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REGULAR PAPER

Multiple and mass introductions from limited origins: genetic diversity and structure of *Solidago altissima* in the native and invaded range

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Abstract Understanding the origins and diversity of invasive species can reveal introduction and invasion pathways, and inform an effective management of invasive species. Tall goldenrod, *Solidago altissima*, is a herbaceous perennial plant native to North America and it has become a widespread invasive weed in East Asian countries. We used microsatellite and chloroplast DNA markers to obtain information on neutral processes and on genetic diversity in native and invaded populations of *S. altissima* and to infer how it invaded and spread in Japan. We found that introduced ($n = 12$) and native ($n = 20$) populations had similar levels of genetic diversity at nuclear SSR loci. Genetic structure analysis indicated that at least two independent colonization events gave rise to current *S. altissima* populations in Japan. The majority (68 %) of the Japanese *S. altissima* were genetically similar and likely shared a common origin from a single or a small number of populations from the southern USA populations, while the populations in Hokkaido were suggested to arise from a different source. Our results suggest that multiple and mass introductions have contributed to the persistence and rapid adaptation of *S. altissima* promoting its widespread establishment throughout Japan.

Keywords Genetic diversity · Invasion history · Microsatellite · Phylogeography · Population genetics · *Solidago altissima*

Introduction

Determining which factors enable exotic plants to proliferate in new environments is a fundamental challenge worldwide (Mitchell et al. 2006; Thuiller et al. 2005). The genetic variation in founder populations is a crucial factor in determining whether an invasive species will successfully adapt to their new locations (Lee 2002). Genetic variation can be introduced into a new geographic area either through multiple introductions of genotypes (Bossdorf et al. 2005; Ellstrand and Schierenbeck 2000; Kelager et al. 2013), or through introduction of a few pre-adapted genotypes with a broad range of physiological tolerance and phenotypic plasticity (Dlugosch and Parker 2008; Lee 2002; Yu et al. 2014).

Phylogeographical studies of invasive species using neutral genetic markers can retrace the possible routes of introduction, and determine the number of introductions, genetic variability of invasive and source populations, and the degree of hybridization among source populations of invasive species (Estoup and Guillemaud 2010; Fitzpatrick et al. 2012; Handley et al. 2011). This information will help determine the relative importance of stochastic and deterministic forces in determining the success of an invasive species (Keller and Taylor 2008; Lavergne and Molofsky 2007; Lee 2002). The level of genetic diversity of exotic plants plays a key role in their ability to invade new areas

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(Dlugosch and Parker 2008; Keller and Taylor 2008; Lambrinos 2004; Vallejo-Marin and Lye 2013). Knowing the origins of invasive plants and how they spread is critical in designing strategies to control the colonization and spread of invasive plants (Estoup and Guillemaud 2010; Roderick and Navajas 2003).

Solidago altissima L. (Asteraceae), is a perennial herbaceous plant belonging to the *Solidago* subsect. Triplinervae. It is a dominant plant in the early stages of secondary succession in prairies, woodland edges, and old fields throughout North America in a broad geographic range (Semple and Cook 2006). It is among the most invasive introduced plants in the East Asian countries of Japan, China, Korea, and Taiwan (Huang and Guo 2004; Kil et al. 2004; Li 1978; Shimizu 2003). In its native range, *S. altissima* occurs as diploid, tetraploid, and hexaploid (2n = 18, 36, 54; Halverson et al. 2008). However, in Japan only hexaploids have been found (Sakata et al. 2013a). Semple et al. (2015) recognized three varieties of *S. altissima*. These varieties are associated with cytotypic variation, with *S. altissima* var. *gilvocanescens* reported as diploid and tetraploid, and *S. altissima* var. *altissima* and *S. altissima* var. *pluricephala* primarily as hexaploid with a few tetraploids reported at the western edge of their distribution and across the southeastern USA. *S. altissima* var. *altissima* and var. *pluricephala* occur from the eastern edge of the Great Plains to the Atlantic coast, while var. *altissima* are found predominately from 35° to 50° N latitude, *var. pluricephala* primarily south of 35° N latitude. *Solidago altissima* var. *gilvocanescens* is found in the Great Plains (Semple et al. 2015).

Solidago altissima was first introduced to Japan as an ornamental plant in 1897, but it was not until the 1980s that it became naturalized throughout the country (Fukuda 1982), and it is still rare on the island of Hokkaido. *S. altissima* reproduces through obligate outcrossing via pollination by a wide range of insects (Melville and Morton 1982), and it produces large numbers of wind-dispersed seeds. Once established, it spreads almost exclusively through vegetative reproduction (Meyer and Schmid 1999). Two closely related species, *S. canadensis* L. and *S. gigantea* Aiton, have also become invasive throughout Europe (Weber 1997; Weber and Jakobs 2005). *Solidago altissima* has been studied for its phenotypic traits such as growth, allelopathic, and defensive traits in its invaded range in Japan (Ito et al. 1998; Sakata et al. 2014). Despite *S. altissima*'s status as a globally important invasive species, little is known about its invasion history, and how its genetic diversity has changed through the invasion process. Information on invasion history would allow comparisons of phenotypic traits between native ancestors of the invasive populations and allow inferences to be made about the evolution of plant traits in the invasive populations (Keller and Taylor 2008).

In order to obtain information on genetic diversity in populations of *S. altissima* in both its native and invaded range, and to identify the source populations of lineages invasive in Japan to infer how it was introduced and spread in Japan, we studied the genetic diversity and structure of multiple *S. altissima* populations in their native and invaded ranges. We used both chloroplast DNA (cpDNA) markers and recently-developed nuclear simple sequence repeat (nSSR) markers, which differ in their mode of inheritance (maternal only vs. biparental) and mutation rate (higher at nuclear markers), and therefore give complementary insights into the invasion history and population dynamics (i.e., changes in size and age of populations) of the species.

