REVIEW

Autopolyploidy in angiosperms: have we grossly underestimated the number of species?

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Many species comprise multiple cytotypes that represent autopolyploids, or presumed autopolyploids, of the basic diploid cytotype. However, rarely has an autopolyploid been formally named and considered to represent a species distinct from its diploid progenitor (*Zea diploperennis* and *Z. perennis* represent a rare example). The major reasons why autopolyploids have not been named as distinct species are: (1) tradition of including multiple cytotypes in a single named species; and (2) tradition and convenience of adhering to a broad morphology-based taxonomic (or phenetic) species concept. As a result, plant biologists have underrepresented the distinct biological entities that actually exist in nature. Although it may seem "practical" to include morphologically highly similar cytotypes in one species, this practice obscures insights into evolution and speciation and hinders conservation. However, we do not suggest that all cytotypes should be named; each case must be carefully considered. A number of species comprising multiple cytotypes have been thoroughly investigated. Drawing on the literature, as well as our own experience with several autopolyploids (*Tolmiea menziesii*, *Galax urceolata*, *Chamerion angustifolium*, *Heuchera grossulariifolia*, *Vaccinium corymbosum*), we reassess the traditional view of plant autopolyploids as mere cytotypes. When considered carefully, many "unnamed" autopolyploids fulfill the requirements of multiple species concepts, including the biological, taxonomic, diagnosability, apomorphic, and evolutionary species concepts. Compared to the diploid parent, the autopolyploids noted above possess distinct geographic ranges, can be distinguished morphologically, and are largely reproductively isolated (via a diversity of mechanisms including reproductive and ecological isolation). These five autopolyploids (and probably many others) represent distinct evolutionary lineages; we therefore suggest that they be considered distinct species and also provide a system for naming them.

KEYWORDS: autopolyploidy, nomenclature, polyploidy, species, sympatric speciation, taxonomy

POLYPLOIDY IN PLANTS

Genome doubling (i.e., polyploidy) has frequently been associated with evolution and diversification in plants and has been a major factor in the evolution of other lineages of eukaryotes, including yeast (Kellis & al., 2004) and many groups of vertebrates and invertebrates (reviewed in Levin, 2002; Wendel & Doyle, 2005; Adams & Wendel, 2005; Gregory & Mable, 2005; Tate & al., 2005). Polyploidy in angiosperms has been studied for nearly a century, dating to the early genetic work of De Vries on the angiosperm *Oenothera lamarckiana* mut. *gigas* (Onagraceae), which was discovered to be a tetraploid (Lutz, 1907; Gates, 1909), and to the early suggestion of an ancient chromosome duplication in maize (*Zea mays*) (Kuwada, 1911). Early reviews of polyploidy in plants include those by Müntzing (1936), Darlington (1937), Clausen & al. (1945), Löve & Löve (1949), and Stebbins (1947, 1950, 1971, 1985). Following the work of Stebbins (1947, 1950) and Grant (1971, 1981), polyploidy became a major focus of biosystematic research. As a result, plant scientists have long recognized that polyploid lineages may show complex relationships with each other and their diploid ancestors, making application of species concepts problematic.

Systematists and evolutionary biologists have typically recognized two general categories of polyploidy, allopolyploidy and autopolyploidy. Although the definitions and boundaries of these have been controversial

(Kihara & Ono, 1926; Clausen & al., 1945; Lewis, 1980; Jackson, 1982; reviewed in Soltis & Rieseberg, 1986; D. Soltis & Soltis, 1993, 1999; Levin, 2002; Ramsey & Schemske, 2002; Bennett, 2004; Tate & al., 2005), following the taxonomic definition, autopolyploids are generally considered to be derived from within a single species, whereas allopolyploids arise via hybridization between two species. Allopolyploidy has long been considered more important than autopolyploidy in natural populations of angiosperms (e.g., reviewed in D. Soltis & Soltis, 1993, 1999; P. Soltis & Soltis, 2000).

The past decade has seen a dramatic resurgence in the study of polyploidy (e.g., see volume edited by Leitch & al., 2004; also reviewed in Soltis & al., 2004; Adams & Wendel, 2005; Tate & al., 2005; Wendel & Doyle, 2005), with renewed interest in the mechanisms of polyploid formation and establishment (Ramsey & Schemske, 1998, 2002; Husband, 2004), the frequency of recurrent polyploidization (e.g., D. Soltis & Soltis, 1999; P. Soltis & Soltis, 2000), the ecological effects of plant polyploidy (reviewed in Thompson & al., 1997, 2004), and the genetic, epigenetic, chromosomal, and genomic consequences of polyploidization (e.g., Liu & Wendel, 2003; Bowers & al., 2003; Osborn & al., 2003; Leitch & Bennett, 2004; Adams & Wendel, 2005; Rapp & Wendel, 2005). Such work has increased our knowledge of autopolyploid dynamics and elevated estimates of the frequency of autopolyploids in natural populations (D. Soltis & Soltis, 1993, 1999). However, the recognition of autopolyploidy as a major speciation mechanism has not been part of these recent developments.

Here we summarize the historical treatment of autopolyploidy in systematics and evolutionary biology. We then discuss criteria that would establish autopolyploids as distinct species, and present examples for a number of systems where autopolyploids appear to meet these criteria. We conclude that autopolyploidy is an important mechanism of speciation in plants (see Lewis, 1980; D. Soltis & Soltis, 1993; Ramsey & Schemske, 1998), and that the failure to name autopolyploids as separate species has resulted in a serious underestimate of the role of polyploidy in plant speciation. This is particularly significant, given that polyploids are produced in sympatry with their progenitor cytotypes, and thus polyploid species are unambiguously the product of sympatric speciation, a mechanism that has been the subject of longstanding debate in the study of speciation in animals.

