	Leaf length (A) (cm)	Fiber cable length (B) (cm)	B/A	Leaf width (mm)
1	52.6	12.9	0.25	9.0
2	73.4	32.1	0.44	12.0
3	88.5	49.1	0.55	12.5
4	101.9	59.9	0.59	13.0
5	108.7	58.2	0.54	13.5
6	110.7	54.9	0.50	13.5
7	110.1	60.4	0.55	13.5

Sterile zone, 1.2 cm; leaf sheaths, auriculate; pollen, monads; female part of the inflorescence, 20.4 cm × 2.1 cm, chestnut; stigmas, more filiform than spatulate; abortive pistil, truncate. Analysis of variance shows that the longest fiber cable length is significantly correlated with the leaf length ($p<0.0001$) and significantly correlated with leaf width ($p<0.0001$). The correlation coefficient (r) is 0.973 for the longest fiber cable length and leaf length and $r=0.982$ for the longest fiber cable length and leaf width. Analysis of covariance shows that the longest fiber cable length is significantly correlated with the leaf length and width together ($p=0.001$), but not to width alone ($p=0.117$) or length alone ($p=0.310$).

While in *T. × glauca*, there is a correlation between the presence of fiber cables in the last leaf formed before the fertile spike and a consensus of the morphological characters that define *T. angustifolia*, and there is a correlation between the absence of fiber cables in the last leaf formed before the fertile spike and a consensus of the morphological characters that define *T. latifolia*, there seems to be no correlation between any single character in *T. × glauca* and the presence or absence of fiber cables in the last leaf formed before the fertile spike in *T. × glauca*.

While the presence or absence of fiber cables in the last leaf formed before the fertile spike in *T. × glauca* is a dichotomous

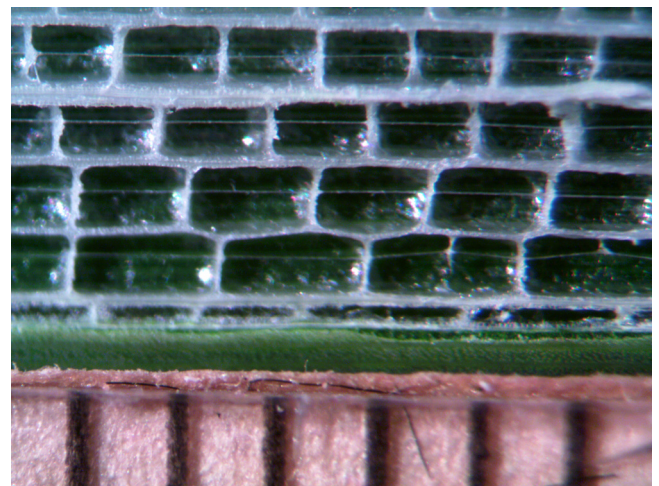


Fig. 4. Presence of fiber cables in the lacunae of the last leaf blade produced before the fertile spike in *T. × glauca* observed with a stereo microscope 20 cm above the sheath attachment. The scale is calibrated in millimeters.

Table 5
Length and width of leaf blades and longest fiber cable length and B/A ratio of an individual of a "latifoloid" *T. × glauca* collected from Newman Arboretum.

Leaf number	Leaf length (A) (cm)	Fiber cable length (B) (cm)	B/A	Leaf width (mm)
1	71.3	0	0	18.0
2	95.4	0	0	21.0
3	112.2	25.3	0.23	23.0
4	121.2	48.1	0.40	25.5
5	130.1	58.5	0.45	26.0
6	136.8	58.4	0.43	27.0

Sterile zone, none; leaf sheaths, auriculate; pollen, tetrads; female part of the inflorescence 37.2 cm × 2.4 cm, dark brown; stigmas, more spatulate than filiform; abortive pistil, oval-shaped. Analysis of variance shows that the longest fiber cable length is not significantly correlated with the leaf length ($p=0.084$) but is significantly correlated with leaf width ($p=0.027$). The correlation coefficient (r) is 0.973 for the longest fiber cable length and leaf length and $r=0.916$ for the longest fiber cable length and leaf width. Analysis of covariance shows that the longest fiber cable length is not significantly correlated with the leaf length and width together ($p=0.222$), nor to width alone ($p=0.375$) or length alone ($p=0.838$).

