PLANT POLYPLOIDY AND INSECT/PLANT INTERACTIONS

John N. Thompson,[1,2,*] Bradley M. Cunningham,[2] Kari A. Segraves,[1]
David M. Althoff,[2] and Diane Wagner[2,†]

[1]Department of Botany, Washington State University, Pullman, Washington 99164; [2]Department of
Zoology, Washington State University, Pullman, Washington 99164

Abstract.—We used flow cytometry and extensive geographic surveys of herbivore attack to test whether repeated evolution of autotetraploidy in the perennial herb *Heuchera grossulariifolia* Rydb. (Saxifragaceae) has created evolutionary barriers to attack by the specialist moth herbivore *Greya politella* (Prodoxidae). We found that the moth has colonized tetraploid as well as diploid populations, has colonized tetraploids of separate evolutionary origin, and, at least under some conditions, is more likely to attack tetraploids than diploids. Plant polyploidy therefore provides a potential route out of specialization as an evolutionary dead end in phytophagous insect taxa as well as a potentially important route to subsequent phylogenetic and geographic diversification of plant/insect interactions.

Polyploidy is one of the major ways by which plant taxa have diversified in species (Grant 1981; Masterson 1994; Soltis and Soltis 1995). Its continuing importance in plant evolution is indicated by the local co-occurrence of two or more cytotypes within described species or species complexes and in the documented cases of new polyploid taxa that have arisen during the past century (Keeler et al. 1987; Lumaret and Barrientos 1990; Abbott 1992; Soltis and Soltis 1993; Soltis et al. 1995). Nevertheless, the ecological effects of polyploidy on shaping interspecific interactions within natural communities are largely unknown. Hence, it is one of the largest gaps in our understanding of the evolution—and coevolution—of interactions between plants and their enemies.

Closely related plant species differing in ploidy often differ in physiology, life history, and, in some cases, morphology (Levin 1983; Schoen et al. 1992; Thompson and Lumaret 1992; Warner and Edwards 1993; Bretagnolle and Thompson 1996). These changes caused by polyploidy have been exploited routinely in agriculture, producing polyploid varieties of some of the most important crop plants (Hilu 1993). Experimental studies have also indicated that some, but not all, polyploids are more resistant to attack by pathogens, insects, and nematodes than closely related diploids (Burdon and Marshall 1981; Reinert et al. 1986; Schoen et al. 1992; Busey et al. 1993). Hence, at least some polyploid

* To whom correspondence should be addressed; E-mail: jnt@wsu.edu.

† Present address: Department of Biological Sciences, Stanford University, Stanford, California 94305.

events may create a barrier to attack by enemies. These few studies, however, have not been designed to evaluate systematically the effect of polyploidy on the geographic pattern of attack of plant enemies across populations. Consequently, whether plant polyploidy can actually create a geographic and evolutionary barrier to enemy attack remains untested.

The evolutionary barrier hypothesis requires testing because where polyploidy does not immediately create a barrier to attack, polyploid events may broaden the host range of some specialist enemies, at least temporarily, until diploid and polyploid populations diverge further in traits. Hence, the alternative hypothesis is that polyploidy may act as a route to further diversification of plants and their enemies. Under both hypotheses there is a high but unevaluated potential for polyploidy to shape the population and geographic structure of interactions between plants and their enemies within and among natural communities, thereby contributing to the geographic mosaic of coevolution between these taxa (Thompson 1994).

The *Heuchera grossulariifolia* (Saxifragaceae) complex of populations is one of several complexes within the Saxifragaceae that have undergone autopolyploid evolution in parts of their geographic ranges (Soltis and Rieseberg 1986; Ness et al. 1989; Wolf et al. 1989, 1990). The descendent polyploid populations are completely or partially reproductively isolated from their diploid ancestors. Such autopolyploid events are particularly valuable for evaluating how polyploidy shapes the ecology and evolution of a population and its interactions with other species. The alternative route to polyploidy—allopolyploidy—involves both polyploidy and interspecific hybridization, making it difficult to separate the ecological effects of polyploidy from the known effects of hybridization (Strauss 1994; Whitham et al. 1994).