Materials and methods

Population sampling

Samples were collected from 20 populations of *S. altissima* from its native range in North America, and 11 populations from its invaded range in Japan, and one population in Korea during June to August in 2011–2013 (Table S1). In each population, samples of 10–24 (22.3 on average) leaves of *S. altissima* were collected from plants that were at least 5 m apart. Because *S. altissima* in Japan are all hexaploid, we collected throughout the hexaploid range in the USA. Because of the possibility that hexaploid plants were derived from the hybridization between diploids and tetraploids plants after their invasion of Japan, diploid (CA: California, USA) and tetraploid plants (EF: Oklahoma, USA) were also collected to examine the genetic relationship among plants of different ploidy levels (Table S1). We determined the ploidy level of plants in the Midwestern USA since other ploidy level individuals occur sympatrically. We collected and cultivated rhizomes of 5 to 10 individuals that we had used for leaf samples in the Midwest populations (HB, FB, CL, PE, CG, EF, I20, and HIL). Fresh leaf samples were collected from these cultivars to determine the ploidy levels by using chromosome counts, flow cytometry as described in Sakata et al. (2013a). In addition, allele numbers with nSSR genotyping were also used to determine the ploidy level of individuals without rhizome samples and plants in Korean populations. We also collected two individuals of *Solidago virgaurea* (subsection Solidago; from northern Honshu, Japan), 24 individuals of *Solidago gigantea* (subsection Triplinerviae; from Hokkaido, Japan), and six individuals of *Solidago canadensis* (subsection Triplinervae; from Jena, Germany) as outgroups. We collected larger number of samples of *S. gigantea* compared to other outgroup species to determine whether they have hybridized with *S. altissima* since they co-occur with *S. altissima* in the Hokkaido region in Japan.

DNA extraction and nSSR genotyping

Total genomic DNA was extracted from 1.0 cm^2 of plant tissue using a modified CTAB (cetyltrimethyl ammonium bromide) method (Milligan 1992). Fifteen nSSR markers out of 16 markers developed for *S. altissima* except for Salt 9 (Sakata et al. 2013b) were scored in all samples ($N = 713$; Table S1). The nSSR loci were polymerase chain reaction (PCR) amplified following Sakata et al. (2013b) and loaded on an ABI Prism 3130 Genetic Analyzer (Applied Biosystems Foster City, California, USA), and scored using GENEMAPPER (Applied Biosystems). Of the 15 nSSR primer pairs, two loci (Salt 6 and 7) did not amplify well on the diploid population (CA) and *S. gigantea*. Therefore, the two loci were excluded from the analysis of outgroups and different ploidy level populations.

Chloroplast DNA sequencing

First, we screened cpDNA variation in intergenic spacers with 20 sets of PCR primers from which six: psbH-psbB, rps12-rpl20 (Shaw et al. 2005), psbJ-petA, rpl-trnL, rps16-trnK, and trnQ-rps16 (Shaw et al. 2007) were selected due to amplification and variable sites and were sequenced for 142 samples (i.e., four samples per population and two samples per outgroup species). PCRs were performed on 20 μL samples containing 50 ng of template DNA, 2 μL of 10 × PCR buffer, 1.6 μL of 2.5 mM dNTP, 0.1 μL of 50 μM each primer and 0.5 unit of TaKaRa Ex Taq™ (TaKaRa, Shiga, Japan). The PCR cycle for all six fragments was as follows: template denaturation at 94 °C for 3 min, followed by 35 cycles of denaturation at 95 °C for 1 min, annealing at 50 °C for 1.5 min and extension at 72 °C for 1.5 min; followed by a final extension of 72 °C for 7 min. PCR products were sequenced using reverse primers with ABI Prism BIGDYE Terminator Cycle Sequencing Ready Reaction kit v. 3.1 (Applied Biosystems), and electrophoresed on an ABI Prism 3130 Genetic Analyzer (Applied Biosystems).

Genetic diversity, differentiation, and demographic analysis

For nSSR analysis, it was not possible to determine genotypes and allele frequencies from peak heights due to the high ploidy level. Therefore, only genetic diversity statistics that are not affected by genotype ambiguity were calculated. The number of maximum alleles per locus (*A'*), Shannon diversity index (*Shannon*), and genetic differentiation statistics G'_{ST} (Hedrick 2005) were calculated at each nSSR locus using the software GenoDive 2.0b19 (Meirmans and Van Tienderen 2004) and POLYSAT v. 1.3-2 (Clark and Jasieniuk 2011) in R v. 3.0.1 (R Development Core Team 2013). To measure the level of within-population genetic diversity, we calculated the following statistics: number of alleles per locus (N_a), gametic heterozygosity (H_o) (Moody et al. 1993), and Shannon diversity index (*Shannon*). Genetic differentiation statistics: G_{ST} (Nei 1973), G'_{ST} (Hedrick 2005), and D_{EST} (Jost 2008) were calculated per population per loci using GenoDive 2.0b19. For cpDNA sequence, the number of haplotypes (H), haplotype richness (H_R) and G_{ST} were calculated using CONTRIB v. 1.02 (Petit et al. 1998).

To assess whether populations in the native and invaded regions experienced past population expansions, mismatch distribution analysis (Rogers and Harpending 1992) was performed using Arlequin v. 3.11 (Excoffier et al. 2005). This analysis detects past population expansions and declines by measuring the signature of molecular changes (i.e. the frequency distribution of pairwise nucleotide or restriction site differences) that follow population fluctuations. The sum of square deviations between the observed and expected mismatch distributions and the raggedness index of the observed distribution were used as statistics to validate fit of the models (Harpending 1994; Rogers and Harpending 1992).

We calculated pairwise genetic differences between individuals averaged over loci with POLYSAT (Clark and Jasieniuk 2011) using two distance measures appropriate for polyploids: a band-sharing dissimilarity index (one minus the similarity index in Eq. 1 of Lynch (1990)) and a measure taking into account mutational distance between microsatellite alleles (Bruvo et al. 2004). Because the hexaploid *S. altissima* is considered an autopolyploid (J. Semple personal communication), we calculated both Bruvo and Lynch distance matrices. We assessed the hierarchical partitioning of genetic variance within and among populations and between the two regions (native and invaded regions) by performing analysis of molecular variance (AMOVA) (Excoffier et al. 1992) on the basis of the two distance matrices using GENALEX 6.4 (Peakall and Smouse 2006). The same distance matrices were used to estimate pairwise Φpt, an analogue of F_{st} (Weir and Cockerham 1984), between populations. Pairwise Φpt were estimated using GENALEX 6.4 (Peakall and Smouse 2006). We also estimated pairwise Φpt using the cpDNA sequence data. We tested for correlations between geographical and genetic distance $[\Phi_{pt}/(1 - \Phi_{pt})]$ following a classical isolation by a distance method in each region using Mantel tests performed with GENALEX 6.4 (Peakall and Smouse 2006).