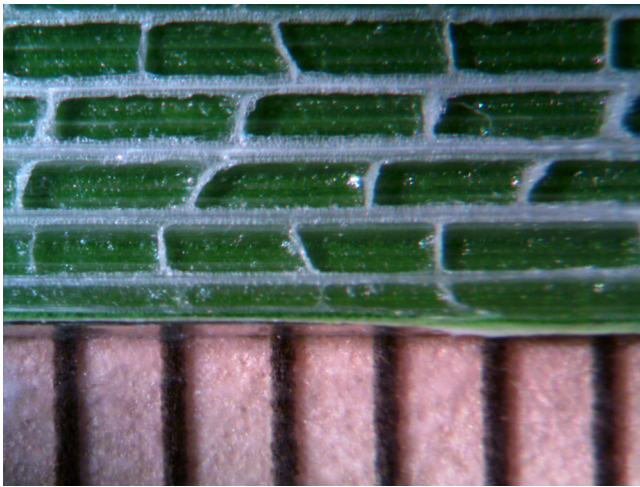


Fig. 5. Absence of fiber cables in the lacunae of the last leaf blade produced before the fertile spike in *T. × glauca* observed with a stereo microscope 20 cm above the sheath attachment. The scale is calibrated in millimeters.



Fig. 7. Variation in the color and size of the female parts of the inflorescences of *Typha* collected from the Newman Arboretum. The isolated 10 cm segment of the fertile spike serves as a scale bar.

character that distinguishes affinity with *T. angustifolia* or *T. latifolia*, the rate in which the fiber cables decrease as the plants proceed developmentally into the flowering phase also varies (Fig. 6). The greater the number of last formed leaves that lack the fiber cables in an individual of *T. × glauca*, the greater the affinity of that individual to *T. latifolia*. The presence of fiber cables is generally but not absolutely correlated with the color and morphology of the fertile spike in *T. × glauca* (Fig. 7). In the leaves of plants represented by the female parts of the inflorescences shown in Fig. 7, there were no fiber cables in the last 3–5 leaf blades of the four "latifoloid" plants on the left, there were fiber cables in all leaf blades of the