Here we evaluate whether repeated evolution of autopolyploidy in *H. grossulariifolia* has created evolutionary barriers to attack or potential evolutionary routes to diversification in the specialist moth herbivore, *Greya politella* (Prodoxidae). Attack of the diploid/autotetraploid complex of *H. grossulariifolia* populations by *G. politella* was chosen for five reasons. First, previous work had confirmed that the polyploid populations were of autopolyploid origin (Wolf et al. 1989). Second, *H. grossulariifolia* has a geographic distribution restricted to the wilderness core of central Idaho and western Montana and surrounding river drainages. This distribution allowed an assessment of insect attack throughout the plant's geographic range in a region that encompasses the largest area of relatively undisturbed environments remaining in the United States outside of Alaska. Hence, the geographic pattern of attack on plants could be more readily interpreted than in the more recently fragmented habitats of many plant species.

Third, previous work on interpopulational patterns of allozyme distribution and restriction-site analysis of chloroplast DNA indicated that autopolyploid populations had arisen separately in two different areas of Idaho: once or twice in western Idaho along Rapid River and an adjacent section of the lower Salmon River near Riggins, Idaho, and once in eastern Idaho in the Bitterroot mountains (Wolf et al. 1990). The origin of autopolyploidy in two separate geographic

areas allowed an assessment of whether polyploids arising from geographically distinct populations differ in creating a barrier to insect attack.

Fourth, as *Greya* populations have radiated onto Saxifragaceae, they have encountered barriers and opportunities in incorporation of new hosts and diversification of species. Six *Greya* species are known to attack Saxifragaceae (Davis et al. 1992), and all are restricted to a small clade of saxifrage genera known as the *Heuchera* group (Soltis and Kuzoff 1995). Several of these *Greya* species are specialized to different *Lithophragma* and *Heuchera* species (Davis et al. 1992; Thompson and Pellmyr 1992; Pellmyr et al. 1996). *Greya politella* is the most widespread and geographically complex of these *Greya* species. It is a locally host-specific, geographically differentiated complex of populations restricted to a small group of closely related *Lithophragma* species and *H. grossulariifolia.* Analysis of mitochondrial DNA restriction length polymorphisms and the sequencing of part of cytochrome oxidase-I in *G. politella* had suggested that this specialist insect probably originated on *Lithophragma* and that some populations later incorporated *H. grossulariifolia* in the part of its geographic range where it encountered this plant species complex (Brown et al. 1997). *Greya politella* pollinates and oviposits into *Lithophragma* populations (reproductively isolated to varying degrees) along the west coast of North America (Thompson and Pellmyr 1992; Thompson 1997). In northern Idaho and western Montana, where it encounters *H. grossulariifolia,* some populations use both of these plant taxa, although preliminary evidence suggests that local populations on the two hosts may not be panmictic (B. M. Cunningham and J. N. Thompson, unpublished data). Prior to this study, it was unknown whether the moths have been able to colonize both diploid and autotetraploid plants.

Fifth, attack on plants could be readily assessed. The whole life cycle of this moth is intimately associated with its local host plant. The moths are diurnal, and adult females spend much of the day and night resting on flowers of their host plant when not ovipositing, allowing the distribution of moths on host plants to be surveyed. Like its close relatives, the yucca moths, *G. politella* oviposits into the flowers of its host plant, and the larvae feed on the developing seeds (Pellmyr and Thompson 1992; Thompson and Pellmyr 1992). Hence, capsules can be collected from many sites and dissected for presence of eggs, larvae, or seed damage. No other insect feeds internally on the seeds of this plant species.

MATERIAL AND METHODS

Study Regions

Heuchera grossulariifolia grows primarily on steep rock faces and rocky soil along rivers and streams. The geographic distribution of *H. grossulariifolia* was grouped into 14 regions corresponding to the major separate river drainages or river systems, or geographically separated parts of major river drainage systems, in which this species complex occurs: St. Joe = St. Joe River; North Fork of Clearwater = North Fork of Clearwater River, lower Kelly Creek, and sur-

rounding tributaries; Lochsa = Lochsa River and tributaries; Lower Selway = Selway River from mouth upstream to Selway Falls; Upper Selway = upper Selway River near Magruder, Idaho, and surrounding creeks; South Fork of Clearwater = South Fork of Clearwater and tributaries; Upper Salmon = Salmon below North Fork, Idaho; Lower Salmon = Salmon River from Riggins east to Vinegar Creek; Rapid River = lower Rapid River; South Fork of Salmon = lower Secesh River, East Fork of South Fork of Salmon River, and section of South Fork connecting Secesh and East Fork; Payette = Middle Fork of the Payette, Silver Creek, and Clear Creek; Bitterroot and Clark Fork = Bitterroot River and tributaries, and Rock Creek and Schwartz Creeks off the Clark Fork River; Rye = Rye Creek off the Bitterroot River; West Fork of Bitterroot = West Fork of Bitterroot River and tributaries.

