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Clonal Structure of Invasive Cattail (Typhaceae) Stands in the Upper Midwest Region of the US

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Abstract There is mounting evidence that the clonal dynamics of foundational plant species, including exotic invaders such as hybrid *Typha* x *glauca*, have a profound effect on wetland function. Here, we report on the clonal structure of five intensively sampled *Typha* stands from the Upper Midwest region where invasions have been especially disruptive. Each of these stands consisted of a large proportion of F_1 hybrids between *T. latifolia* and *T. angustifolia*, although backcrosses to both parents were also observed, and provided a means of determining relative age of invasion. We found clonal richness, measured as the proportion of ramets representing distinct genets, to vary positively with age of invasion over a range from 0.20 to 0.45, whereas Simpson's Evenness was relatively consistent among sites due to a pattern of dominance by a few large clones accompanied by many smaller clones. Ramets were significantly clumped within genets over a range of approximately 20 m, although many clones included ramets separated by as much as 60 to 90 m, suggesting some degree of clone fragmentation over time. Related genets were significantly clumped over approximately 10 m, suggesting that seedling cohorts may frequently recruit in close proximity to one another.

Keywords Clonal diversity · Clonal structure · Hybridization · Invasive species · Spatial autocorrelation · *Typha*

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Introduction

The structure of wetland ecosystems throughout the world, whether freshwater or brackish in nature, is often dominated by graminoids and sedges, which are inherently clonal in their growth habits. For wetland types that are dominated by just one or a few primary producers, such as the *Spartina*- and *Juncus*-dominated salt marshes of the Gulf of Mexico and Atlantic Coasts of North America, it may be impossible to discern clonal boundaries, and thus clonal diversity and dispersion, through field-based observations. Yet, a growing body of work has shown that these sorts of clonal dynamics, as they relate to native foundational species (*sensu* Bruno and Bertness 2001), can play a critical role in determining both population viability (e.g., Travis et al. 2004), as well as community functional diversity (e.g., Proffitt et al. 2005).

Where introductions of non-native graminoids into wetlands have occurred, clonality has proven to be a critical facet in the evolution of invasiveness (Kolar and Lodge 2001). For example, European haplotypes of *Phragmites australis*, distinguished from native North American *Phragmites* on the basis of chloroplast DNA (Saltonstall

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2002), harbor the capacity to spread rapidly through tidal wetlands by vegetative, or clonal, means (Lathrop et al. 2003). In the case of invasive cattails in the genus *Typha*, which are becoming increasingly dominant among the freshwater wetlands of the Upper Midwestern US (Frieswyk et al. 2007), partially sterile hybrids between *T. latifolia* and *T. angustifolia* appear to rely primarily on clonal growth during their initial expansion phase within newly colonized sites (Travis et al. 2010). This expansion typically has the effect of supplanting native vegetation (Boers et al. 2007) and limiting the ecosystem services provided by the wetland to wildlife populations (e.g., Kaminski and Prince 1981).

In an earlier paper (Travis et al. 2010), we reported on the apparent role of hybridization in the invasive spread of *Typha* in northern North America, but left open the question of how invasive *Typha* stands are structured from a clonal standpoint. We characterized five wetland sites in the Upper Midwest region, ranging in character from a bog through several pond- and lake-margin sites, and determined that the *Typha* monocultures found growing at each site consisted predominantly of first-generation (i.e., F_1) hybrid cattails, or *T.* x *glauca*. In addition, we confirmed that hybrid cattails are capable of backcrossing with both of their parental species, as well as crossing among themselves to produce advanced-generation hybrids, although the combined occurrence of these individuals was highly variable among sites. Buggs (2007) suggested that introgression resulting from the backcrossing of fertile hybrids with their parental species will occur to an increasing degree as a hybrid population ages beyond the point of initial contact between the hybridizing species, and simulation modeling tends to bear this out (Currat et al. 2008). Following the same logic, fertile hybrid stands founded from imported seed in areas where no preexisting stands occurred would be expected to produce an increasing number of advanced-generation hybrids over time. Thus, in the absence of independent information on the absolute ages of our hybrid populations, we were able to gauge their relative ages on the basis of the prevalence of backcrossed and advanced-generation hybrids, and to report on the relationship between relative stand age and a variety of standard metrics of clonal diversity and dispersion.