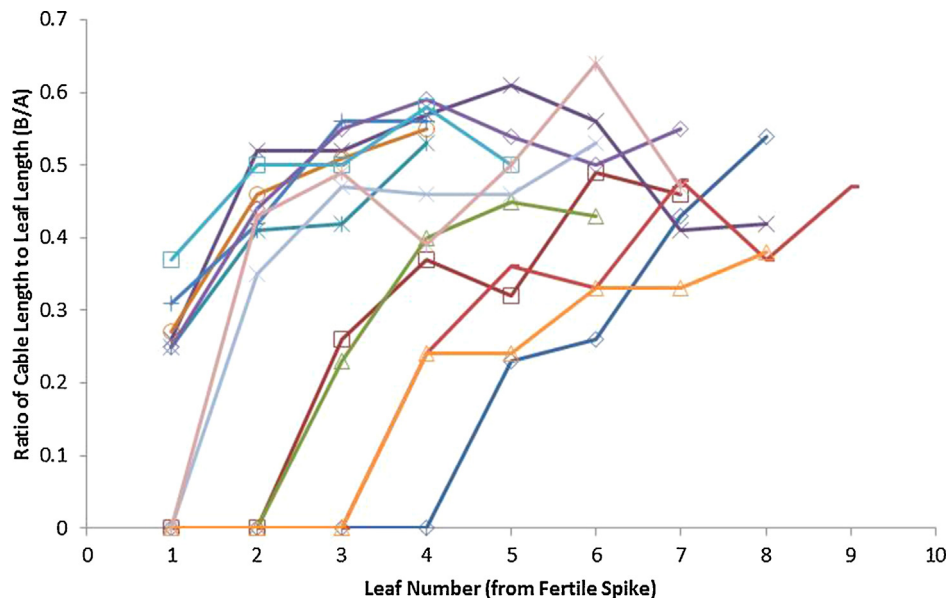


Fig. 6. The ratio of length of the longest fiber cable to leaf blade length in the leaves of various individuals of *T. × glauca* plotted against leaf number from fertile spike. Each color represents a different plant.

four “angustifolioid” plants on the right. There were fiber cables in the last two leaf blades in one of the four center plants—the one on the right and no fiber cables in the last two leaf blades of the other three plants in the center.

4. Discussion

According to Kuehn and White (1999), “Accurate identification of the cattail taxa has become increasingly important over the past several decades as it appears that *T. × glauca* stands are expanding throughout northeastern and central North America.” However, accurate identifications of the taxa are difficult as a result of introgression. While “The cattail genus *Typha* is perhaps the best-studied example of hybridization in water plants from an experimental perspective” (Les and Philbrick, 1993), any additional easily-determined character would be useful in the accurate identification of cattail taxa.

In a study of fiber cables that traverse the lacunae in leaf blades of *T. domingensis*, *T. angustifolia*, *T. × glauca* and *T. latifolia*, we noted that all leaf blades of non-flowering individuals bore fiber cables (Witztum and Wayne, 2014). *T. angustifolia* also bore fiber cables in all leaf blades of both non-flowering and flowering individuals. By contrast in flowering individuals of *T. latifolia*, the last 4 or 5 leaves formed lack fiber cables entirely.

We originally found that in plants from a morphologically uniform stand of *T. × glauca* fiber cables were present in all the leaves of non-flowering individuals and in all or most of the leaves of flowering individuals (Witztum and Wayne, 2014). In the present work, where we studied mixed stands in a variety of habitats where many intermediates between *T. angustifolia* and *T. latifolia* grew together, we found that the presence or absence of fiber cables in the last leaf produced before the fertile spike is a variable character that may indicate an affinity to one or the other parental species that gave rise to *T. × glauca*. The presence of fiber cables in the last leaf produced before the fertile spike is an indication of an affinity with *T. angustifolia* and the absence of fiber cables in the last leaf produced before the fertile spike is an indication of an affinity with *T. latifolia*. In addition, the greater the number of leaves that lack fiber cables before the fertile spike, the greater is the affinity with *T. latifolia*.

While Hotchkiss and Dozier (1949) considered *T. × glauca* Godr. to be a definite and readily distinguished species, more recent work has suggested that *T. × glauca* is neither a distinct species nor a result of a single hybridization event between *T. angustifolia* and *T. latifolia* (Smith, 1962, 1967, 1987, 2000). As a result of introgression (Wiegand, 1935; Anderson, 1949; Mason, 1957), *T. × glauca* is a genotypically and phenotypically diverse collection of individuals that make up a hybrid swarm between *T. angustifolia* and *T. latifolia* (Fassett and Calhoun, 1952; Bayly and O’Neill, 1971; Krattinger, 1975; Lee, 1975; Sharitz et al., 1980; Kuehn et al., 1999; Kuehn and White, 1999; Tsyusko et al., 2005; Snow et al., 2010; Travis et al., 2010, 2011; Kirk et al., 2011; McKenzie-Gopsill et al., 2012; Ball and Freeland, 2013; Freeland et al., 2013; Nowińska et al., 2014). Indeed, *T. × glauca* was the first taxon in which a graphical method was used to show introgressive hybridization (Fassett and Calhoun, 1952; Anderson, 1953). Variability in the presence of the fiber cables in the lacunae of the leaves produced before the fertile spike supports the claim that *T. × glauca* is a diverse collection of individuals that have undergone introgressive hybridization to make up a hybrid swarm.

