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Plant polyploidy and host expansion in an insect herbivore

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Abstract Polyploidization has played an essential role in the diversification of seed plants and often has profound effects on plant physiology and morphology. Yet, little is known about how plant polyploidization has shaped the ecology and evolution of interactions between phytophagous insects and their hosts. Polyploidization could either facilitate or impede colonization of new hosts. *Greya politella* (Lepidoptera: Prodoxidae) is highly specialized on plants in the genus *Lithophragma* (Saxifragaceae) throughout most of its geographic range. In central Idaho, some populations have shifted to the related *Heuchera grossulariifolia*, a plant that has repeatedly undergone autopolyploidization. Previous studies have shown that populations feeding natively on *H. grossulariifolia* prefer tetraploids to diploids in naturally mixed stands. We investigated whether this difference is caused by an inherent preference for tetraploids, or if the preference in present *Heuchera*-feeding populations has evolved over time. Moths from a strictly *Lithophragma*-feeding population were tested for preference of diploid or tetraploid *H. grossulariifolia*, using a combination of field experiments and caged choice trials. In all trials, attack rates on these non-hosts were very low, with no significant difference between ploidies. In addition, there was little evidence that females manipulated their clutch sizes when ovipositing into different plant species or ploidy levels. Hence, the local shift from *Lithophragma* to *Heuchera* in central Idaho is not due to failure of the moths to discriminate between these plant species. Furthermore, the higher attack rates on tetraploids in native *H. grossulariifolia*-feeding populations cannot be caused by a higher initial preference for these plants, but must

instead be a result of differences in plant phenology and/or selection acting on local populations.

Keywords Clutch size · *Greya politella* · Oviposition preference · *Saxifragaceae* · Specialization

Introduction

The repeated evolution of polyploidy has been one of the major causes of plant diversification; it has been estimated that as much as 70% of all angiosperm species have had polyploidization in their lineages (Masterson 1994). Closely related plant species differing in ploidy often differ in physiology, life history, morphology, and geographic distribution (Schoen et al. 1992; Thompson and Lumaret 1992; Bretagnolle and Thompson 1996; Segraves and Thompson 1999). As a result, the potential impact of polyploidization on interspecific interactions could be substantial. Nevertheless, the extent to which plant diversification through polyploidy influences interspecific interactions and the subsequent diversification of insect/plant relationships is still largely unknown. In some cases, it could lead to a higher resistance to herbivore or pathogen attack, possibly creating a barrier to colonization and thereby providing a means for the plant to escape from enemies (e.g., Reinert et al. 1986; Schoen et al. 1992; Busey et al. 1993). Alternatively, polyploidization could also lead to wider host ranges in some enemies, who continue to use plants of both ploidies as hosts, offering a route to increased diversification in host use (Thompson et al. 1997).

The geographically complex interactions between the pollinating, flower-feeding prodoxid moth *Greya politella* and its closely related host plants in Saxifragaceae provide a useful model system for studying the role of polyploidization in structuring species interactions and coevolution (e.g., Thompson 1997, 1999; Thompson et al. 1997; Segraves and Thompson 1999; Segraves et al. 1999). Throughout much of its geographic range, *G. politella* feeds exclusively on the genus *Litho-*

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phragma (Saxifragaceae). In central Idaho, some populations of *G. politella* have incorporated or shifted to the closely related plant *Heuchera grossulariifolia*. Recent studies have shown that *H. grossulariifolia* is a biogeographically complex set of diploid and autopolyploid populations, with up to seven possible separate origins of tetraploidy from diploid populations (Wolf et al. 1990; Seagraves et al. 1999). Although *G. politella* moths attack diploids and tetraploid plants, previous work has shown that the moths are more likely to attack tetraploids at sites with mixed ploidy (Thompson et al. 1997; Nuismer and Thompson 2001). Within all studied areas, nearby local moth populations also feed on the alternative host *L. parviflorum*.