POLYPLOIDY AND SYMPATRIC SPECIATION

Evolutionary biologists have long struggled with the importance and prevalence of sympatric speciation. Reviews have provided few concrete examples of sympatric speciation in animals (see Futuyma, 1998; Coyne & Orr, 2004; but see Savolainen & al., 2006). Examples include a Darwin's finch, *Geospiza conirostris* (Grant & Grant, 1979); indigo birds, *Vidua* spp. (Sorenson & al., 2003); crater lake cichlids, *Amphilophus* (Schliewen & al., 1994); and host-plant races of the apple maggot, *Rhagoletis pomonella* (Filchak & al., 2000), European corn borer, *Ostrina nubilialis* (Thomas & al., 2003), and pea aphid, *Acyrthosiphon pisum* (Via, 1999). Mechanisms of sympatric speciation proposed in animals include host switching (e.g., Sorenson & al., 2003; Thomas & al., 2003), as well as assortative mating and disruptive selection (e.g., Udovic, 1980; Turner & Burrows, 1995; Kondrashov & Shpak, 1998; Kondrashov & Kondrashov, 1999; Doebeli & Dieckmann, 2000; Via, 2002; Via & Hawthorne, 2002; Arnegard & Kondrashov, 2004; van Doorn & al., 2004). Although long considered rare in animals, sympatric speciation is considered relatively common in the plant world (e.g., Schemske, 2000), a view prompted by the frequent occurrence of polyploidy in plants.

The association between polyploidy and speciation traces to De Vries (1901, 1905). Well known for his contribution to the mutationist theory, De Vries argued that species arise instantaneously through abrupt and discontinuous mutations, which he observed as sports or spontaneous variants. Much of his work was based on observations of *Oenothera* and one particular variant called "gigas" that was generally larger than its parent, *O. glazioviana* Micheli (Syn: *O. erythrosepala* Borb., *O. lamarkiana* De Vries) (De Vries, 1905). This mutant was shown to possess twice the normal somatic chromosome number of 14 and is possibly the first documented example of a polyploidization event in plants (Gates, 1909). In opposition to Darwin's natural selection, De Vries (1901) and others argued that mutations such as this led to the spontaneous origin of new species and that "the ordinary or so-called individual variability can not…lead to a transgression of the species border…" (Mayr, 1982).

Since the Modern Synthesis, autopolyploidy has generally been ignored as a significant mechanism of speciation. Grant (1981) devoted one section of *Plant Speciation* to what he termed "biotically sympatric speciation." His introduction to the topic is still appropriate today: "The problem before us here is whether primary divergence to the species level can take place within the limits of a single breeding population. This is a long-standing, much debated, and unsettled question (pg. 163)." Under "Modes of Speciation," Grant (1981) recognized four types of biotically sympatric speciation but autopolyploidy was not included. In contrast, Lewis (1980) did recognize the importance of autopolyploidy, indicating that "…it contributes markedly to the evolu-

tionary process leading to speciation, particularly among herbaceous perennials…"

There appear to be two main reasons for the widespread omission of autopolyploidy as a recognized speciation mechanism. First, autopolyploidy was traditionally considered extremely rare in nature. Grant (1981) reviewed the earlier survey of Clausen & al. (1945) who recognized only three clear-cut autopolyploids—*Galax aphylla* (= *G. urceolata*), *Biscutella laevigata*, and *Zea perennis*—and only four additional probable autopolyploids—*Vaccinium uliginosum*, *Eragrostis* pallescens, and *Galium mollugo* and *G. verum*. Stebbins (1950) considered *Galax aphylla* (= *G. urceolata*) the only "clear-cut autopolyploid." Other authors have similarly considered autopolyploid species to be very rare. A second, more prominent reason why autopolyploidy has not been considered an important speciation mechanism involves the longstanding adherence of plant systematists to a strict taxonomic (= subjectively applied phenetic approach, stressing morphological features) species concept in which diploids and autotetraploids, as well as other ploidal levels, have traditionally been considered conspecific—as cytotypes of a single species. This approach appears to have been based on the strong morphological similarity of cytotypes and a belief that they were not completely reproductively isolated (Müntzing, 1936; Stebbins, 1950; Grant, 1981; J.D. Thompson & Lumaret, 1992). In his classic treatment on the "evolutionary significance of autoploidy," Müntzing (1936) discussed autopolyploids at length, but he did so under the heading "Intraspecific Chromosome Races."

Löve and Löve (as summarized in Löve, 1964) may have been the only early investigators to advocate strongly that autopolyploids represent distinct species, stating that, like allopolyploids, they are good biological species. Löve (1964) further noted in comparing diploids and autopolyploids that "their few differences rather than perhaps many similarities ought to be strongly stressed…"

There is abundant theoretical evidence that autopolyploidy represents a mechanism of sympatric speciation. As numerous authors have noted, the newly formed autotetraploid must immediately contend with its diploid progenitor (Stebbins, 1950; Grant, 1981; Levin, 1983; D. Soltis & Soltis, 1993). Simulation studies suggest that the conditions that would permit the newly formed autotetraploid to become established are restrictive (Fowler & Levin, 1984; Felber, 1991). The new autopolyploid must either out-compete the diploid parent or establish a new niche. However, the role of geographic separation in the divergence of a polyploid from its diploid parent has not been well tested (Fowler & Levin, 1984). Other simulations indicate that the fate of a tetraploid in a diploid population may vary qualitatively, depending on the relative fitness of triploids, the ploidies of the gametes produced by triploids, the strength of assortative mating (Husband & Sabara, 2003), and the fitness of tetraploids relative to diploids (Husband, 2004). Thus, it is likely that after formation, an autopolyploid cannot persist as a successful lineage unless largely reproductively isolated from its diploid progenitor.

