

**CAREX × CAYOUILLEI (CYPERACEAE),
A NEW INTERSECTIONAL SEDGE HYBRID FROM SOUTHERN QUÉBEC, CANADA**

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ABSTRACT

A putative hybrid of *Carex* (Cyperaceae) was discovered in a swamp in the Montréal region (southern Québec, Canada). A survey of the surrounding vegetation, numerical phenetic analysis, and use of proxies of plant sterility showed that the individuals were sterile intersectional hybrids between sects. *Lupulinae* and *Vesicariae*. We propose the name **Carex** × **cayouettei** A. Bergeron, **hybr. nov.** for the hybrid combination *C. comosa* × *C. lupulina*. Several factors (reproduction time, habitat and natural range) support the assumption that the hybrid is likely more common than suggested by previous knowledge, but difficulties encountered in identification may have limited documentation. This finding strengthens the evidence that *Lupulinae* and *Vesicariae* are closely related.

An unidentified sedge was discovered near a swamp during a survey of an urban forest in the metropolitan Montréal area. The plant did not resemble any known species of the region; we thus suspected that it was a natural hybrid. Initially, *Carex lupulina* and *C. pseudocyperus* seemed to be possible parents (authorities are given in Appendix 1), since both were found in the swamp near the unfamiliar sedge. Such a combination was nevertheless questionable because intersectional hybrids between sects. *Lupulinae* Tuck. ex J. Carey and *Vesicariae* (Heuff.) J. Carey [combined with sect. *Pseudocypereae* (Tuck.) Christ sensu Ball & Reznicek 2002] are uncommon (Cayouette & Catling 1992). In addition, visual analysis of the characters was problematic, particularly in relation to size of vegetative organs, which did not appear intermediate. Although hybrid vigor exists among sedges, the intermediate state or presence of some characters more related to one of the parents is essential to the determination of legitimate intersectional hybrids such as *C. lupulina* × *retrorsa* Schwein. (Dudley 1886; Cayouette & Catling 1992). We therefore examined the sedge vegetation around the unfamiliar plant more closely, and performed a phenetic analysis involving several other putative parents to determine which ones were involved in the hybrid combination.

Study site

The unidentified sedge was found at the Bois-de-Saraguay Nature-Park (45° 30.9' N, 73° 44.5' W), southern Québec, Canada. This Park is one of the best preserved urban forests on the Island of Montréal, not only because of restricted public access, but also because of its size (96 ha). This mature forest is characterized by a mosaic of mesic and hygric habitats with tree associations dominated by *Acer saccharum*, *Fagus grandifolia*, and *Tilia americana* on well-drained soils, swamps dominated by *Acer saccharinum*, and *Fraxinus pennsylvanica* on poorly-drained soils (Domon et al. 1986). In an exhaustive floristic survey (152 person-days) carried out by our research team between June and August 2011, a total of ca. 389 taxa were recorded, which represents a high level of richness for the region. Sedges accounted for a pool of 32 species (Appendix 1). Several rare Québec plants are only present in this park (Bergeron & Pellerin 2011; Bergeron et al. 2013). Despite low levels of past anthropogenic disturbances in this urban context, ca. 21% of florula is composed of naturalized and ephemeral plants.

Fieldwork and laboratory

During the plant survey of an open, flooded swamp on July 7, 2011, we collected the putative sedge hybrid for the first time. On July 14, 2011, we returned to the site to note all sedge species present in the swamp and within radii of 10 and 5 meters of the putative hybrid population. Macromorphological characters were measured *in situ* and *ex situ* on live specimens and those collected; the latter were then dried. Nine to twelve random measurements were taken for each character. In the laboratory, pollen grains were stained with cotton blue (lactophenol) to indicate defective cytoplasm. In order to collect the achenes, we examined the site closely a final time on October 16, 2011.