Flow Cytometry to Determine Plant Ploidy

We collected 855 rhizome samples from plants distributed over every major river system in which the plant occurs. We grew plants from these rhizomes in a greenhouse, and then determined the ploidy of each of them using flow cytometry to assess DNA content. Ploidy was determined by evaluating the DNA content of freshly cut leaves relative to a standard (rainbow trout red blood cells) using the methods described by Arumuganathan and Earle (1991) with two modifications: propidium iodide was not used in the chopping buffer, and 4% polyvinyl pyrrolidone–40 was added to remove phenolic impurities. Samples were analyzed on a Becton-Dickinson FACScan flow cytometer. Analysis of leaves, roots, and flowers of three plants indicated that DNA content is consistent among plant parts within individual plants. All plants gave clear peaks indicating diploid, tetraploid, or, in several instances, triploid DNA content (fig. 1).

Analysis of the original samples showed that diploids and tetraploids co-occurred in several river drainages. We therefore returned to those areas and sampled them more intensively to determine the local distribution of diploids and tetraploids. These analyses provided the basis for comparing the pattern of attack among neighboring populations differing in ploidy level.

Plant and Adult Moth Surveys

We surveyed plants ($n = 19{,}573$ plants) and adult moths along 215.9 km of 4-m wide transects within seven regions distributed over the geographic range of the *H. grossulariifolia* complex (table 1). Plants bloom over a 3–4-wk period within a region, and the surveys were conducted in each region during the middle of the flowering period. Surveys were conducted by walking along the transects and recording all flowering *H. grossulariifolia* clones separated by at least 0.5 m and all adult moths resting, nectaring, or ovipositing on the flowers. Because adult females spend the great majority of their adult lives resting on the flowers of their host plant when they are not ovipositing, these surveys provide a good minimum estimate of the use of *H. grossulariifolia* among river drainages.

Oviposition into Diploid and Tetraploid Flowers

We confirmed attack on plants by dissecting 5,209 floral capsules distributed among plants at 97 sites of single ploidy level distributed over the 14 regions
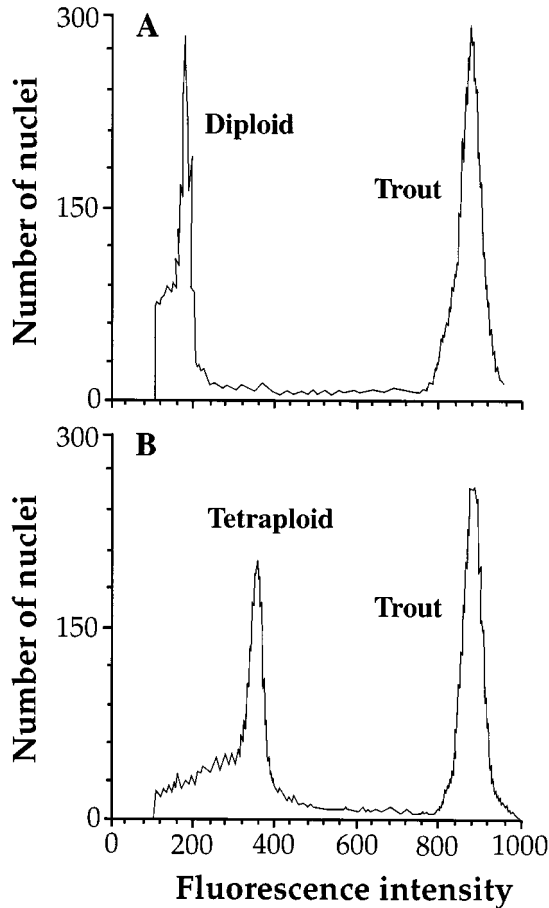
Fig. 1.—Examples of DNA content obtained by flow cytometry from diploid and tetraploid *Heuchera grossulariifolia* plants relative to a rainbow trout standard.