Population genetic structure

Both flow cytometry analysis and nSSR genotyping indicated that the outgroup population CA (California, N°39.43, W°120.24) consists of diploid plants and

population EF (Oklahoma) consists of tetraploid plants, and that all other populations were hexaploid. To clarify the genetic relationship with other taxa, we conducted a PCoA analysis based on Bruvo genetic distance matrices among outgroups (*S. gigantea* 4X and *S. canadensis* 2X) and the different ploidy populations. In the PCoA analysis, we included five hexaploid populations (SN, KRF, CG, I20, PAa), including the same geographic areas as outgroups. Because our focus was on the invasion history of *S. altissima* in Japan, we only used the hexaploid populations for the rest of the population analyses with nSSR.

Population structure based on the nSSR markers was examined by both distance and model-based methods. We increased the probability of obtaining correct phylogenetic tree topology (Takezaki and Nei 1996) using pairwise genetic distances of Nei's D_A (Nei et al. 1983), calculated among the 32 populations to construct a neighbor-joining tree (Saitou and Nei 1987) using package APE (Paradis et al. 2004) in R. The application of a simple branching tree model to data, however, can be problematic when systematic errors, such as inappropriate assumptions in the evolutionary model and sampling errors resulting from small numbers of observed loci, exists (Huson and Bryant 2006). Thus, to explore and graphically present these ambiguities, we also constructed a split network (Bryant and Moulton 2004) on the basis of a distance matrix of Nei's D_A (Nei et al. 1983) using SplitsTree4 v. 4.10 (Huson and Bryant 2006). We also used the recently developed discriminant analysis of principal components (DAPC), which is a multivariate analysis that describes clusters of genetically related individuals (Jombart et al. 2010) using adegenet v. 1.3-4 (Jombart and Ahmed 2011) in R using presence–absence (binary) genetic data. To find an optimal number of clusters in our data, we used k-means clustering of the principal components and calculated the statistical fit of the data for a given k, using the function find.clusters in adegenet. The optimal number of clusters in the data was determined using the diffNgroup option, which identifies sharp changes in the fit of models (measured using Bayesian Information Criterion) with different numbers of clusters. We used 10^6 iterations of the model to search for convergence and obtained the likelihood associated with each value of k between 1 and 20. Finally, PCoA analysis using a pairwise Φpt matrix obtained from two distance matrices (Bruvo and Lynch) was conducted with GENALEX 6.4 (Peakall and Smouse 2006). This method produces a few axes containing most of the genetic variation in the data set and separates the populations.

Genetic structure in native and invaded populations was investigated using two model-based Bayesian algorithms implemented in STRUCTURE 2.3 and TESS 2.3.1 (Durand et al. 2009; Pritchard et al. 2000). The STRUCTURE analysis aims to cluster individuals in K genetic groups, using the multilocus genotypes of individuals. We performed ten independent runs with different proposals for K, testing each possible K from 2 to 10 using 100,000 iterations after a burn-in period of 50,000 iterations. All runs were conducted with the admixture model, assuming correlated allele frequencies (Falush et al. 2003; Pritchard et al. 2000) with prior information on the sampling location (Hubisz et al. 2009). To ensure convergence of the Markov Chain Monte Carlo estimates, the consistency of results was checked for the ten replicates performed for each value of K. The most probable number of clusters (K) was then determined using the change in log likelihood of the data between successive values of K, as described in Evanno et al. (2005). Parameters in the method of Evanno et al. (2005) were calculated using the program Structure Harvester v. 6.0 (Earl and vonHoldt 2012). Population genetic structure was also estimated using a spatial hierarchical Bayesian algorithm implemented in TESS 2.3.1, which includes spatial prior distributions on the individual admixture proportions (Durand et al. 2009). We estimated the population structure within the samples using this algorithm by incorporating individual geographic covariates in the prior distributions on the admixture memberships. Ten individual simulations were run for each Kmax (Kmax 2–10), with 10,000 burn-in steps followed by 20,000 Markov Chain Monte Carlo steps.

To identify genetic groups, for cpDNA sequence data, a spatial analysis of molecular variance (SAMOVA) was performed using SAMOVA 1.0 (Dupanloup et al. 2002). Based on a simulated annealing procedure, SAMOVA algorithm iteratively seeks the composition of a user-defined number of groups (K) of geographically adjacent populations that maximizes the proportion of total genetic variance (F_{CT}) as a result of the differences between groups of populations. We set the number of initial condition to 100 with $K = 2$–10.

Phylogenetic relationships

The chloroplast sequence data were edited and aligned using BIOEDIT v. 7.0.8.0 (Hall 1999) and GENEIOUS PRO, version 5.4.6 (Drummond et al. 2011). Variable sites are listed in Table S2. Phylogenetic relationships between cpDNA haplotypes were assessed using a median-joining network with *Solidago virgaurea*, *Solidago gigantea*, and *Solidago canadensis* as outgroups using NETWORK v. 4.6.0.0 (Bandelt et al. 1999). In addition, phylogenetic relationships between cpDNA haplotypes were assessed with MEGA version 3.1 (Kumar et al. 2004), with conducting 1,000 bootstrap replicates to test the robustness of clades in maximum-parsimony trees. We ran analyses excluding and including indels and mononucleotide repeat length variations and found that though the resolution did not change

the inclusion of indels resulted in complicated haplotype networks and the phylogenetic trees that were difficult to interpret. We will report data from analyses excluding indels.

