DIFFERENCES IN SPATIAL DISTRIBUTION, MORPHOLOGY, AND COMMUNITIES OF HERBIVOROUS INSECTS AMONG THREE CYTOTYPES OF SOLIDAGO ALTISSIMA (ASTERACEAE)\textsuperscript{1}

MATTHEW L. RICHARDSON\textsuperscript{2,4} AND LAWRENCE M. HANKS\textsuperscript{2,3,5}

\textsuperscript{2}Program in Ecology, Evolution, and Conservation Biology, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801, USA; and \textsuperscript{3}Department of Entomology, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801, USA

\begin{itemize}
\item \textbf{Premise of the Study:} Polyploidy in plants can result in genetic isolation, ecological differences among cytotypes, and, ultimately, speciation. Cytotypes should be sympatric only if they are segregated in an ecological niche or through prezygotic isolation. We tested whether sympatric diploid, tetraploid, and hexaploid ramets of Solidago altissima L. (Asteraceae) differ in their ecological niche.
\item \textbf{Methods:} We measured how cytotypes were distributed within habitats, their morphology, and the composition of their communities of herbivorous insects at 10 natural field sites. We also conducted a common garden experiment to confirm whether observed differences in morphology or communities of herbivores were due to cytotype or environmental effects.
\item \textbf{Key Results:} Diploid ramets often grew in open areas, relatively far from woody plants, and were associated with a high species richness of herbaceous plants, especially grasses. Hexaploids often grew in heavy shading under woody plants where grasses were scarce. Finally, tetraploids usually grew in transition areas between diploids and hexaploids. Hexaploid ramets also were taller than ramets of other cytotypes and had larger leaves. Two species of insects, the leaf-galling fly Asteromyia carbonifera and the phloem-tapping aphid Uroleucon nigrotuberculatum, were more abundant on hexaploid ramets than on ramets of other cytotypes in the field. When grown in a common garden, however, cytotypes were similar in morphology and communities of herbivores.
\item \textbf{Conclusions:} We conclude that cytotypes of S. altissima differ in their spatial distribution within habitats and that spatial variation in environmental factors influence plant morphology and communities of herbivorous insects.
\end{itemize}

\textbf{Key words:} common garden; niche segregation; polyploidy; tall goldenrod; Uroleucon.

Polyplody is a major source of genetic diversity in plants and may lead to adaptation and phylogenetic diversification (Grant, 1981). In fact, as many as 80% of angiosperm species may have polyploidal origins (Grant, 1981; Masterson, 1994; Soltis and Soltis, 1999). Cytotypic variation (i.e., the number of chromosome sets) within plant species also is common and can influence their morphology (Khare and Kaur, 1983; Vandenhout et al., 1995; Kao and Parker, 2010), physiology (Tiwari et al., 1992), tall goldenrod; Uroleucon.

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\textsuperscript{2}Present address USDA-ARS, U.S. Horticultural Research Laboratory, Subtropical Insects Research Unit, Fort Pierce, Florida 34945, USA.

\textsuperscript{3}Author for correspondence (e-mail: hanks@life.illinois.edu).

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\textsuperscript{5}1980; Warner and Edwards, 1989), phenology of flowering (Tothill and Hacker, 1976; Lumaret et al., 1987; Petit et al., 1997), and other life-history traits (Marks, 1966; Husband and Schemske, 1997), as well as community structure of their associated arthropod pollinators and herbivores (Segraves and Thompson, 1999; Nuismer and Thompson, 2001; Thompson et al., 2004; Thompson and Merg, 2008). For example, different cytotypes of the saxifrage Heuchera grossularifolia Rydb. vary in their morphology, the species of herbivores that feed on them, and the pollinators that visit their flowers (Segraves and Thompson, 1999; Nuismer and Thompson, 2001; Thompson et al., 2004; Soltis et al., 2007).