that had been analyzed for plant ploidy. These 14 regions encompassed all the major river drainage systems in which *H. grossulariifolia* commonly occurs, including the seven in which adults were censused. A site was a 0.5–1.0 km × 4 m wide section of a region. Each site was separated by at least 0.5 km from all other sites. At all these sites an initial sample of at least three plants was taken for analysis of plant ploidy, and more intensive sampling was done subsequently within the few drainages of mixed ploidy to assure that the local sampled population was only of one ploidy. All capsule collections were from sites in which only one plant ploidy level occurred. A current study of the morphology of diploids and tetraploids has identified several reliable differences in plants of different ploidy (K. A. Segraves and J. N. Thompson, unpublished data), and these differences were used as further verification that the plants within each sampling site were of a single ploidy level.

At each site, three capsules per plant were collected from up to 20 plants. Pre-

TABLE 1

SURVEYS OF ADULT *GREYA POLITELLA* MOTHS ON *HEUCHERA GROSSULARIIFOLIA*
FLOWERS ALONG 215.9 KM OF TRANSECTS CONDUCTED IN IDAHO
IN 1994 (EXCEPT AS NOTED)

River Drainage (North to South)	Ploidy	Transect Length (km)	Flowering Plants (*n*)	Adult Moths (*n*)	Average Number of Moths per 100 Flowering Plants
Lower Selway	Diploid	31.7	313	6	1.92
Upper Selway	Mixed	5.5	659	10	1.52
Upper Salmon	Diploid	30.7	843	24	2.85
Lower Salmon, 1994	Mixed	42.3	8,599	86	1.00
Lower Salmon, 1995	Mixed	42.3	3,796	90	2.37
Rapid River	Tetraploid	7.1	820	31	3.78
South Fork of Salmon	Diploid	15.9	1,439	56	3.89
Payette	Diploid	40.4	3,104	21	.67

NOTE.—Average number of adult moths per 100 flowering plants = (number of adult moths)/(number of flowering plants) $\times$ 100.

liminary analyses of 58 sites in which at least 60 capsules/site were dissected indicated that dissection of 40 capsules was sufficient to determine whether any plants were attacked at that site. Only sites in which 40–60 capsules were dissected were included in the analyses of the proportion of sites attacked.

RESULTS

Flow Cytometry

Analysis of plant ploidy using flow cytometry confirmed earlier work indicating the restricted geographic distribution of tetraploids (fig. 2) but showed more evidence of regions of mixed ploidy than was indicated by that study (Wolf et al. 1990). Polyploids occurred in western Idaho along lower Rapid River and adjacent parts of the Salmon River near Riggins, Idaho (fig. 3*A*). In eastern Idaho and western Montana, polyploids and diploids grew as mixed populations along the upper Selway River and along the West Fork of the Bitterroot River (fig. 3*B*). All other sampled populations were diploid, although several triploid plants were found amid diploids along the East Fork of the South Fork of the Salmon River in central Idaho (fig. 2), and several other triploids were found along the main stem of the Salmon River in the region where diploids and tetraploids come together (figs. 2, 3*A*). In all, 12 triploids were found amid the 855 sampled plants (1.4%).