Specifically, we posed the following questions regarding clonal structure within hybrid *Typha* stands. 1) How clonally rich are hybrid *Typha* stands in the Upper Midwest region? 2) Is clonal evenness within hybrid *Typha* stands typified by many small clones or by dominance of a few large clones? 3) Are stems (ramets) spatially clumped within clones (genets) or are they dispersed, as would be expected with clone fragmentation? 4) Are genetically related clones spatially clumped, as would be expected if sibling cohorts settle and germinate together, or are they

dispersed? 5) Are any of these metrics of clonal diversity and dispersion affected by relative stand age?

Methods

Typha Stand Characteristics

We provided a thorough description of the five sites sampled, as well as the molecular protocols used for *Typha* genotyping and species classification, in a previous paper (Travis et al. 2010). Briefly, we intensively sampled leaf tissue from 150 ramets from each of five mixed *Typha* stands growing in or near three US National Parks of the Upper Midwestern region, which we abbreviate as INDU (Indiana Dunes National Lakeshore), SACN (St. Croix National Scenic Riverway) St. Croix Falls, SACN Wolf Lake, VOYA (Voyageurs National Park) Cranberry Bay, and VOYA Sphunge Island. Historical evidence suggests that some form of *Typha* had been present at all of these sites for at least 35 years prior to sampling, although we had no way of determining at what point in time hybrids first began to invade. At Cowles Bog, a bog-fen complex located in INDU, we sampled from three separate 100-m transects chosen to represent different stages in the documented history of the expansion of the cattail population (early, mid, and late). At the four remaining sites, all of which were lake or pond sites, we collected samples at 2-m intervals from three roughly parallel 100-m transects that followed the contours of the shoreline.

All *Typha* ramets and genets were classified at each site on the basis of seven microsatellite loci (Tsyusko-Omeltchenko et al. 2003) as one of the following: *T. angustifolia*, *T. latifolia*, F_1 hybrid (*T.* x *glauca*), backcross to *T. angustifolia*, backcross to *T. latifolia*, or advanced-generation hybrid. Based on these classifications, we found the bulk of the *Typha* genets (56–90%) at each site to be F_1 hybrids (the one exception being SACN St. Croix Falls which was dominated equally by F_1 hybrids and *T. angustifolia*). In addition, we found the prevalence of backcrosses and advanced-generation hybrids to be quite variable among sites, suggesting that the hybrid invasion had been ongoing at some sites for considerably longer than others. For example, backcrossed individuals were extremely rare at the VOYA Cranberry Bay site, accounting for just one genet in 21 (4.8%), whereas backcrosses constituted >40% of the 64 genets at the SACN St. Croix Falls site (Travis et al. 2010; Table 1).

Hybrid Clonal Structure

We employed the methods of Arnaud-Haond et al. (2007a) to calculate the probability of mistakenly assigning two

Table 1 Summary population statistics for five Upper Midwestern wetland sites where *Typha* spp. were genotyped. *Typha* classes were defined as *T. angustifolia*, *T. latifolia*, F$_1$ hybrid *T.* x *glauca*, backcross to *T. angustifolia*, backcross to *T. latifolia*, and advanced-generation hybrid

Site	No. of *Typha* Classes	Total Ramets	Total Genets	No. of Backcrossed Genets	No. of Hybrid Ramets	No. of Hybrid Genets	Expected No. of Misassignments	Edge Effect
INDU	3	146	37	4 (10.8%)	142 (97.3%)	33 (89.2%)	2	–
Transect 1	–	–	–	–	–	–	–	0.15
Transect 2	–	–	–	–	–	–	–	0.90*
Transect 3	–	–	–	–	–	–	–	−0.96
SACN St. Croix Falls	5	123	64	28 (41.2%)	42 (34.2%)	21 (32.8%)	0	0.12*
SACN Wolf Lake	5	98	44	10 (22.7%)	67 (68.4%)	28 (63.6%)	0	0.33*
VOYA Cranberry Bay	3	150	21	1 (4.8%)	148 (98.7%)	19 (90.5%)	1	−0.14
VOYA Sphunge Island	5	150	32	6 (18.8%)	124 (82.7%)	18 (56.2%)	0	−0.03

*$p < 0.05$

ramets to any one genet due to a lack of discriminatory power on the part of our molecular markers, p_{sex} (i.e., the probability that two ramets with matching genotypes were actually produced by separate sexual reproductive events). Note that we did not consider the possibility of inbreeding in these calculations because hybrids are, by definition, outcrossed (see Arnaud-Haond et al. 2007b for further details). We report these results as the number of expected misassignments of ramets to genets at each site, where a p_{sex} value exceeding 0.05 was considered sufficiently high to produce a misassignment.