Cytotypes of polyploid plant species often do not overlap geographically or are restricted to ecotones or contact zones (Rothera and Davy, 1986; Lumaret et al., 1987; Petit et al., 1997; Hardy et al., 2000; Husband and Schemske, 2000; Stuessy et al., 2004). Nevertheless, some cytotypes of a plant species are widely sympatric (e.g., Keefer, 2004; Halverson et al., 2008b), so they may influence each other through competition for resources, wide flow, or gamete wastage due to failed cross-pollination (Levin, 1975; Herrera et al., 2004; Baack 2005a, b; Martonífova, 2006). Sympatric cytotypes also may have community-level effects if herbivores, pathogens, or other species interact or perform differentially across cytotypes (Nuismer and Thompson, 2001; Thompson et al., 2004; Halverson et al., 2008a). Despite the importance of plant cytotype on population- and community-level interactions, it is rarely considered because different cytotypes of autopolyploids may be morphologically indistinguishable (e.g., Borrill and Lindner, 1971; Rothera and Davy, 1986).
Solidago altissima L. (Asteraceae) is a common perennial herb in oldfield habitats throughout North America and comprises diploid, tetraploid, and hexaploid cytotypes (Semple et al., 1984). The tetraploid and hexaploid plants are likely autopolyploids, given their morphological similarity to diploids, the lack of other species with which to hybridize, and the tendency of other species within Solidago to be polyploids (J. C. Semple, personal communication; Esselman and Crawford, 1997). The species is associated with a rich arthropod fauna of herbivores and pollinators (Abrahamson and Weis, 1997), and there is some evidence that cytotype may influence herbivorous insects: gall-making insects often are more abundant on certain cytotypes, although it is unclear whether cytotype or environmental factors determine their abundance (Halverson et al., 2008a).

Eastern populations of S. altissima are apparently composed entirely of the hexaploid subspecies altissima, whereas western populations are of the subspecies gilvocanescens, which may be diploid or tetraploid (Semple et al., 1984). Both subspecies and all three cytotypes are present in Illinois and Iowa, and polyploidy probably arose multiple times from diploid lineages (Semple et al., 1984; Halverson et al., 2008b).

Cytotypes theoretically should be sympatric only if they are segregated in ecological niche or through prezygotic isolation; otherwise, local co-occurrence should be unstable and minority cytotypes should be lost to extinction (Fowler and Levin, 1984; Rodriguez, 1996; Husband, 2000; Kennedy et al., 2006). In this article, we test the hypothesis that three cytotypes of S. altissima, growing in sympatry, differ in their ecological niche. Specifically, we determined whether cytotypes differ in their fine-scale spatial distribution, in their morphology and flowering phenology, and in the community of herbivorous insects that feed on them. Prior work determined that all three cytotypes can be sympatric in Iowa and western Illinois with no difference in their fine-scale distribution (Halverson et al., 2008b). We extend this earlier work by associating structural features of the habitat with spatial distribution of cytotypes, as well as describing the morphology and flowering phenology of the cytotypes. We also use a common-garden experiment to determine whether differences observed among cytotypes in morphology and communities of insect herbivores are based solely on genotype or are mediated by environmental factors.

MATERIALS AND METHODS

Spatial distribution of cytotypes—We surveyed populations of S. altissima for cytotypic composition at four sites in east-central and northeastern Illinois in May 2007 and added another six sites in May 2008 (Appendix S1; see Supplemental Data with the online version of this article). At each site, we haphazardly chose 30–53 individual ramets (n = 367), which were separated by >10 m to minimize the chances of selecting multiple ramets of the same genet (individual genets usually are <10 m in diameter; Abrahamson and Weis, 1997). Ramets were tagged with flagging tape. Study ramets were cytotyped by flow cytometry (following the methods of Annunagathan and Earle, 1991; Bino et al., 1992; Stehlik et al., 2007) using a Beckman-Coulter Epics XL-MCL flow cytometer (Fullerton, California, USA) at Iowa State University in 2007 or a BD FACSCanto flow cytometer (San Jose, California, USA) at the University of Illinois at Urbana-Champaign in 2008. Cytotype was determined by measuring the fluorescence of propidium iodide (425 nm excitation) for approximately 3,000–5,000 nuclei from each ramet. We converted fluorescence to chromosome number by comparing the relative amount of DNA in cells of study ramets with standards of all three cytotypes that were cytotyped by conventional examination of mitotic root-tip squashes and flow cytometry (provided by J. C. Semple, S. D. Hendrix, K. Halverson, and J. D. Nason).