During the past 15 years the polyploidy paradigm has been dramatically altered. Genetic markers have documented that autopolyploidy, based on the presence of tetrasomic or higher-level polysomic inheritance, is much more prevalent in natural populations than proposed by Stebbins (1950), Grant (1971, 1981), and early investigators such as Müntzing (1936) and Darlington (1937) (but see Harlan & De Wet, 1975). In fact, tetrasomic (or higher-level polysomic) inheritance may be one of the most useful criteria for distinguishing autopolyploids from allopolyploids (Soltis & Rieseberg, 1986). Although mode of inheritance clearly depends on chromosomal factors, cytogenetic criteria such as chromosomal pairing relationships cannot be used to distinguish autopolyploids, as species may have bivalent pairing but still display polysomic inheritance through random association of homologs (e.g., Soltis & Rieseberg, 1986; Qu & al., 1998). Thus, if we relied solely on cytogenetic characters we would underestimate the occurrence of autopolyploidy because some display bivalent formation. Although generally considered less prevalent than allopolyploidy, autopolyploidy is certainly quite common, at least in some groups of species (Löve, 1967). Ramsey & Schemske (1998) estimated that rate of autotetraploid formation is high—comparable to the genic mutation rate. Furthermore, autopolyploidy may be particularly prevalent in certain families, for example Saxifragaceae (Soltis, 2006) and Cactaceae (Hamrick & al., 2002).

Lessons from the past. — Although multiple cytotypes exist within many taxonomic plant species, only a small proportion of these have been studied in any detail, and many or most are now presumed to represent autopolyploids. Müntzing (1936) considered some of the key features of these cytotypes. While considering the cytotypes to represent "chromosome races" rather than species, he stated, "In some cases, of course, it is difficult to decide where the species limits should be drawn and consequently, whether we have to deal with intraspecific chromosome races or with closely related, but separate species." In considering 58 examples, Müntzing asked many of the same questions that remain of interest today and that we again ask here: (1) Are the chromosome races morphologically different? (2) Are the chromosome races ecologically identical or different? (3) Are the chromosome races separated by barriers of incompatibility and sterility? (4) Are the chromosome races to be considered as auto- or allopolyploid?

It is useful to reconsider Müntzing's (1936) results 70 years later. Importantly, he reviewed cytological data and concluded that intraspecific chromosome races are generally autopolyploid. He also concluded that "intraspecific chromosome races are practically always morphologically more or less different from each other"; he goes on to state that "…not a single case is known in which it has been demonstrated that the races are morphologically identical." Both quantitative and qualitative morphological differences may be present, but "the great majority of species consist of races that are quantitatively different." Differences he noted included seed size, flower size, plant size, and leaf size.

Significantly, Müntzing also concluded that "chromosome races are probably always ecologically different." This distinctiveness is reflected either in the ecological characteristics of the cytotypes, or in their different geographic distributions. Of the 58 chromosome races that Müntzing considered, crossing experiments had been undertaken for only 14. Nonetheless, Müntzing found that "chromosome races are generally separated from each other by barriers of incompatibility and sterility." Thus, Müntzing summarized substantial data for a diverse array of taxa with multiple chromosome races and provided compelling evidence that most were reproductively isolated; furthermore, most seem to represent separate lineages with distinct evolutionary trajectories (i.e., evolutionary species; see below). Nonetheless, following the tradition of that time (as well as that of the present day), he maintained these cytotypes as races within a single species.

Insights from the California Flora. — Further insight into the possible frequency of autopolyploidy, as well as the number of unnamed polyploid species, has been provided using the California Flora as a database (J. Ramsey & B.C. Husband, unpublished). Of 2,647 species from 346 genera in 62 angiosperm families, 334 species (13%) have multiple cytotypes (i.e., clear 3*x*, 4*x*, or higher multiples of the base chromosome number for the genus). Most of these are presumed to be autopolyploids, but all would require careful study. Because some of these 334 chromosomally polymorphic taxonomic species actually have more than two cytotypes, if each cytotype represented a distinct species, the total number of unrecognized species is actually 483. We feel that this or any estimation of the occurrence of multiple cytotypes from the literature (e.g., *The Jepson Manual;* Hickman, 1993) could be a low minimum estimate. When taxonomic species are studied cytologically in detail across their geographic ranges, new polyploids within species are often detected. At least some of those instances of polyploidization within a species are likely to involve multiple origins of polyploidy (see below), further increasing the number of polyploid lineages. On the other hand, multiple cytotypes may, nonetheless, truly be conspecific, as a result of frequent gene flow between cytotypes, e.g., resulting from the frequent production of unreduced gametes (e.g., *Dactylis glomerata*, J.D. Thompson & Lumaret, 1992; *Hyla versicolor*, Holloway & al., 2006). The true number of unrecognized polyploid species is therefore difficult to assess, and specific status for any given polyploid must be determined on a case-by-case basis.

AUTOPOLYPLOID SPECIATION

Reviews of polyploidy and speciation by Grant (1981), Stebbins (1950, 1971), and other authors make it clear that researchers typically do not consider autopolyploidy to result in the formation of new species. The phrase "autopolyploid speciation" is, in fact, rarely used in the literature (e.g., Ramsey & Schemske, 1998; Soltis & Rieseberg, 1986; D. Soltis & Soltis, 1993, 1999). Whereas there are numerous examples in plants of multiple ploidal levels included within a single taxonomic species, examples in which both a diploid and its autotetraploid derivative have been named as distinct species are rare. Perhaps the only example involves *Zea perennis,* a tetraploid ($2n = 40$). Iltis & al. (1979) discovered and described a diploid ($2n = 20$) species, *Zea diploperennis,* that is morphologically similar to *Zea perennis*. *Zea perennis* is now generally thought to be an autotetraploid derivative of a *Zea diploperennis*-like ancestor (reviewed in Tiffin & Gaut, 2001).