Phenetic analysis

After a summary examination of macromorphological measurements, we classified the putative hybrid as belonging to the group of “bladder” and “bottlebrush” sedges (*sensu* Hipp 2008). The specimens bore long and inflated perigynia, which distinguish the sect. *Lupulinae* and pistillate scales with scabrous awns characterizing, *inter alia*, the sect. *Vesicariae*. Furthermore, the broad vegetative blades on the putative hybrid could place it not far from the broadly construed sect. *Paludosae* (Heuff.) Christ (Ball & Reznicek 2002).

For phenetic analysis, we first checked the sedge list for the Bois-de-Saraguay (Appendix 1) to select the putative parents among *Carex* sects. *Lupulinae*, *Vesicariae*, and *Paludosae*. We included species belonging to the three sections, with the exception of *C. grayi* (globular spikes) and *C. pellita* (pubescent perigynia), which have characters too distant from the putative hybrid. Second, we included five species forming hybrid combinations according to Cayouette and Catling (1992) and with documented occurrences in the Montréal region and southern Québec (A. Bergeron, unpub. data; Brouillet et al., 2010+). *Carex lupuliformis* Sartwell ex Dewey was not selected due to its rarity and remote populations well-researched in the context of the Pellerin’s team’s project, “Rescuing false hop sedge” (Environment Canada 2014). Finally, we included three species exhibiting some ornamental qualities, unlisted for Québec but possibly present due to escape from cultivation. In order of selection as described above, the 13 species are the following: *C. intumescens*, *C. lacustris*, *C. lupulina*, *C. pseudocyperus*, *C. retrorsa*, *C. comosa* Boott, *C. hystericina* Muhl. ex Willd., *C. lurida* Wahlenb., *C. utriculata* Boott, *C. vesicaria* L., *C. acutiformis* Ehrh., *C. gigantea* Rudge, and *C. hyalinolepis* Steud.

Measurements of macromorphological characters related to the 13 possible parents were compiled from the literature (Gleason & Cronquist 1991; Hill 2006; Ball & Reznicek 2002; Jones 2010). Data analysis was performed by Principal Coordinates Analysis (PCoA) with Cailleux correction (Legendre & Legendre 2012, p. 493) on the mid-point of min and max values of each character. The PCoAs were calculated on character tables rescaled in Gower’s dissimilarity matrix (Legendre & Legendre 2012, p. 278), and then multiplied with an *F*-ratio weighting (Adams 1972, 1982). With the min and max values of each character, an *F*-ratio (intergroup variance ÷ intragroup variance) was calculated from an ANOVA between the species. Derived from the literature, these ranges of values establish the true boundaries of the species, which guarantees the validity of the calculations even if the intragroup variance were computed on only two degrees of freedom. In fact, we also tried the PCoAs without weighting (Adams 1972, 1982), which did not alter our conclusions. However, the weighting with the *F*-ratios gave the greatest amount of explained variance on the first two PCoA axes, which justified the use of this procedure. Note also that these numerical methods are not statistical hypothesis tests. We used the weighted PCoAs to synthesize information and draw a conclusion based on decisions. All analyses were performed using the R language (R core team, 2013).

Preliminary analysis

Eighteen selected characters known to discriminate sedges within and between the three sections were used (Table 1) in a preliminary analysis which aimed to reduce the number of putative parents to be examined in detail. By excluding the putative hybrid, we calculated *F*-ratios for weighting each of the 18 characters (Table 1). Ordination of the first two PCoA axes with the 14 taxa including the putative hybrid (80% of explained variance) made it possible to segregate sedge sections and identify species with characters too distant from the putative hybrid. All members of sect. *Paludosae* were discarded. We then calculated two other PCoAs that led to the successive removal of species distantly related to the putative hybrid. The last preliminary PCoA was performed on seven taxa (94% of explained variance) and placed the putative hybrid approximately in the middle of the PCoA axis I, the *Lupulinae* being on one side and *Pseudocypereae* [incl. within sect. *Vesicariae*] on the other.