The observed patterns could have arisen in any of several ways. *Lithophragma parviflorum*-feeding moths could have colonized both ploidy levels of *H. grossulariifolia* and later developed a preference for tetraploid plants. *L. parviflorum*-feeding moths may inherently prefer tetraploids to diploids. Or, *L. parviflorum*-feeding moths may show no preference among the two plant species, and the pattern results only because the tetraploids are more likely than the diploids to overlap in flowering time with *L. parviflorum*, thereby increasing the probability of attack on tetraploids. Distinguishing among these hypotheses is important for understanding if the origin of polyploidy has the potential to drive diversification of phytophagous insect species. Toward that end, we evaluate here whether a local population of *G. politella* that is confined to *L. parviflorum* is more likely to accept tetraploid than diploid *H. grossulariifolia* when offered plants of both ploidy levels.

Materials and methods

Study system and field site

The entire life cycle of the moth is closely associated with its host plant. The moths mate on the host and the females oviposit into the seed capsules, where the young larvae feed on the developing seeds. Hence, the potential for host-race formation is high (cf. Feder et al. 1994; Wood et al. 1999). After eating through the outer wall of the capsule, the larvae crawl down the stem to hibernate. After hibernation, the larvae feed on leaves and eventually pupate in the leaves.

A female lays its eggs in small clutches in the flower capsules of the host. To reach the seeds, a female must stretch down through the narrow flower, where her abdomen comes into contact with both stamens and stigma, thereby pollinating the plant. The extent to which the interaction is mutualistic or parasitic depends in part on the local presence of alternative pollinators (Thompson and Pellmyr 1992; Pellmyr and Thompson 1996).

Although *L. parviflorum* inhabits a wide range of open habitats, ranging from California to British Columbia, and eastward to South Dakota, *H. grossulariifolia* is endemic to the mountainous regions of Idaho and Montana (Brown et al. 1997) and grows primarily on steep rock faces and rocky soil along rivers and streams. The two host plants are sympatric in central Idaho, and the presumed shift from *L. parviflorum* to *H. grossulariifolia* has probably occurred in this region (Brown et al. 1997). Along the Salmon River in west central Idaho occur populations of *L. parviflorum* as well as diploid and tetraploid *H. grossulariifolia*. The plant species and ploidy levels overlap to different extents in different parts

of the river. Moth populations occur on both species and both ploidy levels of *H. grossulariifolia*, with local population levels of the moths varying considerably along the river (Seagraves et al. 1999).

The study site was located at the confluence of the Wind River and Salmon River. It is a south-facing slope, with locally dense patches of *L. parviflorum* growing among grasses and low herbs with scattered shrubs and trees. The site was chosen for several reasons. First, it is in the general geographic region where the shift from *Lithophragma* to *Heuchera* has probably taken place (Brown et al. 1997), providing a natural setting for the experiments. Second, the *G. politella* population at the Wind River site uses *L. parviflorum* exclusively. The nearest populations on *H. grossulariifolia* are found within a few kilometers from the site on the other side of the river, where plants of both ploidy levels occur. Third, the site has been included in a long-term project where *L. parviflorum* plants have been sampled for *G. politella* eggs for several years (J. N. Thompson and B. M. Cunningham, unpublished data), and where it is therefore known that a well-established local moth population occurs on *L. parviflorum*.

Survey of eggs on *L. parviflorum*

We investigated the background attack rates on the local natural host, *L. parviflorum*, by collecting seed capsules from plants throughout the study area. Four *L. parviflorum* plants were sampled around each pair of diploid and tetraploid *H. grossulariifolia* set out for field exposure trials (see next section of Materials and methods). Several to ten flowers are produced sequentially on one to two floral scapes, and we collected capsule 2, 3 and 4 from one floral stalk on each plant (Thompson et al. 1997). A total of 336 capsules from 112 plants were thus collected and dissected to search for eggs.