We compared hybrid clonal richness and evenness among sites in order to determine variation due to relative stand age. We calculated clonal richness within each stand as (G-1)/(N-1), where G is the number of multilocus genotypes, and N is the total number of ramets (Dorken and Eckert 2001). We measured evenness using the Simpson Evenness Index, V (Hurlbert 1971). In addition,

we calculated the edge effect, E_e, proposed by Arnaud-Haond et al. (2007b) as an estimate of the upward bias in genotypic richness introduced by the sampling scheme, particularly the undersampling of large clones lying along the edge of a transect.

We measured clonal dispersion using spatial autocorrelation statistics. Specifically, we plotted mean kinship coefficients, calculated according to Lynch and Ritland (1999), against distance classes at each site and tested whether these coefficients, as well as their overall slope relative to distance, were significantly different from zero using permutation tests (random assignment of locations to ramets). Probabilities were assigned to observed kinship coefficients and slopes on the basis of 10,000 permutations per site. Similarly, we assessed spatial autocorrelation among genets within sites via permutation testing by keeping all ramets in the analysis, but removed from the dataset all distances among replicates of the same genet.

Table 2 Summary of hybrid clonal diversity and dispersion statistics for five Upper Midwestern wetland sites where *Typha* x *glauca* were genotyped

Site	Richness (G-1/N-1)	Evenness	Clonal Subrange (m)	Spatial Autocorrelation (Ramets)	Spatial Autocorrelation (Genets)
INDU	0.25	0.83	88	–	–
Transect 1	–	–	–	−0.02***	−0.01*
Transect 2	–	–	–	−0.04****	−0.03****
Transect 3	–	–	–	−0.02**	−0.01
SACN St Croix Falls	0.52	0.90	58	−0.04****	−0.04****
SACN Wolf Lake	0.44	0.80	58	−0.03****	−0.02****
VOYA Cranberry Bay	0.13	0.83	70	−0.08****	−0.06****
VOYA Sphunge Island	0.21	0.87	57	−0.10****	−0.06****

Clonal subrange represents the maximum separation among ramets within a genet; spatial autocorrelation represents the slope of the regression of kinship coefficient on natural log of distance.

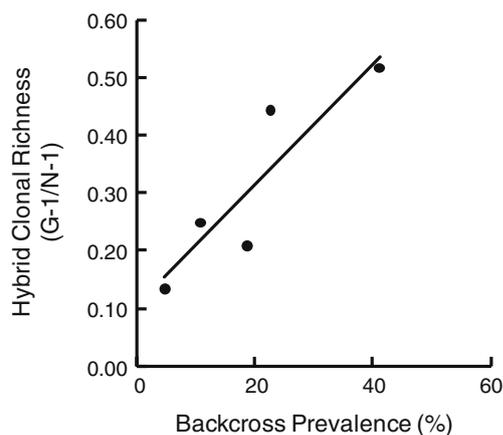*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ****$p < 0.0001$

Fig. 1 The relationship between hybrid clonal richness and the prevalence of backcrossed and advanced-generation hybrid individuals at five Upper Midwestern wetland sites where *Typha* spp. were genotyped

All clonal diversity and spatial autocorrelation statistics were calculated using GenClone 2.0 (Arnaud-Haond and Belkhir 2007).

In order to determine whether hybrid clonal diversity or dispersion was impacted by relative stand age, we ran a series of correlation tests. Specifically, we tested for a significant correlation between the proportion of genets classified as backcrossed and advanced-generation hybrids, as a surrogate of absolute stand age, and each of the

following metrics: hybrid clonal richness, evenness, clonal subrange (defined simply as the estimated diameter of the largest hybrid genet within a site), and the slope of kinship against the log of distance when all ramets were included or when only genets were included. All correlation tests were run using the STATS package in R, version 2.5.1 (R Development Core Team 2009).