Plant and Adult Moth Surveys

The 215.9 km of survey transects showed that adult moths occurred on plants in diploid, tetraploid, and mixed-ploidy regions (table 1). On average there were 2.3 (SD = 1.20, *n* = 8 surveys) adult moths per 100 plants among the 19,573 surveyed plants.
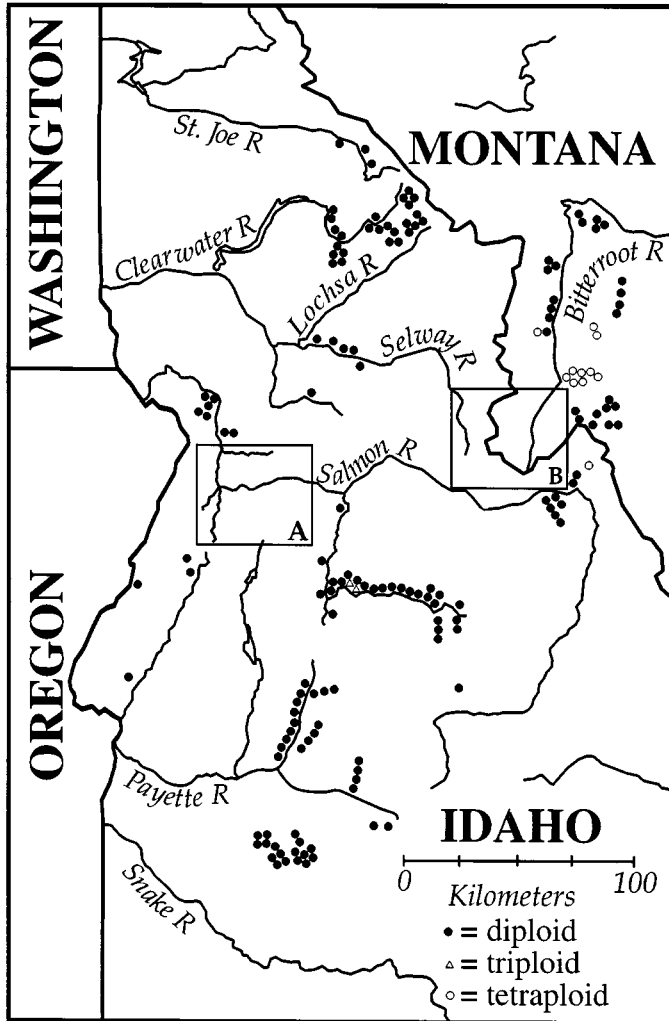
FIG. 2.—The geographic distribution of *Heuchera grossulariifolia* plants sampled for ploidy level. Each dot represents three sampled plants. Areas *A* and *B* are shown in detail in figure 3.

Oviposition into Diploid and Tetraploid Flowers

Dissections of floral capsules confirmed *Greya politella* attack on autotetraploid as well as diploid *H. grossulariifolia* individuals (table 2). Plants were attacked in all 14 regions and at 79.4% of the 97 sites, including regions with only diploids, only tetraploids, or a mix of the two ploidy levels (fig. 4*A, B*). The two purely tetraploid regions on the eastern and western edges of the geographic range had a lower percentage of capsules attacked than some other diploid and mixed regions in central Idaho (fig. 4*B*), but these percentages alone could not distinguish the effects of ploidy from other geographic causes.
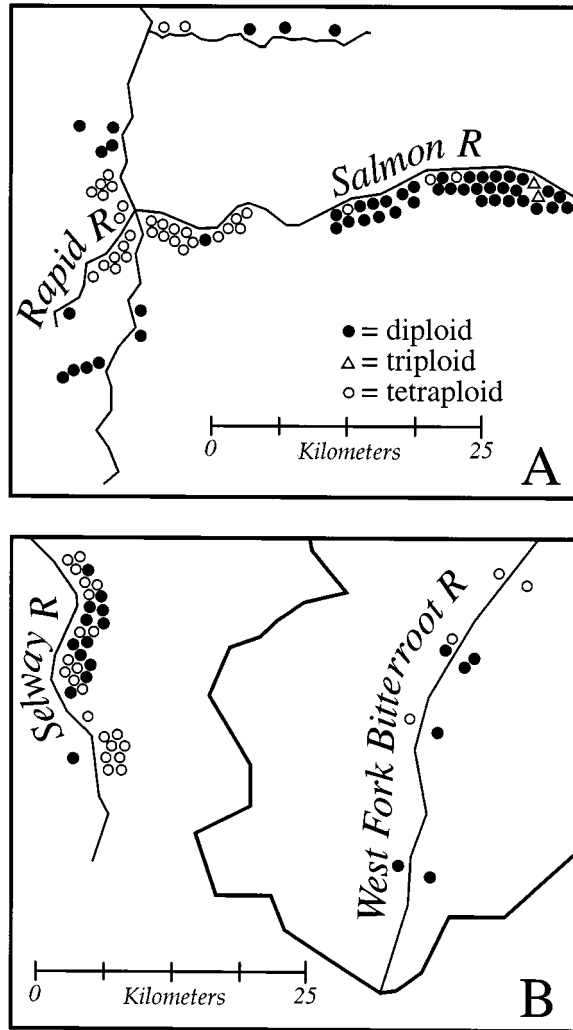
Fig. 3.—The areas in which diploid and tetraploid *Heuchera grossulariifolia* populations occur near to one another or overlap in geographic distribution: Rapid River/Salmon River; Upper Selway River; West Fork Bitterroot River. See figure 2 for geographic placement of these areas.