Results

Genetic diversity and differentiation

The number of alleles observed in the native and invaded range per locus varied 9 to 29 (18.3 on average) and 7 to 31 (15 on average), respectively (Table 1). Out of the 306 different alleles found across the whole data set, 69 were unique to the native and 19 to the invaded range (Table 2). In the population genetic analysis, we used only the values averaged for all loci (Table S1). The invaded populations had lower mean number of alleles per locus within populations and a lower Shannon diversity index, whereas the observed heterozygosity was higher than the native populations. The genetic differentiation was higher in the invaded range ($G_{ST} = 0.03$) than the native range ($G_{ST} = 0.011$, which was also true with alternative estimators of genetic differentiation G'_{ST} and D_{EST} (Table 2).

The concatenated cpDNA sequence had a length of 4417 bp with 21 substitutions (Table S2). Among the 32 haplotypes found in the total data set, seven haplotypes were found in outgroups (H6 and H10: *S. virgaurea*, H7: *S. gigantea*, H19 and H20: *S. canadensis*, H31: diploid, H12: tetraploid). There were five haplotypes shared with both native and introduced ranges (H9, H24, H25, H26, and H30), two haplotypes unique to the introduced range (H5 and H23), and 20 haplotypes unique to the native range (Table 2; Fig. 1). Overall genetic differentiation was low in both ranges: $G_{ST} = 0.24$ and 0.27 in the native and invaded range, respectively (Table 2). Haplotype richness was smaller in the invaded range (Table 2: 3.15 and 2.54 in native and invaded range, respectively).

Analysis of mismatch distributions, which shows a large increase between 0_0 and 0_1 (Table 2) revealed support for recent expansion in both ranges. Non-significant sum of square deviations (SSD) and the raggedness index (HRI) of the observed distribution indices were obtained for both ranges ($P > 0.05$), while both indices and observed value of time since divergence (tau) in the invaded region showed lower values than those in the native region (Table 2).

The AMOVA analysis showed little genetic differentiation among individuals between the two ranges (4 and 5 %), while there was a large genetic differentiation among individuals within populations (85 and 82 %). The genetic divergence between the invasive and native groups was significant (Table 3).

We found a weak but significant association between genetic and geographic distance with the cpDNA markers in the native range (Fig. S1a: $R^2 = 0.02$, $P < 0.001$), but a non-significant association in the invaded range (Fig. S1b: $R^2 = 0.002$, $P = 0.42$). With the two genetic distance matrices obtained with the nSSR analysis, significant association between genetic and geographic distance was found for both ranges (Fig. S1c–f; Native: $R^2 = 0.15$ for Bruvo,

Table 1 Characteristics of the 15 microsatellite loci examined in this study

Locus	Native ($N = 443$)			Invaded ($N = 270$)		
	A'	*Shannon*	G'_{ST}	A'	*Shannon*	G'_{ST}
Salt1	26	2.66	0.146	21	2.31	0.357
Salt2	19	1.86	0.057	10	1.29	0.085
Salt3	28	2.83	0.128	31	2.49	0.307
Salt4	16	1.83	0.063	12	1.57	0.132
Salt5	29	2.46	0.076	21	2.09	0.164
Salt6	24	2.57	0.074	14	1.98	0.265
Salt7	13	1.29	0.018	13	1.28	0.191
Salt8	16	2.28	0.064	17	2.09	0.084
Salt13	13	2.01	0.025	7	1.78	0.068
Salt14	9	1.61	0.029	9	1.11	0.121
Salt16	15	1.49	0.021	17	1.08	0.083
Salt17	18	1.78	0.05	18	1.58	0.086
Salt18	18	1.95	0.079	12	1.59	0.066
Salt19	12	1.73	0.095	8	1.44	0.053
Salt21	19	2.01	0.048	15	1.72	0.123
Overall	275	2.88	0.052	225	2.67	0.126

A', number of maximum alleles per locus; *Shannon*, Shannon diversity (mean across population); G'_{ST}, standardized genetic differentiation index (mean across population) (Hedrick 2005)

Table 2 Genetic diversity of cpDNA (upper half) and nSSR (lower half) analysis, and the results of the mismatch distribution analyses of the native and invaded populations of *S. altissima*

	Native	Invaded
cpDNA		
H	25 (2X: H31, 4X: H12)	7
H_R	3.15	2.54
G_{ST}	0.238	0.272
SSD	0.087 (0.45)	0.064 (0.26)
HRI	0.401 (0.62)	0.319 (0.34)
tau	1.71	0.94
θ_0	4.2×10^{-3}	2.9×10^{-4}
θ_1	5.8×10^{4}	7.0×10^{4}
nSSR		
N_a	9.68	7.92
A	275	225
Ho	0.863	0.873
P_R	69	19
Shannon	2.88	2.67
G_{ST}	0.011	0.03
G'_{ST}	0.052	0.13
D_{EST}	0.041	0.099

N_a, H_o, Shannon, G_{ST}, G'_{ST}, and D_{EST} are mean values across loci and population. Values in parentheses in *H* represent haplotypes of diploid (2X) and tetraploid (4X) samples. Values in parentheses in SSD and HRI represent *P* values

H number of haplotype, H_R, haplotypic richness, G_{ST} genetic differentiation index (Nei 1973), *SSD* the sum of square deviations between the observed and expected distributions (Rogers and Harpending 1992), *HRI* the raggedness index of the observed distribution (Harpending 1994), *tau* the time parameter to the population expansion, θ_0, θ before population expansion, θ_1, θ after population expansion, pairwise difference of population after growth, N_a number of alleles per locus per population, *A* total number of alleles, H_o gametic heterozygosity (Moody 1993), P_R number of private alleles, *Shannon* Shannon diversity, G_{ST} genetic differentiation index (Nei 1973), G'_{ST} standardized genetic differentiation index (Hedrick 2005), D_{EST} standardized genetic differentiation index (Jost 2008)

and 0.16 for Lynch, $P < 0.001$ for both; Invaded: $R^2 = 0.17$ for Bruvo, and 0.26 for Lynch, $P < 0.001$ for both), indicating genetic isolation by geographic distance.