The view of diploids and autopolyploids as representing "races" within a single species persists. For example, J.D. Thompson & Lumaret (1992) stated "but in the case of autopolyploids, polyploidy may simply represent a microevolutionary process generating and maintaining genetically based variation within individual species." They further stated that "…reproductive isolation as a result of autopolyploidy may be insufficient for the maintenance of a completely independent unit. In such cases polyploidy is not a mechanism of speciation." This statement summarizes well some of the rationale behind the longstanding tradition among plant biologists to consider autopolyploids as merely cytotypes of a diploid species complex. But is this statement truly representative of all or most plant autopolyploids? Are these cytotypes reproductively isolated? Are they distinct evolutionary units? Do they conform to any of the variously recognized species concepts (e.g., biological, phylogenetic, taxonomic, etc.)? If the answer to most of these questions is yes, then many autopolyploids should be named as distinct species.

Lewis (1980) also considered the issue of naming autopolyploids. His statement of 25 years ago remains

appropriate today. "How to differentiate infraspecific polyploids … is not a simple task. Speciation may have proceeded sufficiently in some instances to designate confidently populations of sibling species with appropriate Latin binomials, but in others no significant and readily detectable… changes may yet accompany polyploidy. In these cases there is little justification for insisting that taxonomy reflect the polyploid genome. Anyone planning wholesale naming of thousands of cytotypes with specific epithets ought to reconsider this approach before flooding the taxonomic literature with impractical names simply to satisfy man's interpretation of a biological species concept. A better way might be to tag cytotypes with a ploidy level (2*x*, 4*x*, etc.) following a legitimate binomial."

We concur with Lewis (1980); we do not maintain that every cytotype or autotetraploid should automatically be named a new species. Rather than "flooding the literature with new names," we advocate here a more careful case-by-case consideration of the topic. Actual naming of diploid and autopolyploids as distinct species should occur only after studies, like several of the examples provided here, show that these populations follow the guidelines of prominently used species concepts. If autopolyploid populations are following their own evolutionary paths, separate (mostly) from diploids, and are also largely reproductively isolated and morphologically diagnosable, species status is certainly merited. Triploids may occur, and some introgression may occur, but if the diploid and autopolyploid are mostly functioning as independent lineages, then they should both be named as species. In fact, the situation is no different from a pair of morphologically similar diploid species (cryptic species) that occasionally hybridize (Grundt & al., 2006). We assert that we need to take autopolyploidy seriously as a mechanism of speciation, but we do not maintain that every case of autopolyploidy results in instantaneous speciation.

THE SPECIES PROBLEM AND SPECIES CONCEPTS IN PLANTS

The fact that autopolyploids are typically not recognized as distinct species, but as chromosomal races within a cytologically polymorphic species, may reflect the species concepts of the investigators. Do autopolyploids meet the expectations of any of the commonly employed species concepts? We review here several of the most widely used concepts and consider their applicability to autotetraploids and their diploid progenitors. Comprehensive reviews of species concepts are given in Grant (1981), Templeton (1989), Baum (1992), Rieseberg (1994), Baum & Donoghue (1995), Davis (1997), Levin (2000), Wheeler & Meier (2000), Coyne & Orr (2004), and Futuyma (1998, 2005). The issue of when two entities should be considered distinct species has been a longstanding controversy (reviewed in Grant, 1981; King, 1993; Wilson, 1999; Levin, 2000; Wheeler & Meier, 2000). The question of what constitutes a species has been particularly problematic in plants.

The most well-known and widely employed approach to species is the biological species concept (Mayr, 1963; the isolation species concept of Templeton, 1989), which maintains that a species is "a group of interbreeding (or potentially interbreeding) populations that are reproductively isolated from other such groups." The biological species concept has been the prevailing view of species in animals (e.g., Coyne, 1992; Coyne & Orr, 2004) and has also played a major role in views of plant species as well. However, it has long been maintained that the application of the biological species concept is difficult in plants due to frequent hybridization. However, some hybridization between species and gene flow do not necessarily imply that two entities must be considered a single species (e.g., Coyne & Orr, 2004). In part because of frequent hybridization between plant species, many plant systematists have largely abandoned the biological species concept (e.g., Ehrlich & Raven, 1969; Mishler & Donoghue, 1982; Donoghue, 1985; Nixon & Wheeler, 1990; Davis & Nixon, 1992; Baum & Shaw, 1995; McDade, 1995; Judd & al., 2002). However, the biological species concept continues to have strong advocates in plant evolutionary biology (e.g., Schemske, 2000), and recent analyses suggest that plant species may be more likely than animal species to represent reproductively isolated lineages (Rieseberg & al., 2006).

The evolutionary species concept (Simpson, 1961) is based on the recognition of evolutionary lineages, an ancestral-descendant sequence of populations that evolves separately from other such lineages and has its own ecological niche. This concept was further developed by Wiley (1978) and Wiley & Mayden (2000): a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate. Hybridization can be taken into consideration in the evolutionary species concept. If hybridization occurs, but the two entities do not merge, they still represent distinct species (Simpson, 1961; Grant, 1981).

The morphology-based taxonomic species concept has been widely used: an assemblage of morphologically similar individuals that differs from other such assemblages (Grant, 1981). Although practical for taxonomic purposes, this system is subjective—the amount of difference that "is worthy of species rank cannot be prescribed objectively" (Grant, 1981). Different taxonomists may have different criteria; many systematists

may only consider obvious morphological differences and not cryptic characters that separate population systems. A less subjective system based on morphological variation is the phenetic species concept (Sokal & Crovello, 1970), which also rests on the assumption that members of one species share an overall similarity and are separated from other species by a gap in variation (Judd, 1981).