Results

The discriminatory power of our microsatellite markers to assign hybrid ramets to genets was generally very high, such that we expected few or no misassignments with a probability of >5% at any of our sites (Table 1). Specifically, we expected zero misassignments at three of our five sites (including both SACN sites and VOYA Sphunge Island), whereas we expected no more than one misassignment among the 148 hybrid ramets at VOYA Cranberry Bay, and no more than 2 misassignments among the 142 hybrid ramets at INDU. Thus, the margin of error in our estimates of hybrid clonal structure should have been no more than approximately 5% owing to our microsatellites. A potentially greater concern was the edge effect we observed at several sites, which suggested that we may have overestimated hybrid clonal richness for some transects because they happened to be located along the outer
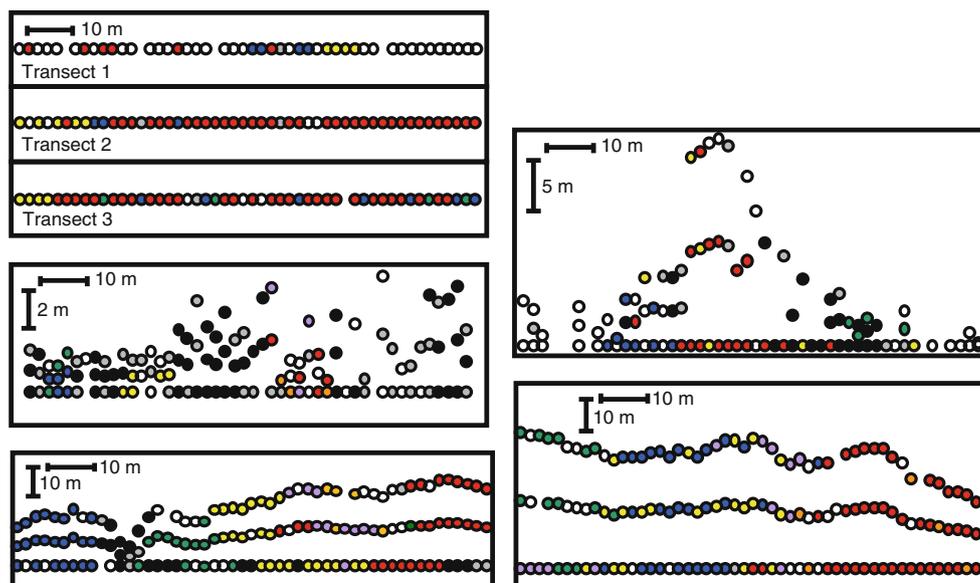

Fig. 2 Clonal structure at five Upper Midwestern wetland sites where *Typha* spp. were genotyped. The top, left panel represents clonal structure by transect at INDU (where transect 1 represents the first area of Cowles Bog to be colonized by *Typha* and transect 3 represents the last); the middle, left panel represents SACN St. Croix Falls and the top, right panel represents SACN Wolf Lake; the bottom, left panel represents VOYA Sphunge Island and the bottom, right panel represents VOYA Cranberry Bay. The position of each ramet sampled

from this *Typha* stand is indicated by an oval. The most common hybrid genets at each site are shown in color; all remaining hybrid genets are represented by unfilled ovals. Ramets representing backcrosses and advanced-generation hybrids are shaded gray, whereas those representing pure *T. angustifolia* or *T. latifolia* are blacked out. Note that the bottom-most transect in the middle and bottom panels, which represent the lakeward transect in each case, has been straightened for ease of presentation

edges of otherwise rather large clones. We detected an edge effect at both of our SACN sites, as well as for one of three transects at INDU (Table 1). Notably, because our SACN sites were far higher in hybrid clonal richness than all other sites (nearly twice as rich as all remaining sites; see below), any overestimates due to an edge effect would have been unlikely to change the actual rankings among the sites.