In 1844, Dominique-Alexandre Godron (1844) described a plant in Europe that was intermediate between *T. angustifolia* and *T. latifolia*. However, intermediate types between *T. latifolia* and *T. angustifolia* were observed even before 1844. In his “A Flora of the State of New-York” Torrey (1843) cited a posthumous contribution of Ludovici Claudii Richard (1833) which described specimens

growing together that connect the two parent species. Torrey (1843) noted that he “also found similar intermediate forms in New-York.” Likewise, Henry David Thoreau noticed on July 31, 1859 a “remarkable large and tall *Typha*, apparently *T. latifolia* (yet there is at least more than an inch interval between the two kinds of flowers. . .). It is seven or eight feet high. . .much taller than any I see elsewhere as to appear a peculiar species. . .They are what you may call the tallest reed of the meadows. . .” (Thoreau, 1906). It is possible that the tall plant Thoreau saw on July 31, 1859 was the hybrid *T. × glauca* (Angelo, 2014).

In the first edition of the “Manual of the Botany of the Northern United States,” Asa Gray (1848) considered *T. angustifolia* L. and *T. latifolia* L. to be separate species. In subsequent editions, Gray (1856, 1859, 1870) considered the possibility that *T. angustifolia* was a “mere variety” of *T. latifolia*. In Gray’s “New Manual of Botany” (seventh edition; Robinson and Fernald, 1908), *T. angustifolia* and *T. latifolia* are included but *T. × glauca* Godr. does not appear. There is no mention that *T. angustifolia* may be a “mere variety” of *T. latifolia*. Intermediates between *T. angustifolia* and *T. latifolia* were becoming more recognized. Knowlton et al. (1909) observed that “where the two species grow together there are all kinds of intermediate forms” that are “especially noticeable in the big swamps at West Cambridge” and Muriel Roscoe (1927) noted that the formation of “angustifolioid” and “latifolioid” intermediates were widespread. In the eighth edition of “Gray’s Manual of Botany,” revised by Fernald (1950), *T. × glauca* Godr. is included and its great stature is noted. In a recent note, Gibson (2012) presented a photograph of *Typha* growing in the Meadow at Harvard University’s Arnold Arboretum that is *T. × glauca* and may be similar in appearance to the plant that Thoreau saw in 1859.

T. × glauca is considered to be an aggressively invasive wetland taxon (Bohlen, 1990; Galatowitsch et al., 1999; Trebitz and Taylor, 2007; Tulbure et al., 2007; Tuchman et al., 2009; Lishawa et al., 2010; Mitchell et al., 2011; Larkin et al., 2012; Ciotir et al., 2013; Freeland et al., 2013; Farrer and Goldberg, 2014), however, as a taxon, it is highly diverse. Molecular markers have been used to characterize the diversity in *Typha* (Lamote et al., 2005). We are beginning to use the fiber cables as a biomechanical marker to characterize the diversity in *Typha*. Since the lengths of the longest fiber cables in *T. angustifolia* and the “angustifolioid” *T. × glauca* are significantly correlated with the lengths of the leaves while they are not correlated with the lengths of the leaves in *T. latifolia* and the “latifolioid” *T. × glauca*, the presence of fiber cables may play a role in the fitness of individuals with tall thin leaves and the absence of fiber cables may play a role in the fitness of individuals with shorter and wider leaves. Being able to distinguish the “angustifolioid” type or the “latifolioid” type may be useful in understanding the ability of each type of this protean taxon to invade wetland habitats. Our morphological and biomechanical approach complements the molecular approaches used to characterize the diversity in the protean taxon referred to *T. × glauca* Godr. (pro sp.), and we hope that this morphological and biomechanical analysis will be extended throughout its wide distribution in order to characterize better, the fiber cables and their biomechanical role in this invasive taxon.

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