The prevalence of phylogenetic thinking prompted the development of several phylogenetic species concepts. According to the phylogenetic species concept, as defined by Cracraft (1983), a species "is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent." Likewise, species are considered "the minimal elements of hierarchic descent systems" (Davis, 1997). Operationally, species are defined as "the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states" (Nixon & Wheeler, 1990; Davis & Nixon, 1992; Wheeler & Platnick, 2000). That is, species are defined as separate lineages, which must be diagnosable (on the basis of morphological or non-morphological characters; the diagnosability species concept, Judd & al., 2002), the states of which must be invariant within each recognized species. A second phylogenetic species concept (Donoghue, 1985; Mishler, 1985; Mishler & Theriot, 2000) has also been called the apomorphic species concept (Judd & al., 2002), as apomorphies (either molecular or morphological) are employed in species diagnosis. Species are recognized on the basis of monophyly and are defined as "the least inclusive taxon recognized in a formal phylogenetic classification" (Mishler & Theriot, 2000; but see also Donoghue, 1985; Mishler, 1985). Variants on these phylogenetic concepts have been proposed (e.g., De Queiroz & Donoghue, 1988; Baum & Donoghue, 1995; Davis, 1997), but discussion of them is beyond the scope of this paper.

One of the biggest apparent challenges to the argument that autopolyploids are distinct species is that each autopolyploid may, in fact, be of "multiple origin." Recent genetic studies have shown that many polyploids (allopolyploids and autopolyploids) have formed repeatedly (D. Soltis & Soltis, 1993, 1999; P. Soltis & Soltis, 2000). Following the evolutionary and phylogenetic species concepts, some might prefer that each new lineage be recognized as a species (see D. Soltis & Soltis, 1999), which may best reflect evolutionary history but seems highly impractical on many grounds. Alternatively, these independent polyploid lineages may be interfertile, and thus interbreed when they come into contact, and could be grouped as one biological species. Furthermore, gene flow among these lineages may fairly rapidly homogenize any differences due to independent ancestry and result in a single polyploid entity that could be recognized as a species under a number of species concepts.

Below we consider several examples of autopolyploids and their diploid parents and discuss which species concepts fit each case. An important issue in applying the biological species concept to diploids and autopolyploids is how one estimates reproductive isolation. Husband & Sabara (2003) have discussed this matter for *Chamerion,* and their study serves as a model for applying this approach.

We argue that the persistence and widespread application of the taxonomic (or phenetic, as traditionally applied) species concept to plants has been a major disservice to plant systematists and evolutionary biologists. This system is based on convenience, facilitating identification for the field taxonomist. Although it may seem "practical" to include morphologically highly similar cytotypes in one species, this practice obscures insights into evolution. For example, by lumping cytotypes into a single species, the complex interactions between pollinators, herbivores, pathogens, etc. and diploids and tetraploids can be overlooked; as a result, comparative investigations are not pursued (see recent findings summarized below for *Heuchera grossulariifolia*). Furthermore, this approach underrepresents biodiversity, potentially thwarting conservation efforts (e.g., Soltis & Gitzendanner, 1999) and masking many potentially significant genetic and ecological processes that create new species.

Several plant systems comprise multiple cytotypes that exhibit largely distinct ranges and are largely reproductively isolated. We review several examples below and also suggest a system for naming the diploid and autopolyploid lineages when appropriate. The issues raised here apply to all unnamed cytotypes—those of allopolyploid origin as well as autopolyploid origin. However, we focus here only on autopolyploids; they represent a well-defined issue and the heart of the problem. Unnamed cytotypes of allopolyploid origin certainly exist, but allopolyploids typically combine attributes of morphologically distinct parents. Hence, because they are morphologically distinctive and combine divergent parental genomes, they are more easily recognized and are therefore more often described as independent species.

We draw on evidence from the literature as well as our own experience with several polyploid complexes to reassess the traditional view of plant autopolyploids. We conclude that the major reasons why autopolyploids have not been named as distinct species are twofold: (1) tradition of including cytotypes in a single named species; and (2) tradition and convenience of adhering to a broad morphology-based taxonomic species concept.

EXAMPLES OF AUTOPOLYPLOID SPECIATION

Many unnamed autotetraploids fulfill the requirements of multiple species concepts, and there is no reason why they should not be named as distinct species. Based on our own research in North America, *Tolmiea menziesii*, *Galax urceolata*, *Chamerion angustifolium*, and *Heuchera grossulariifolia* represent excellent examples of the detailed study needed to evaluate species status, and the *Vaccinium corymbosum* group exemplifies the potential complexity of polyploidy and reticulation (Table 1). For *Tolmiea*, we will offer in a separate publication a formal nomenclatural change to illustrate the process of recognizing diploids and autotetraploids as distinct species. Other diploid-autotetraploid pairs that have been well studied could similarly be critically evaluated, as done here, and a recommendation may, in some instances, be justified for recognizing the diploid and autotetraploid each as distinct species. Examples from the European flora include *Ranunculus cassubicifolius* (Hörandl & Greilhuber 2002; Paun & al., 2006), *Parnassia palustris* (Wentworth & Gornall, 1996; Borgen & Hultgård, 2003), *Galium pusillum* (Samuel & al., 1990), and *Biscutella laevigata* (Tremetsberger & al., 2002). As observed in the taxa discussed here from North America, these examples have diploids and polyploids that exhibit geographic separation, but little morphological differentiation. There are other examples of autopolyploids that also merit careful evaluation—e.g., *Larrea tridentata* (Cortes & Hunziker, 1997), *Thymus loscosii* (Lopez-Pujol & al., 2004), and *Vaccinium oxycoccos* (Mahy & al., 2000). Several of the North American examples we have reviewed in detail provide a framework for the critical research that is still needed on many diploid-autopolyploid complexes, including those just listed above. For example, what is the degree of reproductive isolation between diploids and autopolyploids? If reproductive isolation is present, what are the reproductive barriers? Do the diploid and autopolyploid meet the requirements of multiple species concepts?