We found hybrid clonal diversity, particularly as it was reflected in hybrid clonal richness, to be highly variable from site to site, which was explained, in part, by stand structure (Table 2, Figs. 1, 2, 3, 4). Richness varied by region, with the SACN sites exhibiting much higher richness than all other sites (SACN: clonal richness >0.44; all other sites: clonal richness <0.25), although the existence of a significant edge effect at SACN may have resulted in an upward bias to these estimates (Table 1). Nevertheless, the SACN sites were 79–285% higher in clonal richness than all other sites. The VOYA sites were consistently low in clonal richness (<0.21), with the INDU site only slightly higher at 0.25. Clonal richness was significantly correlated with the prevalence of backcrossed and advanced-generation hybrids at a site, a measure of the relative age of the hybrid stand, accounting for >80% of the variation in hybrid clonal richness ($r=0.8977$; $t=3.5$, $df=3$, $p=0.0387$; Fig. 1).

Our Simpson evenness estimates were much less variable than our richness estimates, ranging from 0.80 to 0.90. This was the result of a consistent pattern of dominance by a small number of large hybrid clones at each site, accompanied by many smaller hybrid clones (Fig. 2).

We observed spatial autocorrelation at all sites, owing to the clumped dispersion of ramets within hybrid genets (Table 2), although the distance classes within which mean kinship coefficients were significantly greater than zero varied from site to site (Figs. 3 and 4), and all sites exhibited very large clonal subranges (Table 2). Our observation of subranges varying from 57 to 88 m (mean ± SD=66.20±13.31 m), coupled with significant mean kinship coefficients generally occurring only at distances of less than 20 m (with the exception of VOYA Cranberry Bay where significant autocorrelation occurred at up to 40 m; Figs. 3 and 4), indicated that hybrid clones are not cohesive over the entire extent of their component ramets.

We also observed spatial autocorrelation due to the clumped dispersion of genetically related hybrid genets within sites (Table 2), although mean kinship coefficients were generally significant over shorter distances of less than 10 m (again, with the exception of VOYA Cranberry Bay where significant values were observed at up to 22 m; Figs. 3 and 4). Patterns of spatial autocorrelation were strikingly similar between ramets and genets (Figs. 3 and 4), with the exception of transect 3 at INDU, suggesting

that related cohorts of hybrid seedlings recruit very near one another.

Discussion

Our characterization of F_1 hybrid T. x glauca clonal richness within the mixed Typha stands of northern North America revealed somewhat reduced mean values compared to an earlier study of pure T. angustifolia and T. latifolia stands in eastern Europe (Tsyusko et al. 2005). Whereas we found
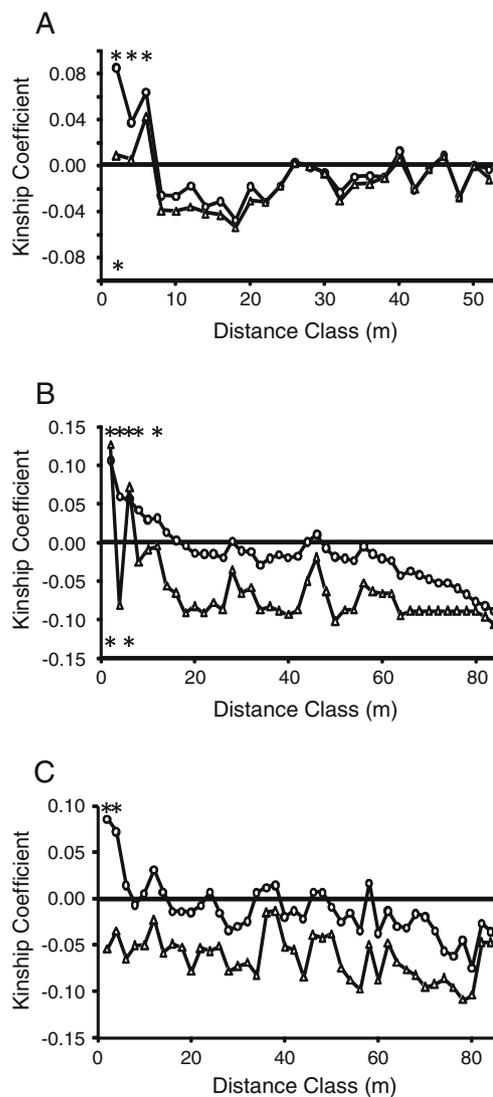

Fig. 3 Spatial autocorrelation of F_1 hybrid Typha by transect at INDU Cowles Bog, as indicated by the relationship between mean kinship coefficient and distance class (A: Transect 1; B: Transect 2; C: Transect 3). Two lines are plotted on each graph, one representing spatial autocorrelation owing to ramets within genets (circles), and one owing to genets within sites (triangles). Asterisks running along the top of each graph indicate significant kinship coefficients for the ramets plot, whereas those running along the bottom of each graph correspond to the genets plot