Field exposures of *H. grossulariifolia*

Diploid and tetraploid *H. grossulariifolia* were reared in a greenhouse in plastic boxes approximately 10×15×35 cm in size, so that flowering times of diploids and tetraploids could be as synchronized as possible. Each plant produces one or more flowering scapes. All but four of the flowering scapes were cut off the plants before they were exposed in pairs at the study site. Twenty-eight diploid/tetraploid pairs of *H. grossulariifolia* were placed within natural patches of flowering *L. parviflorum*, and the pairs were exposed to the moths for between 7 and 14 days, with a mean of 11.4 days. They were left out during the time of moth activity each day (the moths are strictly diurnal), but were moved to mesh cages during the nights, to protect them from being grazed by deer and bighorn sheep. At the end of each trial, all seed capsules were collected from the plants (4,923 capsules in total), and dissected to search for eggs.

Preference trials

We used two types of experimental protocols for testing oviposition preference: (1) a no-choice trial, where the female moths were presented with only one plant type, and (2) a pairwise choice trial, where both types of plants were presented to the ovipositing female simultaneously.

Female moths for the preference experiments were caught close to the study site, while avoiding collection within the patches used in the field exposure experiment. Experienced moths were used in the experiments to simulate the conditions likely in the shift from *L. parviflorum* to *H. grossulariifolia* in the U.S. northern Rockies: colonization of local populations of *H. grossulariifolia* by experienced moths searching for the much more abundant *L. parviflorum* plants in nearby sites. Females were caught from flowers of *L. parviflorum* in the afternoon the day before the initiation of the trial and were kept at cool ambient temperature during

Table 1 Patterns of attack by ovipositing *Greya politella* on natural stands of *Lithophragma parviflorum* compared with three experimental set-ups of *Heuchera grossulariifolia*: pairwise field exposures and caged choice- and no-choice preference trials

Host	<i>L. parviflorum</i>	<i>H. grossulariifolia</i>		No-choice trials		Choice trials	
	Field survey	Field exposures		Diploid	Tetraploid	Diploid	Tetraploid
		Diploid	Tetraploid				
Attacked scapes	49% (<i>n</i> =112)	5.4% (<i>n</i> =112)	2.7% (<i>n</i> =112)	21.4% (<i>n</i> =56)	23.2% (<i>n</i> =56)	20.6% (<i>n</i> =63)	23.8% (<i>n</i> =63)
Attacked capsules	21% (<i>n</i> =336)	0.3% (<i>n</i> =2,696)	0.2% (<i>n</i> =2,227)	2.1% (<i>n</i> =779)	1.5% (<i>n</i> =992)	3.4% (<i>n</i> =1,116)	1.8% (<i>n</i> =980)
Clutch size	4.5 (<i>n</i> =55, SE=0.3)	4.3 (<i>n</i> =7, SE=0.4)	4.2 (<i>n</i> =4, SE=1.1)	5.3 (<i>n</i> =12, SE=0.3)	9.2 (<i>n</i> =13, SE=0.8)	4.1 (<i>n</i> =13, SE=0.9)	5.1 (<i>n</i> =15, SE=0.9)

the night. This minimized differences in motivation between the wild-caught females that could otherwise bias the results of the no-choice trial. Females were placed individually in cages made from clear plastic tubes, 30 cm high and 8 cm in diameter. In the no-choice trials, one flowering stalk of either diploid or tetraploid *H. grossulariifolia* was placed in aqua-culture in the center of the tube and the cage was sealed with nylon mesh at the top and bottom to prevent the female from escaping. All trials were performed in the field, beginning in mid morning and ending 24 h later. Twenty trials were set up each day. The pairwise choice trials were set up in a similar manner as the no-choice trials, with two exceptions: one stalk each of both diploid and tetraploid *H. grossulariifolia* were placed in the same cage, and these experiments ran for 24–48 h. At the end of each trial, all seed capsules were collected (1,771 capsules in the no-choice trial and 2,042 in the choice trial) and dissected under a microscope to search for eggs.

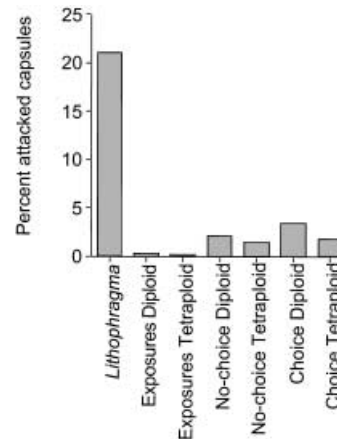
Results

Survey of *L. parviflorum*

The attack rate on the Wind River population of *L. parviflorum* that surrounded the field exposures of *H. grossulariifolia* was 49% (*n*=112), measured as the proportion of flowering stalks that were attacked, and 21% (*n*=336), measured as the proportion of capsules with eggs, across plants (Table 1). Clutch sizes varied between one and 13 eggs, with a mean of 4.5 (*n*=55, SE=0.3).