***Tolmiea*. —** *Tolmiea menziesii* (Pursh) T. & G. (Saxifragaceae), as currently recognized, comprises a single taxonomic species with both diploid ($2n = 14$) and autotetraploid ($2n = 28$) populations (Soltis, 1984). The species was long considered to have a chromosome number of only $2n = 28$ until routine chromosome counting indicated that some field-collected populations have $2n = 14$ (Soltis, 1984). There are no other species of *Tolmiea,* and the genus is distinct among genera of Saxifragaceae in having strongly zygomorphic flowers (rather than actinomorphic) and a unique floral morphology. Hence, based on morphology, the case for autopolyploidy is strong, and no other possible progenitor of the autotetra-

Table 1. Summary of diploid/autotetraploid comparisons in *Tolmiea menziesii*, *Galax urceolata*, *Chamerion angustifolium*, *Heuchera grossulariifolia*, and *Vaccinium corymbosum* for the species concepts examined here.

Taxon	Species concept				
	Biological	**Evolutionary**	**Phylogenetic apomorphic**	**Phylogenetic diagnosability**	**Taxonomic**
Tolmiea menziesii	Yes, complete reproductive isolation	Yes, distinct lineages, distinct geographic ranges	Yes, each cytotype monophyletic	Yes, chromosome number, molecular, morphology	Yes, leaf shape, plant size
Galax urceolata	Probably, triploids present in areas of sympatry between diploids and tetraploids	Yes, appear to be distinct lineages not homogenized by triploid hybrids	Unknown	Yes, chromosome number, morphology (cryptic)	Yes, guard cell size, plant size
Chamerion angustifolium	Yes, reproductive isolation strong despite some triploids	Yes, distinct lineages, distinct geographic ranges, ecological separation	Unknown	Yes, chromosome number, morphology (cryptic); sometimes indistinguishable in field	Yes, leaf shape, pollen size and guard cell size have different means but overlapping distributions
Heuchera grossulariifolia	Yes, some triploids, but different flowering phenology and pollinator behavior	Yes, diverging lineages with distinct pollinators	Unknown	Yes, chromosome number, inflorescence and flower morphology (usually)	Sometimes, inflorescence and flower morphology but sometimes not distinguishable
Vaccinium corymbosum	Yes, triploid block	Yes, diverging lineages, ecological separation	Unknown	Yes, chromosome number	Sometimes, leaf shape and anthocyanins in fruit but often not distinguishable

ploids is known. Phylogenetic analyses confirm the distinctiveness of *Tolmiea* from other Saxifragaceae (Soltis & Kuzoff, 1995; Soltis & al., 2001).

Chemical, isozyme, and DNA data also support autopolyploidy (P. Soltis & Soltis, 1986; Soltis & Doyle, 1987; D. Soltis & Soltis, 1989). Inheritance studies confirmed tetrasomic inheritance at all isozyme loci examined (Soltis & Rieseberg, 1986; D. Soltis & Soltis, 1988); tetraploid individuals possessed as many as three or four alleles at a locus and maintained greater heterozygosity per locus than did diploid individuals (D. Soltis & Soltis, 1989). Phylogenetic analysis of cpDNA restriction site and length mutations (Soltis & al., 1989) indicated that the diploid and autotetraploid entities are monophyletic sister taxa, i.e., each is supported by several unique apomorphies and together they constitute a clade.

The diploid and autotetraploid also have distinct geographic ranges (Soltis, 1984; Soltis & al. 1997). The diploid occurs along the western coast of North America from northern California to central Oregon; the tetraploid occurs from central Oregon northward to southeastern Alaska (Fig. 1). The diploid and tetraploid populations do not overlap but abut in central Oregon. There are no obvious differences in habitat or ecology between diploids and tetraploids. The diploid and autotetraploid are reproductively isolated. Extensive artificial crosses between diploid and tetraploid plants yielded very few viable seed; those that were viable produced, when germinated, tetraploid plants, suggesting the production of unreduced gametes by diploid individuals. No triploids were detected via artificial crosses, presumably due to triploid block, and no triploids have been found in natural populations.

Although morphologically similar, diploid and tetraploid *Tolmiea* do differ slightly in some morphological characters. The diploid has leaves that are slightly narrower (in relation to their length) than those of the autotetraploid; the autotetraploid is more robust and produces more plantlets.

Thus, diploid and tetraploid *Tolmiea* each meets the criteria for all of the commonly used species concepts: they are reproductively isolated, so they are biological species; they are distinct evolutionary lineages, so the two cytotypes meet the expectations of the evolutionary species concept; each is monophyletic, so both can be considered phylogenetic (apomorphic) species; they are diagnosable on the basis of chromosome number and several molecular characters, thus fitting the phylogenetic/diagnosability species concept; morphological characters distinguish the two cytotypes (although these may be considered cryptic by some; see taxonomic treatment of Judd & al.), hence they are taxonomic species. The diploid and tetraploid also have distinct geographic ranges; there seems to be no reason *not* to consider the cytotypes of *Tolmiea menziesii* as separate species. Therefore, a formal description of the diploid populations is provided elsewhere (Judd & al., in press).