We tested for differences among cytotypes of S. altissima in their spatial distribution within habitats by estimating the same environmental variables that have been used in earlier ecological studies of polyploidy in plants (Johnson et al., 2003; Raabovi et al., 2008) and to characterize plant community structure (Blouin-Demers and Weatherhead, 2001; Richardson et al., 2008). We measured the following parameters for each tagged ramet that we could relocate in July and August 2007 and 2008 (n = 319): (1) distance to the nearest habitat edge (i.e., the boundary between grassland and forest, cropland, or road); (2) distance to the nearest tree; (3) number of stems of woody shrubs, saplings, and vines within a 1-m radius; (4) number of plant species within a 1-m radius (i.e., species richness); (5) maximum height of ground vegetation within a 1-m radius (estimated during 20–22 August 2008); (6) percentage of ground within a 1-m radius that was covered by grasses, estimated with a sighting tube (a 14 × 4 cm piece of cardboard pipe with cross wires at one end; modified after Winkworth and Goodall, 1962) that was aimed haphazardly within the 1-m-radius area that encircled the ramet (repeated 20 times per ramet). We recorded the percentage of times that grasses were sighted within the cross wire and (7) percent canopy coverage provided by shrubs and trees above a ramet, estimated with the same sighting tube as described above, but angled >45° from horizontal, repeated 20 times and recording the percentage of times that foliage or branches of trees or shrubs were sighted within the cross wire.

We used discriminant function analysis in Systat for Windows version 11 (Systat, Chicago, Illinois, USA) to test differences between cytotypes in these variables. The hypothesis would be supported if cytotypes differed significantly in how their data points were distributed within the function space.

Morphology and flowering phenology of cytotypes—We tested whether the three cytotypes of S. altissima differed in morphology and flowering phenology by measuring the following nine characters that vary with genotype in this plant species and may influence abundance of herbivores (from Weis et al., 1987) in August 2007 or 2008: height of the stem; number of lateral branches; length and width of the longest leaf; mean length and width of three leaves at the middle of the stem; total number of leaves; number of inflorescences (during 2007 only); and timing of the onset of flowering (determined by monitoring each ramet from 5 August through 30 September 2007 to record the ordinal date on which the first inflorescence opened). Data on inflorescences and flowering phenology were not collected in 2008 because we were interested primarily in plant traits that may influence abundance of insect herbivores, and after the 2007 season we determined that the abundant herbivores at our field sites were largely unaffected by these two traits. These data were recorded for each of 94 haphazardly selected ramets across seven field sites where all three cytotypes were present. We tested differences between cytotypes using separate restricted maximum likelihoods (PROC MIXED; SAS Institute, 2002), with individual ramets nested within sites, including the interaction. Differences between pairs of means were tested with the Tukey-Kramer means separation test to control the overall experimentwise error rate (Sokal and Rohlf, 1995).

To confirm that phenotypic traits that we measured were governed solely by cytotype, and not by environmental factors, we grew ramets of each cytotype in a common garden at Phillips Tract, Champaign County, Illinois (a University of Illinois natural area). We established the common garden from rhizomes of 30 clones of each cytotype (30 clones × 3 cytotypes = 90 total clones) during fall 2006 and 2007. Most of the rhizomes were dug with a spading fork from four field sites in east-central Illinois (Appendix S1): fallow pasture (n = 27), Alerton Park (n = 15), Meadowbrook Park (n = 11), and Phillips Tract (n = 15), but we also included stock from a common garden in Pennsylvania (n = 13; provided by M. J. Wise, C. Blair, and W. G. Abrahamson) and potted plants from Iowa (n = 11; provided by K. Halverson and S. D. Hendrix). Because of the scarcity of diploid plants at the four field sites, most diploid clones (n = 19) came from a single site (fallow pasture), whereas tetraploid and hexaploid clones were collected from all four field sites and from Pennsylvania and Iowa. Rhizomes were planted at 3-m spacing, with position randomized within the garden, and plants were watered as needed. Ramets were grown for a minimum of 11 mo in the common garden before measuring morphological characters to reduce maternal effects and the influence of site. We compared the same morphological characters for ramets in the common garden using separate restricted maximum likelihoods (PROC MIXED; SAS Institute, 2002) as described above for wild ramets, except that site was included as a random factor and was dropped from the final analyses because it was nonsignificant (see Milliken and Johnson 1984). We did not control for blooming phenology of cytotypes in the common garden because some ramets did not bloom and usual visual destructions destroyed the inflorescences of many ramets, especially on diploid plants.