Fig. 4 Spatial autocorrelation of F$_1$ hybrid *Typha* by site at SACN and VOYA, as indicated by the relationship between mean kinship coefficient and distance class (A: SACN St. Croix Falls; B: SACN Wolf Lake; C: VOYA Cranberry Bay; D: VOYA Sphunge Island). Two lines are plotted on each graph, one representing spatial auto-correlation owing to ramets within genets (*circles*), and one owing to genets within sites (*triangles*). *Asterisks* running along the top of each graph indicate significant kinship coefficients for the ramets plot, whereas those running along the bottom of each graph corre-spond to the genets plot
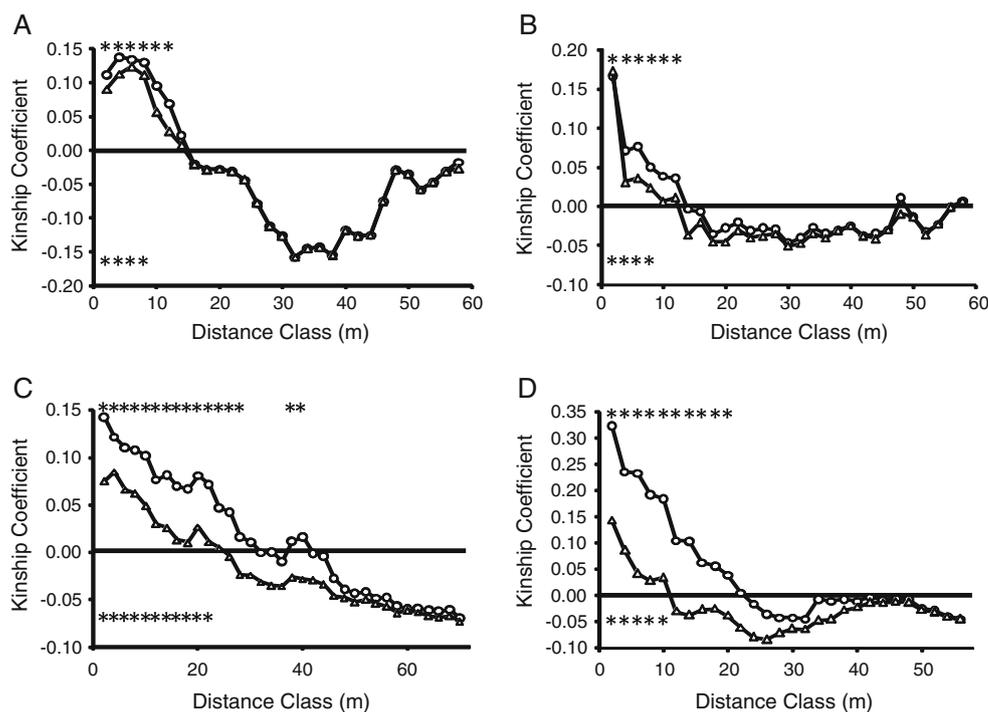
clonal richness to range from 0.13 to 0.52 at five sites, with an overall mean of 0.31, Tsyusko et al. (2005) recorded values of 0.20–0.69 at 13 *T. angustifolia* sites and 0.47–0.86 at 11 *T. latifolia* sites, with means of 0.40 and 0.61, respectively. Several factors may account for these differences. First, although our probability statistics indicated a low probability of misassigning ramets to genets within each of our sampled stands, we used fewer microsatellite loci to identify clones than did Tsyusko et al. (2005)—their 11 and nine loci for *T. angustifolia* and *T. latifolia*, respectively, to our seven loci. This could have led us to slightly underestimate clonal richness (Arnaud-Haond et al. 2007b), although a significant edge effect at our SACN sites would actually have put these richness estimates slightly too high. Second, we were evaluating F$_1$ hybrid clones within predominantly hybrid stands, as opposed to the pure stands observed by Tsyusko et al. (2005), and hybrid clones may either spread more rapidly by vegetative means than pure clones (e.g., Woo and Zedler 2002), or may face greater challenges to sexual reproduction than pure clones (e.g., Smith 1967, 1987, 2000), or both. Third, the fact that historical records for four out of our five sites suggest that cattails have invaded only within the past 100 years makes our sites likely to be much younger than Tsyusko et al.'s (2005) sites, and therefore to have had less time to recruit new genets.