Triplet analysis

To show the intermediate state of the putative hybrid relative to the characters of two sedge species, we only retained the six most likely parents (*Carex comosa*, *C. gigantea*, *C. hystericina*, *C. intumescens*, *C. lupulina*, and *C. pseudocyperus*) found in preliminary analyses. For the final analyses, we included 23 characters to improve refinement of the differences between taxa, and calculated new *F*-ratios (by excluding the putative hybrid) for weighting each of these characters (Table 1). By considering one species of sect. *Lupulinae*, the putative hybrid, and one species of sect. *Pseudocypereae*, we performed nine weighted PCoAs i.e., on all possible combinations of triplets.

Table 1. Description of characters and units used in the phenetic analysis. The *F*-ratios calculated between the putative parents are also shown, i.e. with 13 species for preliminary analyses, and 6 species for triplet analyses.

Characters	<i>F</i> -ratio for 13 spp.	<i>F</i> -ratio for 6 spp.
1. Culm length (cm) ^{*†}	0.0810	0.0433
2. Blade width (mm) ^{*†}	0.3396	0.2444
3. Number of prominent blade veins ^{*†}	0.5833	0.1200
4. Color of basal sheath (510 nm, 615 nm, 650 nm) ^{*†}	0.6360	1.1333
5. Number of terminal spikes ^{*†}	1.6005	0.9059
6. Sexuality of terminal spike (0: staminate, 1: bisexual) ^{*†‡}	0.9167	0.8000
7. Number of lateral spikes ^{*†}	0.1612	0.1294
8. Sexuality of lateral spike (0: pistillate, 1: bisexual) ^{*†‡}	0.7500	0.6000
9. Orientation of perigynium (45°, 90°, 135°) ^{*†}	6.8333	2.4000
10. Orientation of proximal spike (45°, 90°, 135°) ^{*†}	0.4028	0.2857
11. Perigynium length (mm) ^{*†}	2.4608	2.8642
12. Perigynium width (mm) ^{*†}	1.4872	2.3846
13. Perigynium length:width ratio	0.1435	0.1136
14. Length of perigynium beak (mm) ^{*†}	4.7309	5.2116
15. Length of perigynium teeth (mm) ^{*†a}	1.4347	1.6394
16. Number of perigynium veins ^{*†§}	0.9719	0.0342
17. Perigynium shape in cross section (0: trigonous, 1: round) ^{*†}	0.0581	0.1200
18. Apex of pistillate scale (0: acute, 1: acuminate, 2: awned) ^{*†}	0.6852	0.6000
19. Length of pistillate scale (mm) ^{*†}	NA	0.3613
20. Width of pistillate scale (mm) ^{*†}	NA	2.8887
21. Shape of beak teeth (0: straight, 1: outcurved, 2: very outcurved) ^{*†}	NA	4.2000
22. Width of proximal pistillate spike (mm) ^{*†}	NA	0.9464
23. Length of proximal bract (cm) ^{*†}	NA	0.4963

NA = Not applicable. * Characters measured directly on the putative hybrid. Data from [†]Ball and Reznicek (2002), [‡]Jones (2010), [§]Hill (2006), and ^{||}Gleason and Cronquist (1991). ^aFor *C. gigantea*, *C. lupulina* and *C. intumescens*, the length of perigynium teeth was measured in ImageJ (Rasband, 2012) on digital specimens after

imaging improvements (range between spp.: 0.5–1.2 mm); for each species, nine random specimens from AUA, TROY, USF, UWAL, or WIN herbaria (Thiers, 2008+) were used.

RESULTS AND DISCUSSION

The putative hybrid was discovered in a ca. 4000 m² swamp that was home to 10 species of sedges. The companion vegetation was mainly composed of hydrophytes e.g., *Alisma triviale*, *Impatiens capensis*, *Leersia oryzoides*, *Lemnoideae*, and *Onoclea sensibilis*. In an area of 314 m² (10 m radius) around the putative hybrid, we noted the presence of *C. cristatella* Britton, *C. intumescens*, *C. lupulina*, *C. pseudocyperus*, *C. tenera*, and *C. retrorsa*, while only three sedges were present in an area of 78.5 m² (5 m radius) i.e., *C. intumescens*, *C. lupulina* and *C. pseudocyperus*.