Communities of herbivorous insects—We characterized the relationship between host-plant cytotype and relative abundance of herbivorous insects by estimating insect abundance on 313 tagged ramets in the field (Table 1) and all
Table 1. Total number of ramets of Solidago altissima and the number represented by diploid, tetraploid, and hexaploid cytotypes at 10 study sites in east-central and northeastern Illinois (Appendix S1; see Supplemental Data with the online version of this article). Number of ramets sampled for herbivores in parentheses.

<table>
<thead>
<tr>
<th>Site</th>
<th>n</th>
<th>Diploid</th>
<th>Tetraploid</th>
<th>Hexaploid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allerton Park</td>
<td>53</td>
<td>2 (2)</td>
<td>34 (25)</td>
<td>17 (17)</td>
</tr>
<tr>
<td>Clinton Lake</td>
<td>25</td>
<td>0 (10)</td>
<td>20 (14)</td>
<td>5 (0)</td>
</tr>
<tr>
<td>Fallow pasture</td>
<td>37</td>
<td>35 (34)</td>
<td>1 (1)</td>
<td>22 (21)</td>
</tr>
<tr>
<td>Goodenow Grove Nature Preserve</td>
<td>30</td>
<td>1 (1)</td>
<td>7 (7)</td>
<td>22 (21)</td>
</tr>
<tr>
<td>Iroquois County Conservation Area</td>
<td>29</td>
<td>2 (2)</td>
<td>4 (3)</td>
<td>23 (22)</td>
</tr>
<tr>
<td>Kankakee River State Park</td>
<td>24</td>
<td>0 (0)</td>
<td>33 (3)</td>
<td>21 (21)</td>
</tr>
<tr>
<td>Meadowbrook Park</td>
<td>46</td>
<td>6 (6)</td>
<td>30 (25)</td>
<td>10 (10)</td>
</tr>
<tr>
<td>Phillips Tract</td>
<td>51</td>
<td>6 (6)</td>
<td>35 (30)</td>
<td>10 (10)</td>
</tr>
<tr>
<td>Reserve prairie</td>
<td>30</td>
<td>1 (1)</td>
<td>10 (10)</td>
<td>19 (18)</td>
</tr>
<tr>
<td>Vermilion River Observatory</td>
<td>28</td>
<td>13 (10)</td>
<td>4 (3)</td>
<td>11 (10)</td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>353</td>
<td>6.6 ± 10.8 (62)</td>
<td>17.8 ± 14.1 (121)</td>
<td>13.9 ± 7.6 (130)</td>
</tr>
</tbody>
</table>

RESULTS

Spatial distribution of cytotypes—We were unambiguously able to cytotype 353 of the 367 ramets. All three cytotypes were present at eight sites, but only two cytotypes were present at the remaining two sites (Table 1). The cytotypes overlapped extensively in their spatial distribution, but discriminant function analysis yielded one function that separated most hexaploids from the other two cytotypes and another that separated most diploids from the other two cytotypes (Fig. 1; distribution of data points for cytotypes significantly different: Wilks’s λ = 0.643, F14,462 = 8.24, P < 0.001). Function 1 represents a positive gradient of grass coverage and distance to trees and a negative gradient of numbers of woody stems. Function 2 represents a positive gradient of shade by trees and shrubs and a negative gradient of grass coverage and plant species richness. Therefore, diploids tended to grow in open areas far from trees and other woody plants where they were surrounded by grasses and high species richness of herbaceous plants. Tetraploids, on the other hand, grew in areas that were shadier and had smaller amounts of grass and lower plant species richness. Finally, hexaploids grew in proximity to trees and other woody plants where grasses were not dominant.