Field exposures

In contrast to the very high background rates of attack on *L. parviflorum*, attack rates on both diploid and polyploid *H. grossulariifolia* pairs set amid the *L. parviflorum* plants were very low (Table 1). Of the 4,923 capsules dissected, only nine were attacked, i.e., 0.2% of the capsules, and only 4% of the scapes had eggs in them. Diploid capsules received 30 eggs (seven clutches on six plants), whereas tetraploid capsules received 17 eggs (four clutches on three plants). Hence, in the presence of neighboring *L. parviflorum* plants, the moths were reluctant to oviposit into either diploid or tetraploid *H. grossulariifolia*.

**Fig. 1** Percent attacked capsules by ovipositing *Greya politella* on natural stands of *Lithophragma parviflorum* compared with three experimental set-ups of diploid and tetraploid *Heuchera grossulariifolia*: pairwise field exposures and caged choice- and no-choice preference trials

Preference trials

Attack rates were low in the no-choice trials as well, although considerably higher than in the field exposures (Table 1). Among the 1,771 capsules dissected from the 64 pairs of diploid and tetraploid *H. grossulariifolia*, eggs were found in 31 capsules from 25 scapes (1.8% of the capsules and 19% of the scapes). There was no significant difference in the number of attacks on diploid and tetraploid *H. grossulariifolia* capsules in the no-choice trials (Fig. 1; logistic regression, *n*=128, *df*=1, $\chi^2=0.05$, *P*=0.82) or in the total number of eggs oviposited (Mann-Whitney *U*-test, *n*=128, *U*=1973.0, *P*=0.61). However, the moths laid significantly larger clutches on tetraploids than on diploids (Mann-Whitney *U*-test, *n*=25, *U*=14.5, *P*<0.001). Mean clutch size (\pm SE) for diploids was 5.3 (\pm 0.3) whereas tetraploid clutches averaged 9.2 (\pm 0.8) eggs (Fig. 2).

Attack rates in the pairwise simultaneous choice trials were similar to the no-choice trials (Table 1). Among the 63 pairwise choice trials, eggs were found on 28 plant scapes (22%) and 56 of the 2,042 capsules were attacked

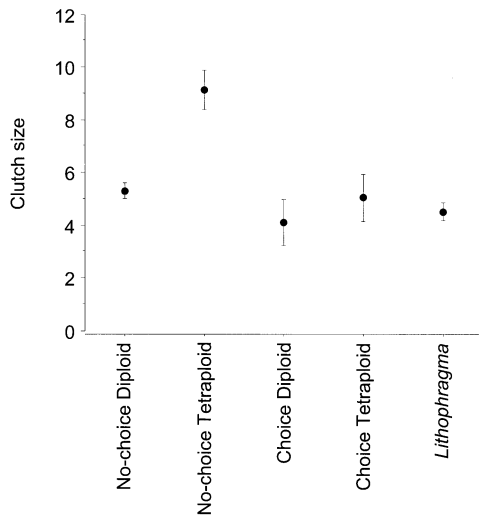


Fig. 2 Mean clutch size (\pm SE) on three experimental set-ups of diploid and tetraploid *H. grossulariifolia*: pairwise field exposures and caged choice- and no-choice preference trials, and on natural stands of *L. parviflorum*

(2.7%). Once again, there was no difference between diploids and tetraploids in neither number of attacks (sign test, $P > 0.99$) nor in total number of eggs oviposited [Wilcoxon signed rank test, N (no. of valid ranks)=23, $Z = -1.14$, $P = 0.25$]. Unlike the no-choice trials however, there was no significant difference in clutch size [Wilcoxon signed rank test, N (no. of valid ranks)=23, $Z = -0.78$, $P = 0.44$].