Population genetic structure and phylogenetic relationships

The PCoA analysis, including other taxa that are outgroups and the different ploidy populations showed that all the taxa were clustered separately from each other, except for the tetraploid *S. altissima*, which partly overlapped with the cluster of the hexaploid *S. altissima* (Fig. S2). The neighbor-joining tree based on the genetic distance of Nei's D_A (Nei et al. 1983) showed distinct differentiation between the native and invaded populations, with the exception of the Hokkaido (SN) population that was rather closely related to native populations (Fig. 2). In the native range, the most closely related populations to the invaded range were the southern populations (LSa, LSb, FLa, FLb). The Midwest USA populations (CL, PE, CG, I20, HIL) were genetically differentiated from other USA populations (Fig. 2). Korean population (KY) was strongly genetically differentiated from the Japanese populations as indicated by length of this terminal clade estimated to be much longer than that of other populations. The population network included many boxes where more than one split and was distinctly non-tree-like (Fig. S3), meaning ambiguity in applying a simple tree model to the data, although the genetic relationship between populations was almost the same as those shown in the neighbor-joining tree. The PCoA analysis appeared to reflect a native–invaded differentiation pattern on the first axis, and a north–south differentiation in the invaded range in the second axis. The southern populations (LSa, LSb, FLa, FLb) in the native range were most closely associated with the invaded populations (Fig. S4), in agreement with the neighbor-joining tree and the population network analyses.

The STRUCTURE analysis showed a clear peak in the modal value of ΔK at $K = 5$ as determined by the method of Evanno et al. (2005), indicating that the most likely number of ancestral gene pools is $K = 5$. A spatial hierarchical Bayesian clustering TESS analysis and the DAPC analysis produced five genetic clusters similar to the genetic clustering pattern of populations with STRUCTURE analysis, although the extent of genetic admixture between populations appeared to be slightly larger than estimated by STRUCTURE analysis (Fig. S5). It suggests that it is unlikely that there was any spurious clustering in the STRUCTURE analysis caused by spatial autocorrelation. The red cluster was dominant in all Japanese populations, except for Hokkaido (SN) and the two other northern Japanese populations. These three populations had very different compositions that characterized by an admixture of more than three gene pools (Fig. 3b). The population in Korea (SY) was a distinct cluster. Native USA populations varied with the green cluster being dominant in the central Midwest populations (CL, PE, CG), while the northern Midwest (HB, FB) and Eastern populations exhibited a highly admixed composition dominated by the purple cluster (Fig. 3b). Only the southern USA populations (LSa, LSb, FLa) and populations in the Atlantic coast (PAa, PAb, MD, VS) had a significant proportion of the red cluster.

The phylogenetic structure among *Solidago* species investigated was shallow, and haplotypes were not grouped to species monophyletically (Figs. 1, S6). The most frequently observed haplotype (H25) was the most common haplotype in both the invaded range and the

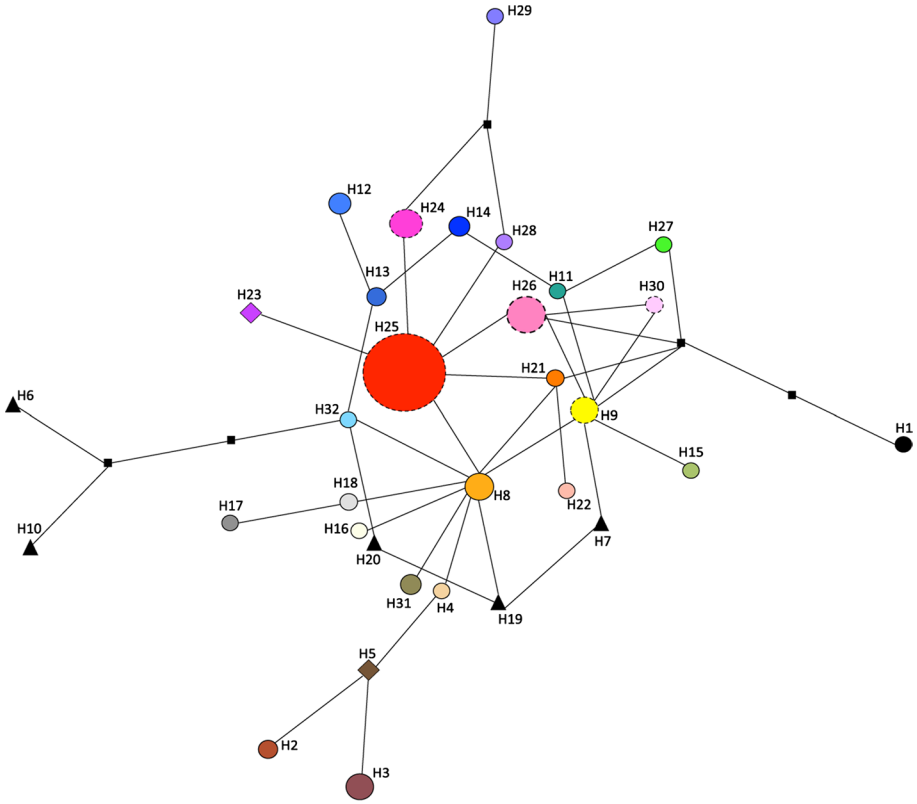

Fig. 1 The haplotype network of *Solidago altissima* based on chloroplast DNA sequence variation. *Circle* size is proportional to haplotype frequency. Each *line* between haplotypes corresponds to one mutational change. *Small black squares* indicate missing haplotypes. Haplotypes found in both native and invaded populations are shown in *dotted outlines*, and haplotypes only found in invaded populations are shown in *diamonds*, and haplotypes of outgroup species are shown in *triangles*: *S. virgaurea*, H6 and H10; *S. gigantea*, H7; *S. canadensis*, H19 and H20 (color figure online)

Table 3 Results of the analysis of molecular variance for both ranges

Distance measure	Source	d.f.	Variance components	%	Fixation indices
Bruvo	Among range	1	0.010	4	$\Phi_{RT} = 0.039$*
	Among population	30	0.027	11	$\Phi_{PR} = 0.113$*
	Within population	681	0.212	85	$\Phi_{PT} = 0.148$*
Lynch	Among range	1	0.012	5	$\Phi_{RT} = 0.047$*
	Among population	30	0.035	13	$\Phi_{PR} = 0.138$*
	Within population	681	0.218	82	$\Phi_{PT} = 0.179$*

* $P < 0.0001$, the probability of obtaining by chance an fixation indices equal to or greater than the observed value, estimated from 999 permutations

native range. All haplotypes observed in the invaded range were closely related to H25 except for H5 (Figs. 1, S6). In the SAMOVA analysis, the F_{CT} value was highest when the number of population groups was defined as three, and included the diploid population (CA) and the tetraploid population (EF) which were detected as a separate group. When these two populations were excluded, the F_{CT} value was highest when the number of population groups was defined as five, and continued to decrease as the number of groups increased. The five groups included two single-population groups and two groups containing two populations, and a large group containing the rest of the populations. However, these groups had no biological consequence.