Two huge clumps of the putative hybrid, in full bloom, had established themselves in mud exposed to direct sunlight (Fig. 1); they were spread over an area of 90 cm by 80 cm and 110 cm by 70 cm, respectively. Clumps of other sedges found in the swamp were smaller, suggesting that the putative hybrid might imply a larger and not inventoried species. No achene was found on the *in situ* specimens or those collected. In the laboratory, the test of pollen colorability with cotton blue was 0%. Grains and their walls were deformed. Anthers were not exerted in the staminate spikes, or the staminate portions of the androgynous spikes. When we returned to the site in October, all infructescences of the two clumps were aborted, whereas achenes were well-developed on the surrounding sedges.



Figure 1. One of the huge clumps of the putative sedge hybrid found in full bloom in an open swamp at the Bois-de-Saraguay Nature-Park (southern Québec), on July 14, 2011.

Examination of 9 triplets using ordinations showed that the first PCoA axes explained the greatest amount of variance (55.8% to 84.2%), which usually located the putative hybrid in the middle of the diagrams. The second axes mostly showed the distinct nature of the putative hybrid by positioning it at one end, and the various putative parents at the other end. Comparison of 9 triplets (Fig. 2) revealed that the “com–hyb–lup” combination explained the most variance, and this combination placed the two species practically equidistant from the putative hybrid on PCoA axis I.