***Galax.* —** *Galax urceolata* (Poiret) Brummitt (formerly *G. aphylla* L.) provides a situation very similar to that described for *Tolmiea* in that there are no other species in the genus *Galax;* it is also a morphologically and phylogenetically distinct entity with no other closely related genera in the eastern United States. In fact, *Galax* was long considered the classic example of autopolyploidy (Baldwin, 1941; Stebbins, 1950). *Galax urceolata* occurs in the southern Appalachian Mountains with most populations in North Carolina through Virginia and additional populations in Georgia, Alabama, Tennessee, West Virginia, and Kentucky (Fig. 2). *Galax* spreads via rhizomatous stems and appears to be highly clonal. The single recognized species comprises both diploid ($2n$ = 12) and tetraploid ($2n$ = 24) cytotypes; there are also occasional triploid populations, each thought to be a clone

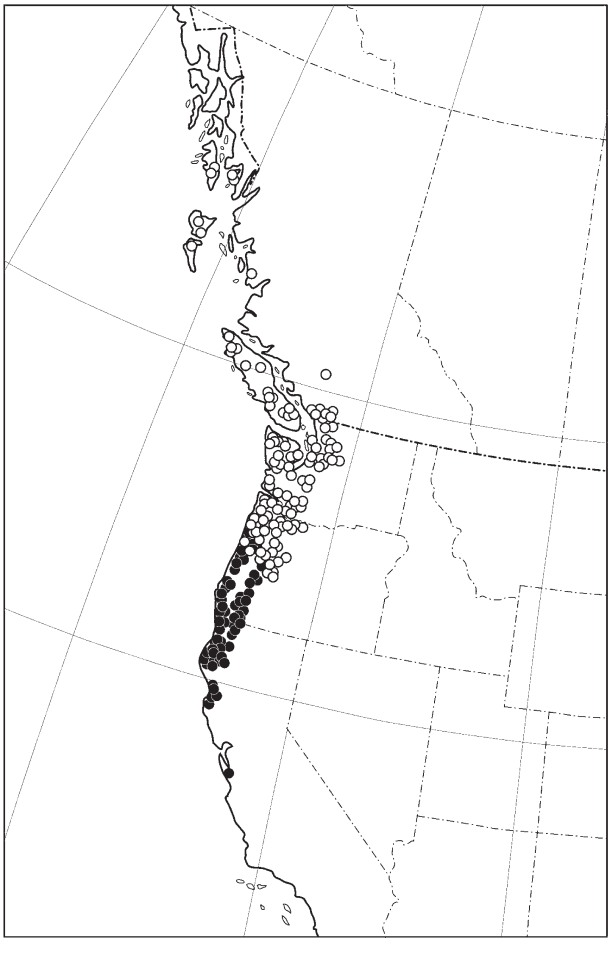

Fig. 1. Geographic distribution of diploid and tetraploid *Tolmiea* (updated from Soltis, 1984). Open circles represent tetraploid populations; black circles designate diploid populations.

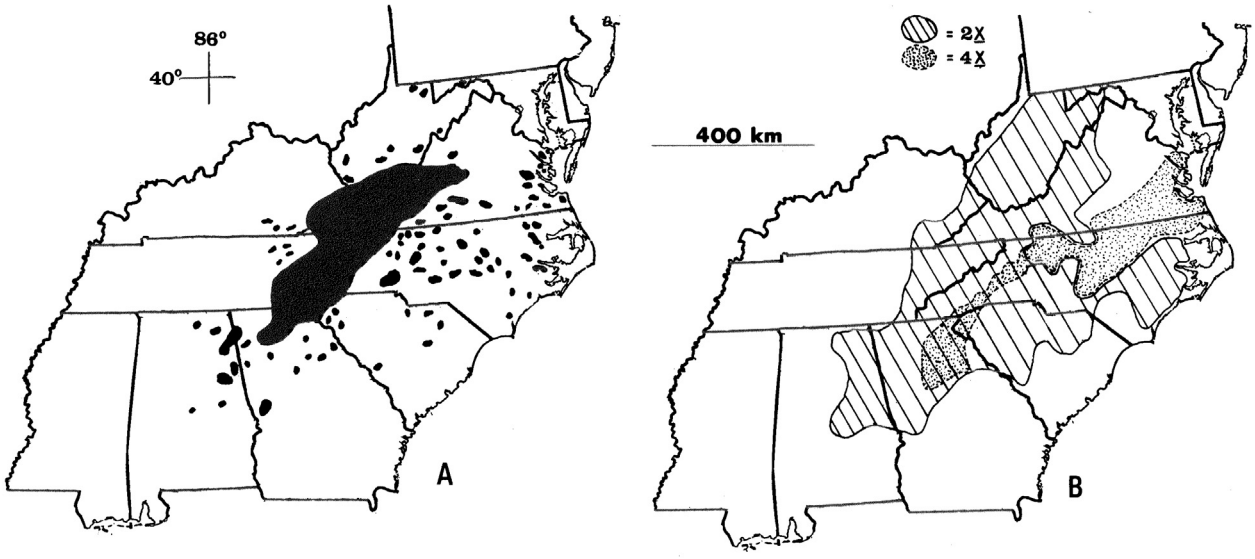

Fig. 2. Geographic distribution of diploid and tetraploid cytotypes in *Galax urceolata* (reproduced with permission from Nesom, 1983). A, main range with isolated, peripheral populations and population systems; B, generalized distribution of diploids and tetraploids.

(Nesom, 1983). Because *Galax* is monotypic, with morphologically highly similar diploids and tetraploids, it has often been considered one of the clearest examples of autopolyploidy in nature (Stebbins, 1950; Grant, 1981). The diploids and tetraploids differ slightly in size, and there is a clear correlation between guard cell size and ploidy (Nesom, 1983).

Nesom (1983) found that diploids occur throughout most of the range of the species, with tetraploids exhibiting a smaller range. Tetraploids are abundant along the Blue Ridge escarpment "sharply bounded on the northwest by the escarpment in northern North Carolina and by the Blue Ridge divide further south" (Nesom, 1983). Tetraploids occur to the exclusion of diploids on the Virginia coastal plain and north-central piedmont of North Carolina.