In three parts of the geographic range of *H. grossulariifolia,* however, diploids and tetraploids occurred together within a region or in two immediately adjacent regions, providing an opportunity for a more direct comparison of the effects of ploidy on attack (fig. 3*A, B*). One of these areas fell within the western Idaho origin of polyploid populations (Rapid River and Lower Salmon River) and the other two fell within the eastern Idaho and western Montana origin (Wolf et al. 1990). Analysis of these three sets of diploid/tetraploid pairs (fig. 5) indicated that plants at tetraploid sites were more likely to be attacked than

TABLE 2

The 14 Regions in Idaho and Western Montana Evaluated for Attack on *Heuchera grossulariifolia* by *Greya politella* through Dissection of Floral Capsules

	Number of Sites			Number of Capsules Dissected
River Drainage	Sampled	Attacked	Ploidy	
Idaho (north to south):				
St. Joe	3	3	D	180
North Fork of Clearwater	10	7	D	621
Lochsa	6	5	D	309
Lower Selway	7	7	D	506
Upper Selway	2	2	M	120
South Fork of Clearwater	8	4	D	479
Upper Salmon	6	6	D	372
Lower Salmon	12	10	M	768
Rapid	6	4	T	305
South Fork of Salmon	6	6	D	311
Payette	14	8	D	223
Montana (north to south):				
Bitterroot and Clark Fork	11	10	D	664
Rye	1	1	T	60
West Fork of Bitterroot	5	4	M	291
Total	97	77		5,209

Note.—D = diploid; T = tetraploid; M = mixture of diploids and tetraploids. Sample sizes shown for ploidy determination are only for the subset of locations in which floral capsules were collected. Overall sample sizes for geographic distribution of polyploidy are given in the text.

plants at diploid sites when they occurred near one another (nominal logistic regression, $P = .0056$, Wald $c^2 = 7.68$, df $= 1$) and that the chance of attack varied among regions ($P = .0035$, Wald $c^2 = 11.32$, df $= 2$). The interaction effect between region and ploidy was nonsignificant ($P = .73$, Wald $c^2 = 0.636$, df $= 2$).

DISCUSSION

We interpret the results conservatively as demonstrating that *Greya politella* has been able to colonize diploid plants and polyploid plants of separate origins in western Idaho and eastern Idaho/western Montana and, at least under some ecological conditions, tetraploids are more likely to be attacked than diploids. Hence, the results do not support the hypothesis that the evolution of polyploidy has acted as an evolutionary barrier to colonization by *G. politella.* Controlled experimental work will be needed to determine the causes for these differences in attack and whether tetraploids are consistently more likely to be attacked than diploids under all ecological conditions. Nevertheless, the results indicate clearly that the evolution of polyploidy in a plant taxon can be important in interpreting the geographic pattern of attack by insect herbivores.