Discussion

Relationships among species and ploidy levels

The genus *Solidago* is known for complex taxonomy and clear differentiation of the species is further complicated, not only by the occurrence of interspecific hybrids, but also because many species are polytopic with overlapping ranges, and several species have multiple cytotypes (Semple and Cook 2006). A recent phylogenetic study of *Solidago* species has revealed a single origin involving reticulate evolution and introgression in an allohexaploid *S. houghtonii* (Laureto and Barkman 2011). While Laureto and Barkman (2011) resolved relationships among Triplinerviae

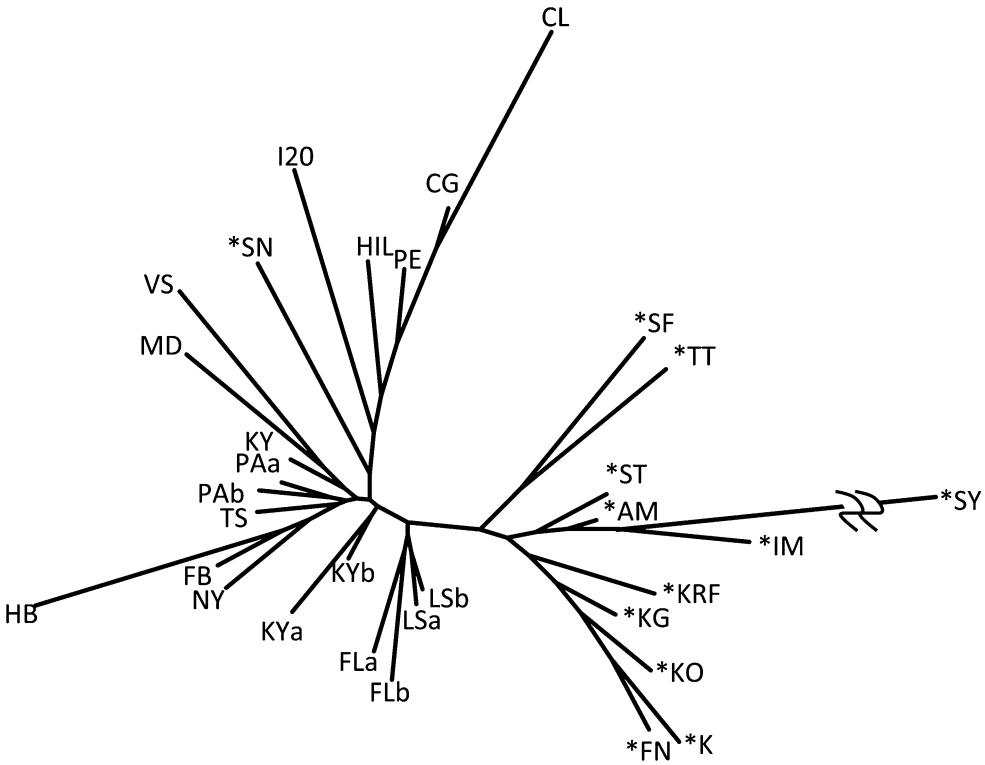

Fig. 2 A neighbor-joining tree summarizing the relationships among hexaploid *S. altissima* populations based on Nei's genetic distance (Nei et al. 1983). *Populations in the invaded range. Abbreviations refer to Table S1

species using chloroplast DNA sequence data, Schlaepfer et al. (2008) could not distinguish between *S. gigantea* and *S. canadensis*, and found that some haplotypes were shared with more than one species. Similarly, our results of the cpDNA sequence data could not resolve relationships among *S. altissima*, *S. gigantea*, and *S. canadensis*. This was consistent even when we included the indels in the DNA sequence for the analysis. We cannot deny the possibility of either incomplete lineage sorting or chloroplast capture by secondary contact, both of which are consistent with recent speciation (Twyford and Ennos 2012). On the other hand, using microsatellite markers, three species were clustered separately and were shown to be genetically distinct. These high-resolution markers can be used to distinguish among polyploid taxa, except for tetraploids and hexaploids.

Genetic diversity and structure in the native range

In the native range, we found high genetic diversity in nSSR markers within populations (Table S1). The genetic structure of nSSR data analyses showed that Central Midwest populations (CL, PE, CG, I20, HIL) were genetically differentiated from the rest of the populations (Figs. 2, 3b). This could be explained by one of the most commonly observed phylogenetic breaks in Eastern North America, which is between the two sides of the Mississippi Valley (Jaramillo-Correa et al. 2009; Soltis et al. 2006). In addition, the genetic differentiation between HB, FB and the other Midwest populations is likely to reflect the southern limit of the Laurentide Ice Sheet. However, since most of our samples are hexaploid plants and include only a few other ploidy plants, we need more diploid and tetraploid samples from other geographic range, to examine the evolutionary history of *S. altissima* in North America. Although the closely related species *S. gigantea* showed the possibility of glacial survival in different refugial areas and separate migration routes on opposite sides of the Appalachian Mountains (Schlaepfer et al. 2008), we did not find any genetic discontinuity in the Appalachian populations. The phylogeographic study of the *Solidago* subsect., *Humiles* suggested Holocene polyploid speciation supported by restriction of endemic polyploid taxa to post-glacial habitats (Peirson et al. 2013). In line with these findings, the cpDNA sequence data showed no pattern in genetic structure among hexaploid populations and the mismatch distribution analysis suggested rapid expansion of the populations (Table 2; Fig. 3a). The significant isolation by distance in both nSSR and cpDNA markers (Fig. S1) shows that genetic differentiation is influenced by geography in North America, and that most subsequent gene flow seems mediated through pollen, as indicated by the much stronger among-populational differentiation at cpDNA (only dispersed by seeds) than nDNA (dispersed by both seeds and pollen) markers (Table 2). Alternatively, this could simply reflect the difference in the effective population size between cpDNA and nDNA markers. From the results of the mismatch distribution analysis