Discussion

General attack rates

Although the background attack rate on the local host plant *L. parviflorum* was high, even in relation to other years at the same site (J. N. Thompson and B. M. Cunningham, unpublished data), the moths were reluctant to oviposit on *H. grossulariifolia*. Almost half of the *L. parviflorum* plants in the survey carried *G. politella* eggs, but the exposed *H. grossulariifolia* plants only had a total of around 3–5% of their flowering scapes attacked (Table 1).

The present study suggests that the differential use of tetraploid *H. grossulariifolia* within natural populations along the Salmon River does not result from an intrinsic preference of *L. parviflorum* moths to attack tetraploids rather than diploids. We were not able to detect any significant difference in oviposition preference for the two ploidies (Fig. 1).

Colonization of *H. grossulariifolia*

Despite the overall reluctance of the moths to use *H. grossulariifolia*, some moths did oviposit into these

plants both in the field exposures and in the oviposition trials. This suggests that the initial incorporation of *H. grossulariifolia* as a host plant in the U.S. northern Rockies need not have involved new mutations that allowed females to recognize either diploid or tetraploid plants as potential hosts. There is no indication that polyploidization in *H. grossulariifolia* renders the polyploids either more or less susceptible to initial attack by *G. politella* adapted to *L. parviflorum*. Thus, if the ecological conditions were right, the Wind River population could conceivably colonize *H. grossulariifolia* of both ploidies. Insect colonization and use of novel hosts have been documented repeatedly (e.g., Tabashnik 1983; Thomas et al. 1987; Carroll and Boyd 1992; Thompson 1993; Singer et al. 1994; Fox et al. 1997). Novel host associations can be caused by any combination of changes in local insect preference, local plant resistance, or local plant availability (Singer and Parmesan 1993; Singer and Thomas 1996).

Two previous studies have shown that *H. grossulariifolia*-feeding populations of *G. politella* preferentially attack tetraploid *H. grossulariifolia*. Thompson et al. (1997) showed higher overall attack on tetraploid *H. grossulariifolia* within three separate geographic areas where diploid and tetraploid plants occur sympatrically. These three geographic areas correspond to three separate origins of polyploidy in *H. grossulariifolia* (Segraves et al. 1999). Consequently, there appears to be something about polyploidy per se rather than the genetics of a particular tetraploid population that has favored this higher level of attack.

More recently, Nuismer and Thompson (2001) undertook a more detailed study of preference for plants of a particular ploidy by analyzing the pattern of attack on pairs of diploid and tetraploid plants set out in the field in a *H. grossulariifolia*-feeding population. This paired experiment controlled for microhabitat and timing of floral availability and was repeated each year over 4 years (1997–2000). Tetraploid plants were much more heavily attacked in 3 of the 4 years, with attack rates reaching almost 80% (~45% for diploids) under the same year that the present study was carried out. The population that was studied during those 4 years occurs approximately 6 km away and across the river from the current study.

If the results from the Wind River population turn out to be generally true, the previously documented preference for tetraploids over diploids in moth populations living on *H. grossulariifolia* may have evolved in situ, probably several times in parallel. Apparently, the role of polyploidization in the shift from *L. parviflorum* to *H. grossulariifolia* is not straightforward. It would seem that the different ploidies are equally possible as novel hosts for a *Lithophragma*-feeding population, but tetraploids may be favored by natural selection over time. *Lithophragma* produces flowers earlier in spring than *Heuchera*, but tetraploid *H. grossulariifolia* generally begins flowering before diploid plants. Tetraploid *H. grossulariifolia* are therefore more likely to overlap with late-flowering *L. parviflorum* at the same site than are diploids, thus making the shift to tetraploids more likely.