Morphology and flower phenology of cytotypes—Cytotypes of S. altissima at the field sites differed in four of the eight morphological characters, and the study-site term also was significant for three analyses, but results for length of the longest leaf and the mean length of three leaves from the midstem are not presented because they were highly correlated with the width of leaves (Table 2). Diploid and tetraploid ramets did not differ in morphology, but hexaploids were taller and had larger leaves (Table 3). Diploids produced flowers about 16–19 d earlier than both tetraploids and hexaploids, but flowering phenology...
variables associated with three cytotypes of \textit{Circles indicate confidence ellipses centered on the centroid for each cytotype woody stems. Function 2 represents a positive gradient of shade by trees and grass coverage and distance to trees and a negative gradient of numbers of against discriminant function 2. Function 1 represents a positive gradient of east-central and northeastern Illinois. Discriminant function 1 is plotted only cytotype had high dance of herbivores at field sites for any of the categories of in field populations. Not determine the abundance of herbivores on individual ramets bivores were evenly distributed across cytotypes of \textit{S. altissima and this was the only term that was significant for the leaf-miners, the crescent morph of \textit{A. carbonifera}, \textit{R. solidaginis}, and \textit{U. luteolum} (overall ANOVA, $F_{1,36} = 18.4$, $P < 0.001$; cytotype, $F_{2,36} = 5.85$, $P = 0.007$; site, $F_{5,36} = 5.54$, $P = 0.04$, respectively). In the common garden, however, all categories of herbivores were evenly distributed across cytotypes of \textit{S. altissima} (all six $P$ values $> 0.23$), which suggests that cytotype alone did not determine the abundance of herbivores on individual ramets in field populations.

Cytotype alone also did not account for the relative abundance of herbivores at field sites for any of the categories of herbivores in the AIC analyses (all AIC models that included only cytotype had high $\Delta$AIC$_c$ values and little support). The AIC model for leaf miners that had the greatest support indicated that they were negatively associated with host plant cytotype (i.e., highest abundance on diploid plants) and positively associated with stem height, the distance from the nearest tree, the proportion of the ground covered by grass, and species richness of nearby plants (Table 4). Multiple models had reasonable support ($\Delta$AIC$_c < 3$), but the most important predictor variables (i.e., in nearly every model that carried weight) were stem height, distance from the nearest tree, and proportion of ground covered with grass ($\Sigma w_i = 0.99, 0.99, 0.94$, respectively). The local abundance of leafminers may also be associated with host plant cytotype or plant species richness, because these variables carried a moderate weight ($\Sigma w_i = 0.63, 0.66$, respectively).

The AIC model for the leaf galler \textit{A. carbonifera} that had the greatest support indicated that they were positively associated with host ramet cytotype (i.e., highest abundance on hexaploid plants) and height of the stem and negatively associated with species richness of nearby plants (Table 4). Cytotype, stem height, and species richness of nearby plants were the most important predictor variables ($\Sigma w_i = 0.87, 0.82, 0.96$, respectively).

The aphid \textit{U. luteolum} was most abundant on diploids that were tall and far from trees (Table 4). Stem height and distance from the nearest tree were the most important predictor variables