Consistent differences in attack between ploidy levels could have any of several potential causes in the interaction between *Heuchera grossulariifolia* and *G. politella.* Current experiments on the life-history consequences of polyploidy in *H. grossulariifolia* indicate that tetraploids within some regions of mixed ploidy
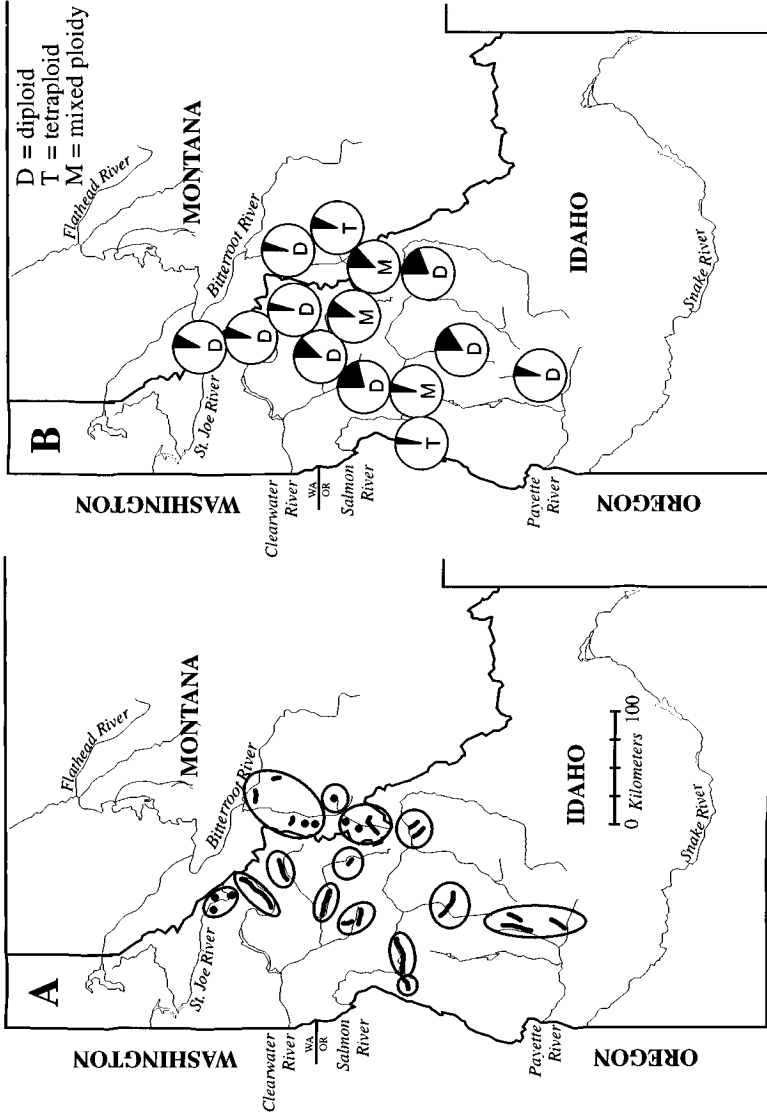
Fig. 4.—Study areas for distribution of attack by the moth *Greya politella* on diploid and autotetraploid *Heuchera grossulariifolia* plants. A, The 14 regions studied within and surrounding the wilderness core of Idaho and Montana. See "Material and methods" for more detailed descriptions of the river drainages included in each region. B, The ploidy of plants found within each region and the percentage of floral capsules attacked (blank region of each pie diagram).
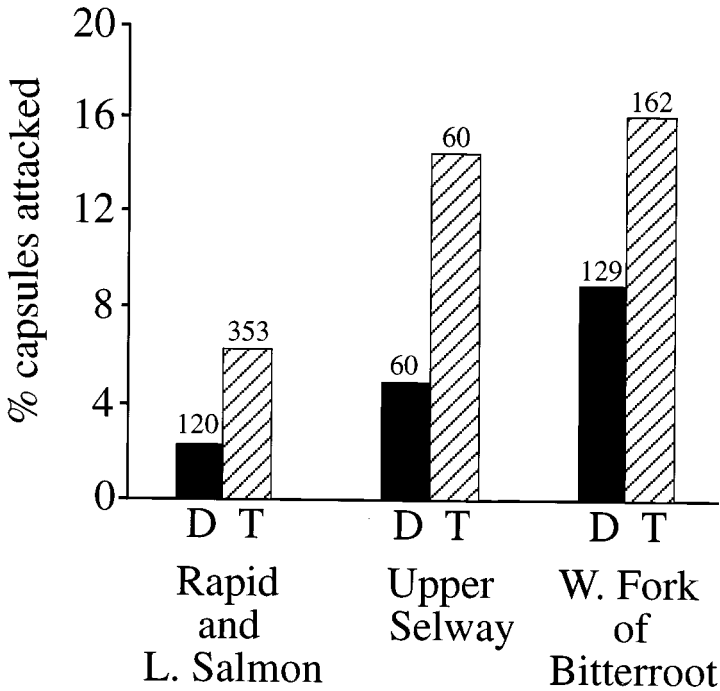
Fig. 5.—Comparison of *Greya politella* attack on diploid and tetraploid *Heuchera grossulariifolia* plants in the three geographic areas where plants of the two ploidy levels occur near one another or overlap in distribution (see fig. 3). Number of dissected floral capsules is given above each bar. Samples sizes for the Upper Selway and West Forest of the Bitterroot correspond directly to the values given in table 2. Sample sizes for Rapid and Lower Salmon are for all plants sampled along Rapid River (where all plants are tetraploid) and the tetraploid section of the Lower Salmon River as compared with plants from the known adjacent diploid section of the Lower Salmon River.