Yet another factor potentially favoring higher use of tetraploid *H. grossulariifolia* over diploids in natural populations along the Salmon River may be differences in nectar composition or other floral attractants. The moths use the same plants as both nectar source and larval host plant. Consequently, an interaction between nectar search and oviposition site search may play a role in shaping the evolution of tetraploid preference. Earlier work along the Salmon River demonstrated that diploid and tetraploid *H. grossulariifolia* differ in floral morphology (Segraves et al. 1999). Moreover, a recent study carried out <10 km away from the current study, showed that neighboring pairs of tetraploid and diploid plants consistently attract different suites of floral visitors, including *G. politella*. In fact, *G. politella* visited flowers of tetraploids about 5 times more frequently than flowers of diploids (Segraves and Thompson 1999).

It is also interesting that the moths had such a low relative preference for *H. grossulariifolia* as compared to *L. parviflorum*. We still do not know if the much higher attack rates on *H. grossulariifolia* in populations that have undergone the shift (Nuismer and Thompson 2001) is caused by a change in relative preference, or if it is entirely caused by local unavailability of the ancestral host. The two host species of *G. politella* typically occupy different habitat types, and colonization of *H. grossulariifolia* in this area may have allowed *G. politella* to expand into new habitat types, without necessarily losing the preference for the ancestral host. Future work should ask whether the different attack rates are caused by changes in relative preference or different host availability (cf. Tabashnik 1983; Thomas et al. 1987; Singer and Thomas 1996).

Clutch size

There was no strong evidence for clutch size regulation in response to host plant quality; clutches were similar in size on the native host *L. parviflorum* as on *H. grossulariifolia* of both ploidy levels (Table 1) under most field and experimental conditions. The only evidence for clutch size manipulation was in the no-choice trials in which the tetraploid *H. grossulariifolia* received substantially larger clutches than did flowers under all other conditions tested. There was no corresponding difference in the pairwise choice trials, or in the field exposures (but here the sample size was very small).

The larger clutch sizes on tetraploid *H. grossulariifolia* in the no-choice trials are puzzling and could of course reflect a chance significance. However, the difference is highly significant. If borne out by future studies, it could have two potential causes. The most commonly demonstrated type of clutch size regulation (e.g., Pilson and Rausher 1988; Vasconcellosneto and Monteiro 1993; Fox et al. 1996) is adjustment to size or quality of the resource (such as seed capsule size) and should thus typically be positively correlated with host

preference. Polyploid flowers are significantly larger than diploid flowers of *H. grossulariifolia*, for this particular origin of polyploidy along the Salmon River (Segraves and Thompson 1999), thereby providing potentially more resources for developing larvae. Nevertheless, the moths laid larger clutches on polyploid *H. grossulariifolia* only in the no-choice trials. Hence, differences in floral size are unlikely to be the sole explanation for the results.

Another possible explanation could be that clutch size is a function of egg load or time since last oviposition (e.g., Pilson and Rausher 1988; Agnew and Singer 2000), as would be the case if the female always lays all her mature eggs at each oviposition (Rosenheim and Hongkham 1996). As time since last oviposition increases, the female will be more likely to accept lower-ranked hosts. Consequently, if egg maturation proceeds continuously during the female's lifetime, she would lay larger clutches on these lower ranked hosts. Hence, increased clutch sizes would be a response to long host-searching times (cf. Agnew and Singer 2000). If this were the case, one would expect a negative correlation between host plant preference and clutch size in no-choice trials (where the females have no alternative hosts), but not in choice trials or field surveys (if they have access to alternative hosts). The necessary life history data needed to evaluate these hypotheses are still not known for *G. politella*. Still, whatever the mechanism may be, the tendency to lay larger clutches in tetraploid *H. grossulariifolia* could facilitate the build-up of populations on tetraploids in the field.

Conclusion

Overall, these results suggest that the high levels of attack found on *H. grossulariifolia* within natural populations along the Salmon River have not developed simply from the failure of moths to discriminate between this species and *L. parviflorum*. At the same time, the higher levels of attack of tetraploids in comparison to diploids within natural *H. grossulariifolia* populations do not seem to result from an intrinsic preference of *L. parviflorum*-feeding moths for tetraploid *H. grossulariifolia*. Instead, the patterns of attack among these two plant species, and two ploidy levels of one of the species, is likely a complex evolutionary result of selection acting on local populations of moths that have different degrees of access to the different hosts.

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