### Table 2. Results of restricted maximum likelihoods that tested differences between three cytotypes of \textit{Solidago altissima} in morphology and date of blooming in seven field sites in east-central and northeastern Illinois.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Term</th>
<th>$F$</th>
<th>df</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Width of longest leaf</td>
<td>Cytotype</td>
<td>3.78</td>
<td>2, 85</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>2.27</td>
<td>6, 85</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>Cytotype x site</td>
<td>0.78</td>
<td>12, 85</td>
<td>0.67</td>
</tr>
<tr>
<td>Mean width of three leaves on midstem</td>
<td>Cytotype</td>
<td>4.08</td>
<td>2, 85</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>0.75</td>
<td>6, 85</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>Cytotype x site</td>
<td>1.61</td>
<td>12, 85</td>
<td>0.11</td>
</tr>
<tr>
<td>Number of leaves</td>
<td>Cytotype</td>
<td>0.27</td>
<td>2, 85</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>6.48</td>
<td>6, 85</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Cytotype x site</td>
<td>1.03</td>
<td>12, 85</td>
<td>0.43</td>
</tr>
<tr>
<td>Number of lateral branches</td>
<td>Cytotype</td>
<td>0.17</td>
<td>2, 85</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>2.92</td>
<td>6, 85</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Cytotype x site</td>
<td>0.68</td>
<td>12, 85</td>
<td>0.77</td>
</tr>
<tr>
<td>Number of inflorescences</td>
<td>Cytotype</td>
<td>1.19</td>
<td>2, 40</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>2.27</td>
<td>2, 40</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>Cytotype x site</td>
<td>2.69</td>
<td>12, 40</td>
<td>0.06</td>
</tr>
<tr>
<td>Height of stem</td>
<td>Cytotype</td>
<td>8.57</td>
<td>2, 85</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>2.17</td>
<td>6, 85</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>Cytotype x site</td>
<td>1.62</td>
<td>12, 85</td>
<td>0.10</td>
</tr>
</tbody>
</table>

### Table 3. Mean (± SE) for morphological traits of three cytotypes of \textit{Solidago altissima} in seven field sites in east-central and northeastern Illinois. Means within rows with different letters are significantly different (Tukey-Kramer means separation test, $P < 0.05$).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Cytotype</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Diploid</td>
</tr>
<tr>
<td>Width of longest leaf (mm)</td>
<td>14.0 (0.95)b</td>
</tr>
<tr>
<td>Mean width of three leaves on midstem (mm)</td>
<td>10.9 (0.91)b</td>
</tr>
<tr>
<td>Number of leaves</td>
<td>153.5 (35.8)</td>
</tr>
<tr>
<td>Number of lateral branches</td>
<td>3.19 (1.10)</td>
</tr>
<tr>
<td>Number of inflorescences</td>
<td>78.7 (21.4)</td>
</tr>
<tr>
<td>Height of stem (cm)</td>
<td>91.1 (6.69)b</td>
</tr>
</tbody>
</table>
Asteromyia carbonifera and the aphid Uroleucon nigrotuberculatum across three cytotypes of S. altissima at 10 field sites in east-central and northeastern Illinois. Means within taxa with different letters are significantly different (Tukey-Kramer means separation test, P < 0.05).

The aphid Uroleucon luteolum was most abundant on tall ramets that were close to trees and surrounded by a low species richness of nearby plants (Table 4). Stem height, distance from the nearest tree, and species richness of nearby plants were the most important predictor variables ($\Sigma w_i = 0.99$; $\Sigma w_i = 0.99$, respectively), and cytotype and proportion of the ground covered by grass also may be important variables ($\Sigma w_i = 0.71$; $\Sigma w_i = 0.59$, respectively).

We tested whether three cytotypes of S. altissima growing in sympathy differed in their ecological niche to provide one possible explanation about how they are able to coexist. Cytotypes of polyploid plant species often do not overlap geographically (Rothera and Davy, 1986; Lumaret et al., 1987; Petit et al., 1997; Husband and Schemske, 2000; Rivero-Guerra, 2008) and should not be able to overlap unless they are segregated in ecological niche or through prezygotic isolation; otherwise, minority cytotypes will be lost to extinction (Fowler and Levin, 1984; Rodriguez, 1996; Husband, 2000; Kennedy et al., 2006). In fact, where two cytotypes of a plant species are sympatric, some studies have shown that competition for resources is apparently limited by subtle differences between them in microhabitat (e.g., Johnson et al., 2003; Raabová et al., 2008). Consistent with these earlier studies, we found evidence that cytotypes of S. altissima differ in how they are distributed within habitats. To our knowledge, this study provides the first evidence that spatial segregation at fine scales can allow more than two cytotypes to coexist in sympatry. The populations rarely are an even mixture of the cytotypes, however, which suggests that random events influence the populations or, perhaps, that there is disruptive selection for chromosome number, as is also apparently the case in the polyploid Galax urceolata (Poir.) Brummit (Diapensiaceae), which has three cytotypes that are sympatric but are not evenly mixed within populations (Burton and Husband, 1999).