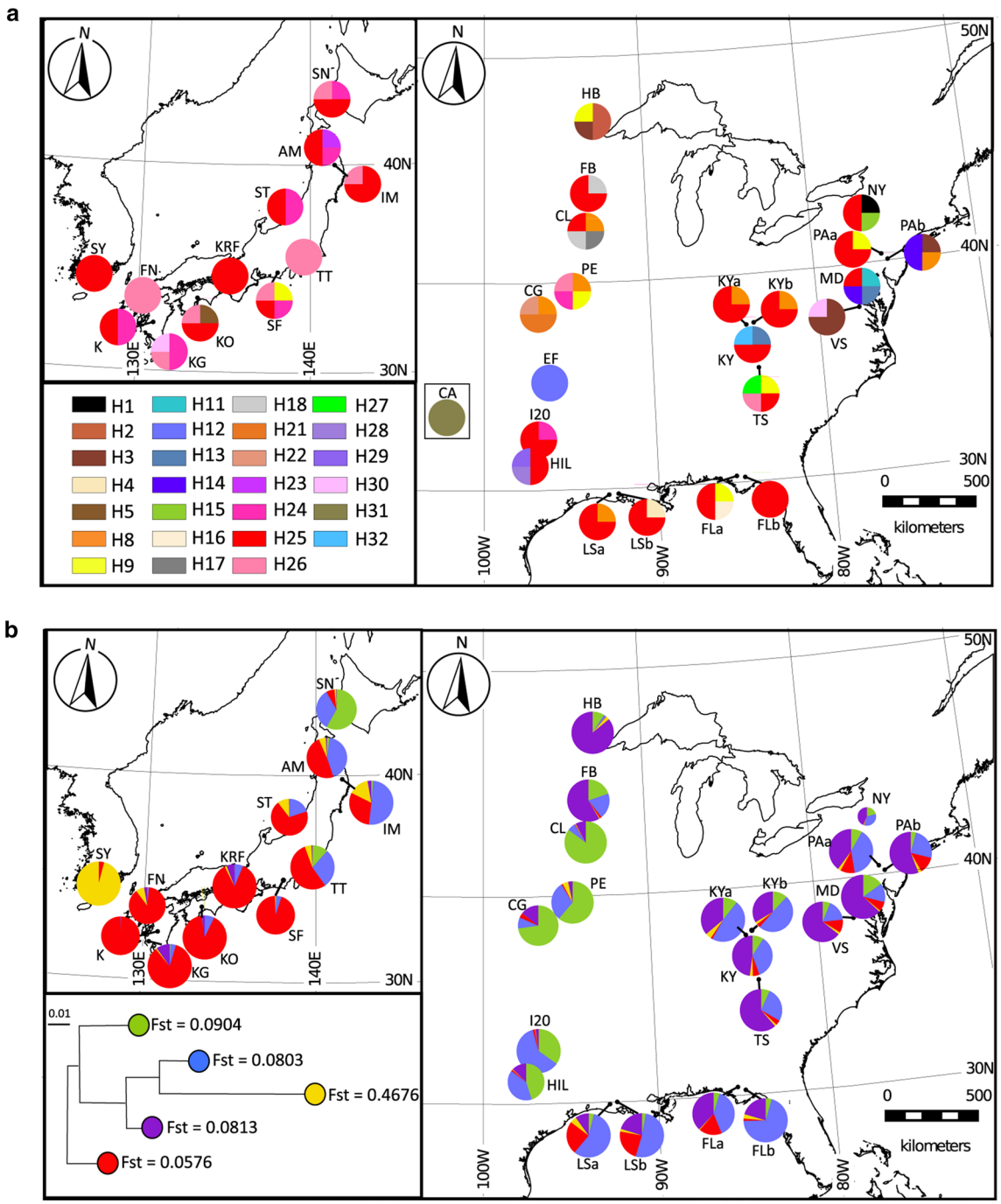

Fig. 3 **a** Geographic distribution of the 27 chloroplast haplotypes found in *S. altissima* populations. H12 is observed in the tetraploid population EF. Haplotype names correspond to Fig. 1. **b** Geographic distributions of five nSSR gene pools estimated by STRUCTURE analysis (Pritchard et al. 2000). A neighbor-joining tree showing the relationships of each gene pool is depicted. The number of samples analyzed per population is proportional to the circle's size

and the fact that the hexaploid *S. altissima* is likely to have multiple origins from different diploid lineages (Halverson et al. 2008), the hexaploid *S. altissima* in North America would have expanded its range recently and the genetic structure been largely shaped through post-glacial migration and gene flow.

Multiple and mass introductions in the invaded range

Many studies have documented that the founding population reduces genetic variation within population, relative to the source population, because of a reduction in population size during colonization (Dybdahl and Drown 2011; Henry

et al. 2009; Okada et al. 2007). However, there is increasing evidence for similar or even higher levels of within-population genetic diversity in exotic populations. This is typically explained by high propagule pressure, multiple introductions or admixture in the introduced range of individuals from different sources (Bossdorf et al. 2005; Dlugosch and Parker 2008; Kelager et al. 2013).