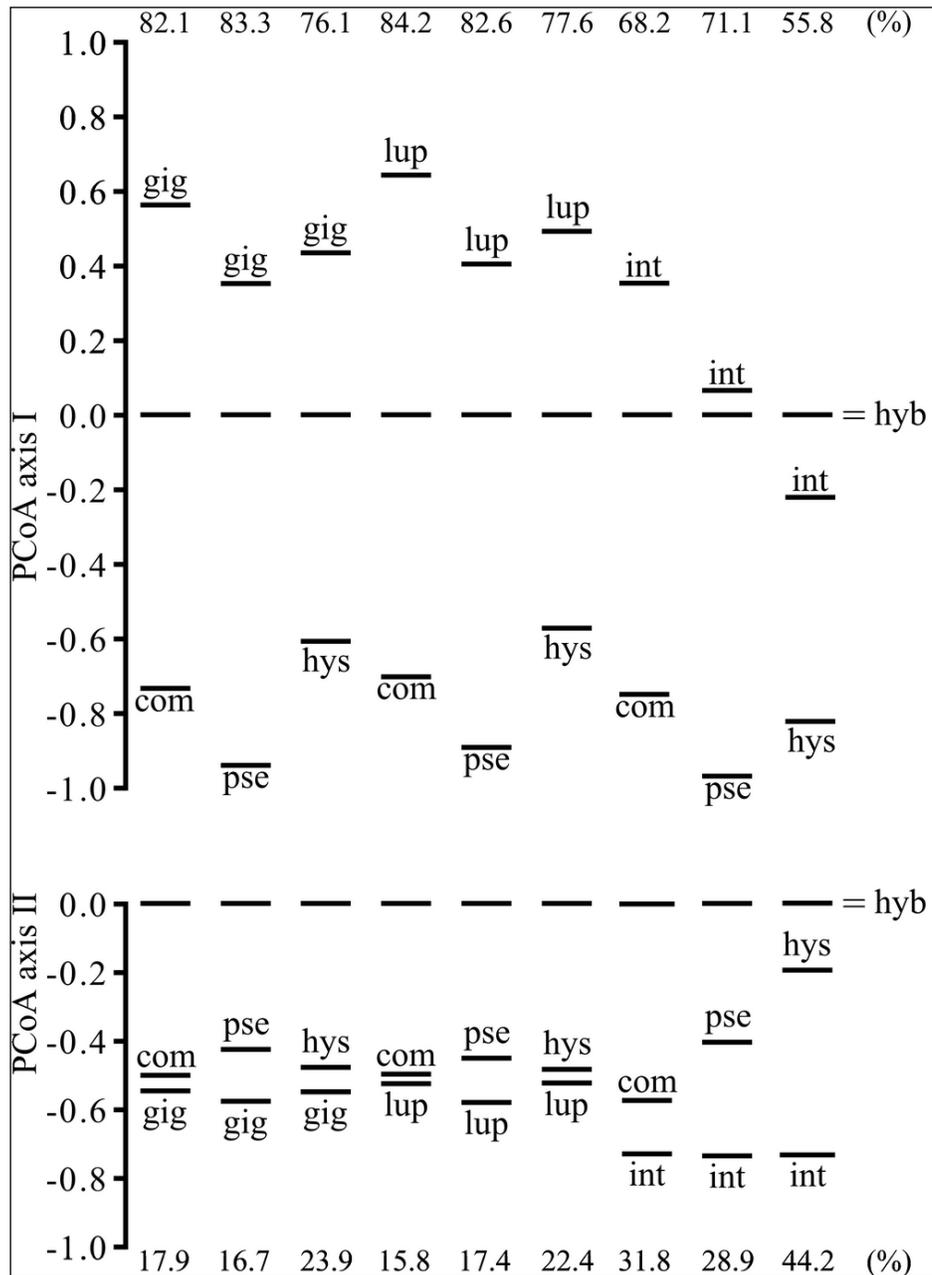


Figure 2. Results of the nine PCoAs performed on the species-by-character tables, rescaled into Gower's dissimilarity matrices and weighted by the *F*-ratios. The upper part of diagram shows the scores (horizontal bar) obtained for each of the nine PCoA axis I, while the lower part shows the scores for each of the PCoA axis II. The putative hybrid (hyb) was located at zero coordinates. The explained variance (%) per axis and for each triplet analysis is shown. The species codes correspond to the first three letters of their specific epithets.

The proxies of sterility (i.e., uncolored grains, undeployed anthers, aborted infructescences) and the set of intermediate characters in the PCoAs confirmed that the taxon was an intersectional hybrid between one smaller *Lupulinae* parent, and one large *Vesicariae* parent. The triplet analyses revealed that the correct hybrid combination (most equidistant position) was *Carex comosa* × *lupulina*. *Carex pseudocyperus* is not involved in the combination, although it was observed a few meters from the hybrid. In fact, visual examination of specimens from the Montréal region (Marie-Victorin Herbarium, MT) showed us that the blade widths of the hybrid (ca. 6–17 mm) were consistent with the morphometry of *C. comosa* (sometimes >13 mm) but not with that of *C. pseudocyperus* (always ≤13 mm). Qualitatively, the broad base of the culm of the hybrid is very similar to that of *C. comosa* in regard to width, texture, and color. Fernald (1950) as well as Cayouette and Catling (1992) have mentioned the combination *C. comosa* × *lupulina*, but there is currently no binomial name. Difficulties encountered in identification may have limited documentation, but it is possible that this taxon is more widespread than suggested by previous knowledge. To help in identification, we provide the morphological description below. Some additional measurements were taken on type specimens.

Carex* × *cayouettei A. Bergeron, **hybr. nov.** Figures 1, 3, 4. **TYPE: CANADA. Québec.** Ville de Montréal: Bois-de-Saraguay dans un marais eutrophe, 508424 mE, 5041055 mN (UTM 18T, NAD 83), 14 Jul 2011, A. Bergeron, M. Charrier, J.-S. Mignot, & E. Bergeron 11104 (holotype: MT; isotype: MICH); 7 Jul 2011, SP069 (paratype: DAO).