**Table 4.** Best-fitting AIC$_c$ models from 63 candidate models for abundance of each herbivore (the dependent variable) with explanatory variables cytotype, local abundance of cytotype, height of ramet, distance to the nearest tree, proportion of the ground within 1 m of the ramet that was covered by grasses, and number of plant species within 1 m of the ramet. The regression coefficient ± SE is given in parentheses for each variable in the best-supported model. K = number of parameters in the model.

<table>
<thead>
<tr>
<th>Herbivore</th>
<th>Model variables</th>
<th>K</th>
<th>Log (L)</th>
<th>$\Delta$AIC$_c$</th>
<th>$w_i$</th>
<th>adj. $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Leaf miners</strong></td>
<td>Cytotype, height of stem, distance to nearest tree, proportion of grass</td>
<td>6</td>
<td>33.7</td>
<td>1.03</td>
<td>0.21</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td>Cytotype, height of stem, distance to nearest tree, proportion of grass, plant richness</td>
<td>6</td>
<td>34.0</td>
<td>0.45</td>
<td>0.29</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td>Cytotype (–0.09 ± 0.06), height of stem (0.01 ± 0.002), distance to nearest tree (0.02 ± 0.01), proportion of grass (0.01 ± 0.002), plant richness (0.05 ± 0.03)</td>
<td>7</td>
<td>35.4</td>
<td>0.00</td>
<td>0.36</td>
<td>0.25</td>
</tr>
<tr>
<td><strong>Asteromyia carbonifera</strong></td>
<td>Cytotype (1.1 ± 0.43), height of stem (0.01 ± 0.00), plant richness (–0.53 ± 0.20)</td>
<td>5</td>
<td>–210.7</td>
<td>0.00</td>
<td>0.25</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td>Cytotype, height of stem, distance to nearest tree, plant richness</td>
<td>6</td>
<td>–210.4</td>
<td>1.66</td>
<td>0.11</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td>Cytotype, height of stem, proportion of grass, plant richness</td>
<td>6</td>
<td>–210.2</td>
<td>1.29</td>
<td>0.13</td>
<td>0.24</td>
</tr>
<tr>
<td><strong>Uroleucon luteolum</strong></td>
<td>Cytotype (–1.6 ± 0.73), height of stem (0.12 ± 0.03), distance to nearest tree (0.29 ± 0.07)</td>
<td>5</td>
<td>–269.7</td>
<td>0.00</td>
<td>0.16</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Cytotype, height of stem, distance to nearest tree, proportion of grass</td>
<td>6</td>
<td>–268.8</td>
<td>0.44</td>
<td>0.13</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Cytotype, height of stem, distance to nearest tree, plant richness</td>
<td>6</td>
<td>–269.4</td>
<td>1.62</td>
<td>0.07</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>Cytotype, local abundance, height of stem, distance to nearest tree</td>
<td>6</td>
<td>–269.3</td>
<td>1.36</td>
<td>0.08</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Height of stem, distance to nearest tree, proportion of grass, plant richness</td>
<td>6</td>
<td>–269.4</td>
<td>1.47</td>
<td>0.08</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Cytotype, height of stem, distance to nearest tree, proportion of grass, plant richness</td>
<td>7</td>
<td>–268.0</td>
<td>1.07</td>
<td>0.16</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>Cytotype, local abundance, height of stem, distance to nearest tree, proportion of grass</td>
<td>7</td>
<td>–267.8</td>
<td>0.64</td>
<td>0.12</td>
<td>0.22</td>
</tr>
<tr>
<td><strong>U. nigrotuberculatum</strong></td>
<td>Height of stem (0.24 ± 0.08), distance to nearest tree (–0.40 ± 0.18), plant richness (–2.1 ± 0.87)</td>
<td>5</td>
<td>–371.1</td>
<td>0.00</td>
<td>0.24</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>Cytotype, height of stem, distance to nearest tree, plant richness</td>
<td>6</td>
<td>–380.0</td>
<td>0.14</td>
<td>0.23</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Local abundance, height of stem, distance to nearest tree, plant richness</td>
<td>6</td>
<td>–380.6</td>
<td>1.26</td>
<td>0.13</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>Cytotype, local abundance, height of stem, distance to nearest tree, plant richness</td>
<td>7</td>
<td>–379.8</td>
<td>1.97</td>
<td>0.09</td>
<td>0.21</td>
</tr>
</tbody>
</table>
We are unsure of the ultimate mechanism that influences spatial distribution of cytotypes, but they may differ in their distribution because of differences in dispersal ability, edaphic factors, or herbivory by insects that vary in abundance across microhabitats. Polyploids also may be more productive and competitive than their diploid ancestors (Lunaret et al., 1987; Lindner and Garcia, 1997; Petit and Thompson, 1997; Sonnleitner et al., 2010). Polyploids of several other plant species often inhabit more nutrient-rich communities with taller and more dense vegetation, whereas diploids tend toward more open habitats in which competition for resources is reduced (Stähleberg, 2009; Sonnleitner et al., 2010). This spatial pattern is similar to what we observed in *S. altissima*: diploids grew in open areas, hexaploids in shaded areas, and tetraploids in intermediate zones. An earlier study concluded that the three cytotypes of *S. altissima* were not spatially segregated within habitats in Illinois and Iowa (Halverson et al., 2008b). Our findings may differ because we measured physical features of the field sites to separate the distribution of cytotypes, whereas earlier researchers did not (Halverson et al., 2008b).