The low haplotype diversity and a few private alleles indicate that introduced populations came from a single or a few independent origins (Table 2 and Fig. 1). Moreover, the introduced populations with the red cluster representing 68 % of the introduced sites in Japan are genetically similar and likely share a common origin, indicating that a single or a few populations were particularly successful in colonizing the invaded range. This can also be suggested as a result of post-invasion selection of genotypes adapted in invaded regions. This scenario has been confirmed in many successful invasive species (Lee 2002; Lombaert et al. 2010). Despite the small numbers of private alleles in the invaded range, the difference between introduced and native populations was significant in the genetic structure analysis (Figs. 2, S2, S4). This may be caused by dissimilarities in allele frequencies rather than allelic identities. Hence, it is likely that high propagule pressure at primary establishment (i.e., mass introductions from few sources) and substantial geneflow through obligate outcrossing and production of large amounts of wind dispersed seeds have co-founded the widely distributed red cluster. This is also indicated in the Korean SY population with the high F_{ST} value of the yellow cluster in STRUCTURE analysis. Although the SY population has genetically differentiated from the other invaded populations, it was most closely related to the northern Honshu populations (Figs. 2, 3). We speculate that the SY population originated from a source in the northern region of Japan, rather than a separate colonization event from the native source.

Our study infers multiple colonization with at least two primary colonization events of *S. altisssima* into Japan. The Hokkaido population (SN) was clustered with the native populations (Fig. 2) and thus was genetically differentiated from the other introduced populations in the population structure analyses (Fig. S5). Fukuda (1982) notes that the Hokkaido populations have been established more recently in Japan compared to other regions. The populations in Hokkaido are more likely derived from an independent colonization event rather than a range expansion from the Honshu populations. In addition, the northern Honshu region showed higher admixture and higher genetic diversity than southern Japan populations (Table S1; Fig. 3). These results indicate that secondary colonization and gene flow (shown in Honshu and Hokkaido clusters) have contributed to the maintenance of high genetic diversity within populations in the invaded range.

The results of the genetic structure analyses in nSSR showed congruent patterns by different methods (neighbor-joining tree, population network analysis and PCoA analysis), which showed that the introduced populations dominated by the red cluster were genetically most related to the South region in North America (LSa, LSb, FLa, FLb), where the highest genetic diversity was observed (Tables S1, S2). However, populations in theAtlantic coast region (PAa, PAb, MD, VS) are also related to populations in the invaded range. Moreover, the cpDNA analysis showed that only two haplotypes (H9 and H25) were shared between the invaded region and South region in North America, while four haplotypes (H9, H24, H25 and H26) were shared with the central Midwest populations. Larger sample size for cpDNA analysis, and analysis with higher resolution markers are necessary to identify the origin of the Japanese population.

Spatial genetic structure in the invaded range and invasive spread during invasion

While the isolation by distance was significant for both cpDNA and nSSR data in the native range, it was only significant for nSSR data in the invaded range. The population differentiation was higher in the invaded range than in the native range for nSSR data (Table 2), but when the Korean (SY) and the Hokkaido (SN) populations were excluded they showed similar low values in both ranges (G_{ST}, 0.011 vs. 0.014; G'_{ST}, 0.052 vs. 0.061; D_{EST}, 0.041 vs. 0.048 in native and invaded range, respectively). There are two possible explanations. First, the multiple introductions from distinct native sources to different regions in Japan (i.e., Hokkaido) may account for the larger population differentiation in the invaded region than in the native range. Second, substantial gene flow has been present and/or genetic drift has been weak in the invaded range. High admixture in the northern Honshu region also suggests this. Gene flow is promoted by the fact that *S. altissima* invaded along railways and roads, which form a highly connected habitat. In addition, the high ploidal nature of the species may have mitigated the effect of genetic drift (Gaudeul et al. 2011). Asai (1970) reported that Japanese bee-keepers have transplanted the naturalized *S. altissima* as honey-bee food plants. It implies that range expansion in Japan occurred by a series of long-distance human-mediated dispersal commonly found in invasive species (Gaudeul et al. 2011; Kelager et al. 2013; Okada et al. 2007).

Our reconstruction of *S. altissima*'s invasion history based on historical records and the results of genetic diversity and structure in both range, suggests that the invaded populations arose from introductions from a few sources potentially in the southern part of North America in early 1900 s by ornamental planting and commercial exchange.

Later, the independent introduction from different native sources to Hokkaido generated admixture between genetic clusters leading to high genetic diversity in the northern region in Japan. Soon after, human-mediated dispersal and the high ploidal nature of the species contributed to the rapid and successful invasion. We summarize that multiple and mass introductions may have contributed to the persistence and rapid adaptation of the species enabling it to be spread throughout Japan. The high genetic diversity maintained within populations in the invaded range is often found in other polyploid plants (Hornoy et al. 2013; Schlaepfer et al. 2008; Vallejo-Marin and Lye 2013). High levels of heterozygosity (and nearly double the effective population size) compared with diploid plants are characterized by autopolyploids as a result of polysomic inheritance (te Beest et al. 2012). Furthermore, the fact that *S. altissima* is perennial may have also increased the effective population size as discussed in other systems (Hornoy et al. 2013). Together with the growing number of studies of invasive polyploid plants, our results also emphasize the significance of considering polyploid as an important trait in invasion models, as polyploids benefit from reduced genetic impact of bottlenecks, and a high evolutionary potential (Lee 2002; te Beest et al. 2012).

Future directions

Determining the mechanisms underlying successful range expansions and rapid adaptive processes including genetic factors, environmental factors, or their interactions is a critical challenge. Closely related *Solidago* species exhibit latitudinal variation in phenology (Weber and Schmid 1998) and enhanced competitive ability (Yuan et al. 2013) in the invaded range. Our previous study on *S. altissima* in Japan showed that plant resistance was rapidly selected when it was re-associated with a recently invaded herbivorous insect, *Corythucha marmorata* from North America (Sakata et al. 2014). The present results support the argument that large genetic variability was introduced and local adaptation is ongoing in the invaded range. Direct ancestor-descendent comparisons of phenotypic traits between native and introduced populations (Keller and Taylor 2008) will clarify whether the adaptation is a result of historical factors or of evolutionary changes involved in the invasion process (i.e., separating the role of stochastic and demographic events from that of selection in shaping the evolution of phenotypes), which is an important focus in future research.

Knowledge of the genetic variation in *S. altissima* in its native and invaded ranges can aid in the development of effective strategies to manage its spread. Information on the amount and distribution of genetic diversity can help to predict its response to chemical and biological control by considering the impacts of genetic variability on the interactions of the invasive species and the biological agents (Garcia-Rossi et al. 2003).

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