Plants cespitose. **Culms** 69–95 cm, scabrous distally. **Leaves:** basal sheaths brownish; blades mid to dark green, flat to W-shaped, 6–17(–19) mm wide. **Inflorescences:** peduncles of proximal spikes 0.9–3.5 cm, scabrous distally; proximal bract 37–53 cm, much longer than inflorescence, blades 6–11 mm wide, glabrous. **Spikes:** lateral 1–3 spikes androgynous, or pistillate, ascending to arching, 85–150-flowered, cylindrical, 45–80 × 16–19 mm; terminal 1–2(–3) spikes staminate, the proximal (if present) often ± forked and androgynous (but few perigynia at the base), 35–64 × 2.5–3.5 mm. **Staminate scales** scabrous-margined. **Pistillate scales** narrowly lanceolate, 6–8.5 × 0.8–1.5 mm, green center with subciliate hyaline margins, sometimes brown colored, apex scabrous-awned. **Perigynia** ascending to spreading, strongly 14–19-veined, slightly stipitate, lance-ovoid, inflated, trigonous to subcircular in cross section, 8–11 × 2.5–3.5 mm; beak, 4–6 mm, bidentate; teeth, fairly straight, 0.5–1.3 mm. **Stigmas** 3. **Achenes** aborted.

The taxon is named in honor of the Québec botanist Jacques Cayouette, who has devoted his life to studying graminoid plants and, in particular, sedge hybrids.

Distinguishing characteristics

Among its congeners, *Carex* × *cayouettei* is placed in sedges with culms and blades reaching a large size; with several spikes per culm having flowers either unisexuals or bisexuals, and bearing perigynia with a glabrous body and 3 stigmas. The pale brown basal sheaths and awned pistillate scales make this nothospecies similar to *C. comosa* from which it differs by its straight and shorter teeth of the perigynium; these latter characters are instead similar to *C. lupulina*. Macromorphological characters with an intermediate state relative to both parents are mainly related to the width and length of the perigynia and their beaks as well as the orientation of the perigynia along the axes of the pistillate spikes (Table 2). Some lateral (or even terminal) spikes of *C. ×cayouettei* are androgynous, which is sometimes observed in *C. comosa* (Hipp 2008). Similarly, the sedge hybrid most frequently bears 2(–3) terminal spikes, which is also sometimes observed in *C. lupulina* (but rarely according to Mohlenbrock 2011). Thus, an interesting feature of *C. ×cayouettei* is that it expresses sexual traits only occasionally encountered in both parents.

Table 2. The most distinguishing characteristics of *Carex* × *cayouettei* relative to its parents (*C. comosa* and *C. lupulina*). See Table 1 for data sources.

Characters	<i>C. comosa</i>	<i>C. ×cayouettei</i>	<i>C. lupulina</i>
Color of basal sheath	Brownish	Brownish	Reddish to brownish
Apex of pistillate scale	Awned	Awned	Acute to awned
Shape of beak teeth	Very outcurved	Straight	Straight
Length of perigynium teeth	1.3-2.8 mm	0.5-1.3 mm	0.5-1.1 mm
Length of perigynium beak	2-3.8 mm	4-6 mm	6-10 mm
Perigynium length	4.8-8 mm	8-11 mm	11-19 mm
Perigynium width	1.1-1.8 mm	2.5-3.5 mm	3-6 mm
Orientation of perigynium	Spreading to reflexed	Ascending to spreading	Ascending