Hexaploid ramets of *S. altissima* may have been larger than the other cytotypes because of the gigas effect (i.e., larger cells in polyploids results in larger organs; Stebbins, 1971) or because they occupy a different microhabitat than the other cytotypes. The common-garden study indicates that the latter is probably true: morphological differences among cytotypes were due to environmental factors that vary over fine spatial scales. For example, hexaploid plants in our field sites may be larger simply because they grow in more shaded habitats. Other plant species that grow in shaded habitats may produce longer stems and leaves (McGuire and Agrawal, 2005; Pugnaire and Valladares, 2007) and also may be larger because rates of herbivory can be lower (Louda and Rodman, 1996).

The common-garden study also suggests that differences between cytotypes of *S. altissima* in the abundance of herbivorous insects are attributable to habitat effects, as is the case for another polyploid plant species (Münzbergová, 2006). To our knowledge, only two other studies have evaluated how herbivorous insects are influenced by host-plant cytotype at multiple study sites: in one case, insects were most abundant on one cytotype across sites (Thompson et al., 1997). In the other case, *S. altissima* and five gallmaking insects were the study system, and of the five gallmaking insects, two, *Eurosta solidaginis* Fitch and *A. carbonifera*, were most abundant on the same cytotype across sites, whereas the abundance of the other four insect species was not influenced by cytotype across sites (Halverson et al., 2008a). Our work in the common garden and statistical modeling provides an explanation for a lack of a strong cytotype effect on herbivores of *S. altissima*. In our statistical models, host-plant cytotype alone did not account for variation in herbivore abundance: herbivorous insects were most abundant on the tallest plants, regardless of cytotype. The ball-galling fly *Eurosta solidaginis* (Fitch) (Tephritidae) also is more abundant on tall ramets of *S. altissima* because tall plants may have higher fitness and may be a higher-quality host (Abrahamson and Weis, 1997).

In conclusion, cytotypes of *S. altissima* are differentially distributed within a field. We are unsure of the mechanism influencing this distribution, but it appears that environmental features that vary across this small spatial scale likely influence the phenotype of cytotypes and their communities of herbivorous insects. The spatial distribution of cytotypes is therefore likely to have important influences on the structure and diversification of terrestrial oldfield and grassland communities.

**LITERATURE CITED**


Münzbergová, Z. 2006. Ploidy level interacts with population size and habitat conditions to determine the degree of herbivory damage in plant populations. *Oikos* 115: 443–452.