Although several previous studies have indicated low seedling recruitment in established *Typha* stands (McNaughton 1966; Grace 1985), our observation of increasing clonal richness with relative stand age suggests that recruitment is an ongoing process. Not only did we

observe a strong correlation between hybrid clonal richness and relative stand age when separate stands were evaluated, but even within stands, namely at our INDU site, where we were able to calculate separate clonal richness statistics for three separate portions of the site varying by age, we found a much higher level of clonal richness, 0.50, within the oldest portion of the stand dated at >65 yrs, than in two much younger portions of the stand, each <30 yrs of age and with clonal richness values measured at approximately 0.10. It remains uncertain when hybrid *Typha* x *glauca* first entered this site, but the rapid expansion of cattail stands since the early 1970's (Wilcox et al. 1985), suggests that hybrids had been present within Cowles Bog for at least 30 years prior to our study. Our high evenness estimates, which averaged 0.85 among sites likely as a reflection of the prevalence of many small, i.e., young, clones that had recently recruited into our sites, also suggested that seedling recruitment is ongoing in the mixed *Typha* stands of the Upper Midwest region. Whether clonal richness increases indefinitely in *Typha* stands, or whether intraspecific competition ultimately becomes so intense as to slow or reverse this trend, as is the case in another clonal wetland graminoid, *Spartina alterniflora* (Travis et al. 2004; Travis and Hester 2005), remains to be seen.

Our results further indicate that hybrid *Typha* clones are cohesive over relatively short distance classes, but become intermingled over larger distances. We observed clones spanning overall distances of up to 88 m, although mean kinship coefficients were generally significantly greater than zero only at distances of <20 m. This pattern could either represent a characteristic pattern of guerilla growth

(sensu Harper 1981) in *Typha*, or clone fragmentation. Both the results of earlier studies (e.g., Dickerman and Wetzel 1985) showing a progressive loss of rhizomatous connections within *Typha* clones, and the cohesiveness that we observed at short distances, would seem to argue for the latter. Fragmentation is a common phenomenon among clonal species (see Pitelka and Ashmun 1985; van Groenendael and de Kroon 1990), and may serve as a form of bet-hedging assuring that severe disturbances, such as systemic infections, do not summarily wipe out entire clones (McCrea and Abrahamson 1985). Fragmentation may also serve as a strategy by which heightened opportunities for outcrossing are afforded the individual ramets within a clone (e.g., Travis and Hester 2005), although this may be less important in *Typha* spp. than in some other clonal plant taxa since *Typha* spp. have been shown to produce viable offspring through self-fertilization (e.g., Grace and Harrison 1986).

Somewhat surprisingly given the many small, buoyant seeds produced by *Typha* spp., as well as the highly developed dispersal capabilities documented for species such as *T. angustifolia* (McNaughton 1966), the spatial autocorrelation that we observed at the ramet level was closely mirrored by that observed at the genet level, suggesting that seedlings may often germinate as cohorts of half or full sibs very near one another. High levels of relatedness in the nearest distance classes are considered an indication of small neighborhood size, i.e., low dispersal (Epperson 2005). This is just one more indication that seedling recruitment, in addition to vegetative recruitment, may play a vital role in the invasive spread of hybrid cattail.

Overall, our results suggest that hybrid *T.* x *glauca* stands grow increasingly clonally diverse over time, with seedling recruitment perhaps coming to dominate over vegetative recruitment as stands age. Initially, however, it appears to be rapid vegetative spread leading to the dominance of a few, large clones that enables *T.* x *glauca* to colonize novel sites and supplant native vegetation. Whether the backcrossed seedlings and advanced-generation hybrids that are also recruited into aging hybrid stands will curb the invasive tendencies of hybrid *Typha* remains to be seen, although presumably the superior competitive abilities of F_1 hybrids, as we documented in an earlier paper (Travis et al. 2010), will prevent other hybrid classes from ultimately gaining sway. Thus, the invasive tendencies of these hybrid stands are likely to persist, and their appropriate management may continue to call for aggressive programs of removal and remediation.

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