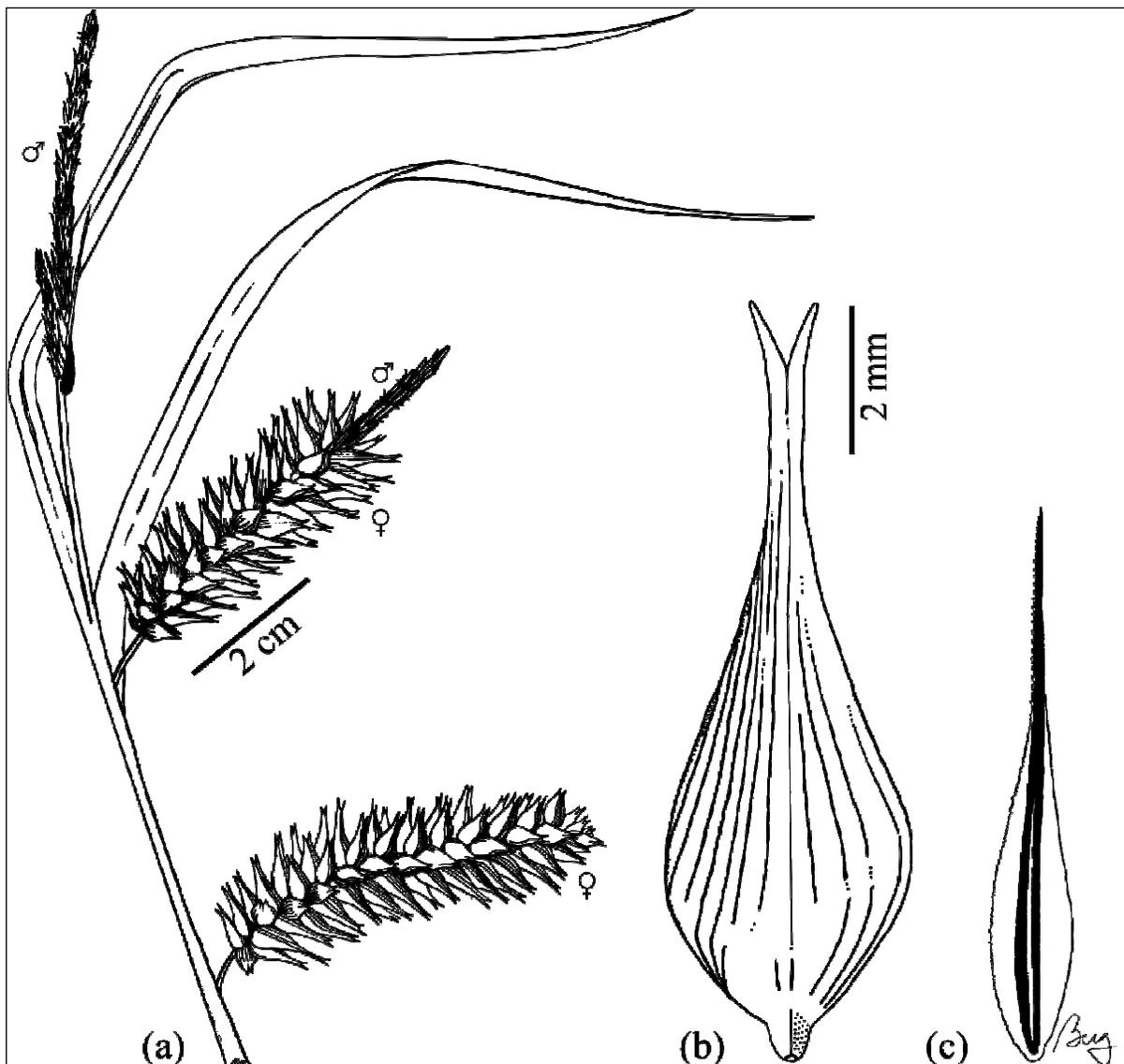


Figure 3. Illustration of *Carex* × *cayouettei* showing (a) the inflorescence with terminal staminate spikes and lateral androgynous and pistillate spikes (b) the perigynium, and (c) the pistillate scale

Carex × *cayouettei* is likely a true sterile hybrid with parents, *C. comosa* ($n = 32$) and *C. lupulina* ($n = 28-30$), having sets of chromosomes of a slightly different count (Wahl 1940; Reznicek & Ball 1974). This suggests that the genome of *C. ×cayouettei* contains irregular meiotic chromosome associations contributing to its complete sterility, as is observed in hybrids of different sections (Cayouette & Catling 1992; Hipp et al. 2009) although some taxa of this kind (e.g., *C. ×langeana* Fernald) can produce achenes in rare circumstances (J. Cayouette, pers. comm.). Further research is needed to verify this point. The sterility of intersectional hybrid sedges acts as a barrier to dispersal of these taxa, which explains their sporadic distribution. Thus, the presence of *C. ×cayouettei* individuals in a given place requires a hybridization event. The likelihood of the occurrence of such events may be more common than suggested by previous knowledge. First, there is a time window, from late-spring until mid-summer, where the reproduction periods of both parents match (Ball & Reznicek 2002). Second, both parents share the same habitat types (e.g., swamps, wet meadows); and third, their respective natural ranges are similar and of considerable size. Indeed, *C. comosa* and *C. lupulina* are obligate wetland species (Lichvar 2013) distributed together at least throughout eastern North America, i.e., from Texas to southern Québec (Ball & Reznicek 2002; NatureServe 2013).