differ from diploids in some life-history and floral traits (K. A. Segraves and J. N. Thompson, unpublished data). For example, in some regions and in our common garden experiments, tetraploid plants generally flower earlier than diploid plants. As a result, flowering of tetraploids partially overlaps the flowering of *Lithragma parviflorum* (the other host of *G. politella* in Idaho and Montana), whereas flowering of diploids generally does not. Hence, there is more of a chance for some females from the local *L. parviflorum*–feeding subpopulations of *G. politella* to lay some eggs in tetraploid *H. grossulariifolia* plants than in diploid plants. The situation, however, is further complicated by recent preliminary results indicating that at least some *L. parviflorum*–feeding populations may not be panmictic with sympatric *H. grossulariifolia*–feeding populations, potentially indicating local host races of these moths. These studies of the complex genetic dynamics of the interactions between *G. politella* and its host plants will provide a basis for further work examining the mechanisms leading to higher attack on tetraploids.

The overall results showing *G. politella* attack both on diploid and autotetra-

ploid populations, and higher attack on tetraploids where plants of both ploidy levels co-occur, have implications for understanding the evolution of specialization in phytophagous insects and diversification of insect/plant interactions. There has been a long-standing argument in evolutionary biology over whether specialization is an evolutionary dead end or a dynamic property of species, expressed in different ways in different populations and subject to continuing natural selection toward greater or lesser specialization (Fox and Morrow 1981; Futuyma et al. 1993; Thompson 1994). *Greya politella* is a group of populations restricted to a small number of related plant species, with populations using different species in different parts of its geographic range. The results reported here indicate that, at least in some cases, a highly host-specific insect species may broaden its host range for some period of evolutionary time in parts of its geographic range as its host plant undergoes divergence through polyploidy. Those populations on novel polyploid hosts may be transient evolutionary events, routes to long-term expansion of host range, or the beginnings of populations that will diverge and become separate species.

Polyploid evolution may therefore play a crucial role in the ongoing evolutionary and geographic dynamics of insect/plant interactions, because polyploidy can change the phenotypic expression of traits and the evolutionary genetics of evolving traits from that observed in ancestral diploids. By having four alleles at a locus rather than two alleles per locus as in diploids, autopolyploid plants can differ from their diploid ancestors in enzyme levels, thereby affecting many aspects of plant physiology, morphology, and life history. Furthermore, mathematical models of autopolyploid populations differ inherently from diploids in the evolutionary dynamics of gene frequencies (Bever and Felber 1992), including the rate of loss of genetic variation within local populations because of random genetic drift (Moody et al. 1993).

Not only may the evolution of interactions between insects and autotetraploids differ from that between insects and the diploid ancestors of those tetraploids, but the evolutionary dynamics of interactions with autotetraploids may also differ from allopolyploids, again as a result of inherent differences in the population genetics (Bever and Felber 1992). Studies of the consequences of polyploidy on interspecific interactions will therefore require analyses of the separate genetic, ecological, and evolutionary effects of autopolyploidy and allopolyploidy.

Finally, recent studies have begun to indicate that the evolution of polyploidy is highly dynamic within some plant taxa, reinforcing the idea that polyploidy may contribute importantly to the geographic mosaic of evolving interactions between insects and plants. Molecular studies have now shown that multiple polyploid populations of different origin may develop from diploid ancestors in different parts of the geographic range of a plant species (Soltis and Soltis 1995; Ehrendorfer et al. 1996), and recent mathematical models have suggested that the ecological and genetic conditions under which a new polyploid can invade a diploid population are less restrictive than once thought (Rodriguez 1996). As indicated by the results for *G. politella,* some of these polyploids are likely to differ from their diploid ancestors in susceptibility to insect attack, setting up the conditions for a variety of alternative routes to the diversification of insect

populations, selection on plant traits, and the evolutionary trajectory of insect/plant interactions.

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