Hence, the discovery of mature individuals of *Carex* × *cayouettei* in a Bois-de-Saraguay swamp indicates that a hybridization event between both parents occurred precisely at this location. Several reasons could explain the absence of *C. comosa* from our floristic inventory. It is possible that the population of this species sensitive to fluctuations in hydrology (NatureServe 2013) has become locally extinct, because the swamp has been profoundly altered by beavers in recent years (A. Bergeron, unpub. data). However, the most plausible explanation is that *C. comosa* remained unnoticed during our fieldwork. It is not unusual for individuals of *C. comosa* bearing narrow pistillate spikes to be interpreted as *C. pseudocyperus* (Bicknell 1908), especially since these two species often grow together (Ball & Reznicek 2002). Moreover, it appears that the invasion strategy of *C. comosa*, a species that can live at least 20 years, is to remain in a vegetative state for a few years before reproducing (Bernard & Seischab 1994). Without a fruiting structure, it can be difficult to properly document the occurrence of *C. comosa*. Its presence in the Montréal region has nevertheless been confirmed by herbarium data (Brouillet et al. 2010+), and it was recently observed in a marsh located ca. 10 km from Bois-de-Saraguay (A. Bergeron, pers. obs.).

There is little doubt that scant documentation of *Carex* × *cayouettei* is largely related to difficulties in identifying it formally. Also, it may be that some botanists aware of the parasitic deformities sometimes found on perigynia of the *Lupulinae* species have assumed that it was such an individual (Reznicek & Ball 1974). To complicate matters, the absence of flowering individuals of *C. comosa* in the vicinity of the hybrid can also lead botanists to false interpretations, as was our case, and moreover, it is possible that the hybrid remains vegetative for many years, like its parent. This feature could contribute to maintaining populations of the hybrid and also could make it a good candidate for inclusion among horticultural plants used in plant engineering or in landscaping of artificial ponds.

Finally, studies of intersectional hybrids have often contributed to revealing the taxonomic relationships within the genus *Carex*. In particular, it is known that *C. lupulina* hybridizes with *C. lurida*, *C. retrorsa*, or *C. vesicaria*, which indicates the affinity between the sects. *Lupulinae* and *Vesicariae* and their positions in a larger group (Reznicek & Ball 1974; Menapace & Wujek 1987; Ball & Reznicek 2002). The documentation of *C. ×cayouettei* is further evidence of the phylogenetic relatedness between these two sections.

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Appendix 1. Sedges found in the Bois-de-Saraguay Nature-Park.

- Carex albursina* E. Sheld.
Carex alopecoidea Tuck.
Carex bebbii (L.H. Bailey) Olney ex Fernald
Carex blanda Dewey
Carex bromoides Schkuhr ex Willd.
Carex cephaloidea (Dewey) Dewey
Carex crinita Lam.
Carex cristatella Britton
Carex deweyana Schwein.
Carex echinodes (Fernald) P.E. Rothr., Reznicek & Hipp
Carex gracillima Schwein.
Carex granularis Muhl. ex Willd.
Carex grayi J. Carey
Carex grisea Wahlenb.
Carex hirtifolia Mack.
Carex intumescens Rudge
Carex lacustris Willd.
Carex leptonevia (Fernald) Fernald
Carex lupulina Muhl. ex Willd.
Carex pedunculata Muhl. ex Willd.
Carex pellita Willd.
Carex plantaginea Lam.
Carex projecta Mack.
Carex pseudocyperus L.
Carex radiata (Wahlenb.) Small
Carex retrorsa Schwein.
Carex rosea Schkuhr ex Willd.
Carex stipata Muhl. ex Willd.
Carex tenera Dewey
Carex tribuloides Wahlenb.
Carex typhina Michx.
Carex vulpinoidea Michx.