Along the escarpment, complex patterns of sympatry involving the diploids, tetraploids, and triploids were often encountered (Nesom 1983). Burton & Husband (1999) later showed that *G. urceolata* forms a mosaic of cytotype frequencies across the species' range. Forty-two percent of populations contained a single cytotype, with diploids more common in the northeast and tetraploids more common in the southwest. Nesom noted that more xeric habitats were occupied by diploids and more mesic sites by tetraploids on the escarpment, but no obvious differences in habitat were noted on the piedmont and coastal plain. Johnson & al. (2003) tested the habitat preferences of diploids and tetraploids suggested by Nesom and found evidence for habitat differentiation. Their results support the hypothesis that environment-dependent selection is at least partially responsible for the geographic separation between diploid and tetraploid *G. urceolata* populations.

The presence of triploids in areas of sympatry between the diploids and tetraploids raises the possibility that the diploids and tetraploids may not be "good" biological species. Little or nothing is known about the crossability and reproductive biology within *Galax;* the degree of reproductive isolation has not been estimated. The presence of occasional triploid patches suggests that diploid × tetraploid crosses may have occurred, although as stressed by Nesom (1983), these triploids could also represent "triploid bridge" populations formed from diploid plants via the result of an unreduced gamete from a diploid fusing with a haploid gamete. Because the cytotypes differ in plant size and stomatal size, they could be considered distinct taxonomic species. They also appear to represent distinct evolutionary lineages because, although triploids may result from hybridization between diploid and tetraploid individuals, they are limited in distribution and do not appear to be homogenizing the diploid and tetraploid cytotypes. Hence, although not as clear as the case for *Tolmiea,* a strong argument could be made for recognizing two species of *Galax*. This genus clearly merits more study.

***Chamerion.* —** *Chamerion* (formerly *Epilobium*) *angustifolium* (L). Holub (fireweed) is a perennial, herbaceous plant that is widely distributed throughout the Northern Hemisphere (Mosquin, 1966) in open and disturbed habitats. In Eurasia, most plants are either diploid ($2n = 2x = 36$) or tetraploid ($2n = 4x = 72$), although some hexaploids have been found in Japan (Mosquin, 1966). Within North America, where most research has been conducted,

both diploids and tetraploids occur commonly (Fig. 3) (Mosquin, 1967), and triploids and pentaploids have also been observed (B.C. Husband, unpublished). Tetraploids are likely autopolyploids based on morphological (Mosquin, 1967), cytological (Mosquin, 1967), phylogenetic (A. Robertson, J. Ramsey & B.C. Husband, unpublished), and genetic (Husband & Schemske, 1997) grounds. Diploids and tetraploids are largely allopatric, with diploids at higher latitudes than tetraploids (Mosquin & Small, 1971). However, there is a contact zone located along the southern border of the boreal forest and in a narrow region along the Rocky Mountains (Mosquin & Small, 1971). In this region, 59% of populations are of mixed cytotype; diploids dominate at high elevations whereas populations are fixed for tetraploids at low altitudes (Husband & Schemske, 1998; Husband & Sabara, 2003; H. Sabara & B.C. Husband, unpublished). Triploids are usually present when diploids and tetraploids co-occur and range in frequency from 2 to 22% within populations.

Despite the presence of triploids, reproductive isolation between diploids and tetraploids is strong and the product of several different reproductive barriers. In an analysis of five pre-zygotic and two post-zygotic barriers, Husband & Sabara (2003) found that total reproductive isolation between the cytotypes was 99.7%. By comparison, Ramsey & al. (2003) estimated that the total isolation between two diploid *Mimulus* species was approximately 99.9%. Pre-zygotic barriers, comprising primarily geographic isolation and pollinator fidelity, accounted for 97.6% of the total. Triploids are produced at low frequency in diploid × tetraploid crosses and have low fertility (Burton & Husband, 2000), suggesting that post-zygotic isolation is also strong. Nonetheless, triploids do produce some euploid gametes with one ($n = x$), two ($n = 2x$), or three ($n = 3x$) chromosome sets, and simulations suggest this may be sufficient to cause recurrent polyploid formation (Husband, 2004). Evidence for or against polyphyly in the tetraploids has yet to be corroborated with phylogenetic evidence.

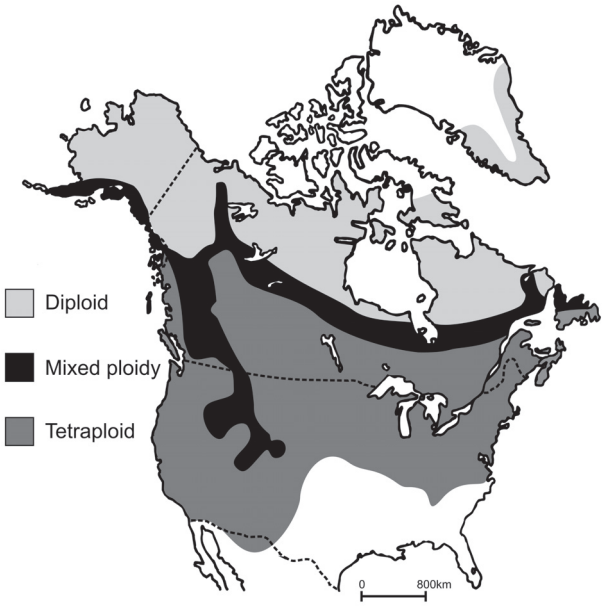

Fig. 3. Geographic distribution of diploid and tetraploid cytotypes in North American *Chamerion angustifolium*, as well as area of overlap of the cytotypes (modified from Mosquin & Small, 1971).

Pre-zygotic reproductive isolation arises largely from ecological and morphological differences between cytotypes. Their differences are primarily one of scale rather than form (cf. Müntzing, 1936). Diploids have significantly smaller flowers, shorter inflorescences, earlier flowering times, and in some cases smaller floral displays than tetraploids (Husband & Schemske, 2000). These differences in phenology and size may contribute to the association between diploidy and higher altitudes/latitudes, which are characterized by shorter growing seasons, extreme temperature fluctuations, and coarse-grained soils. Importantly, the combined effects of clonal structure and differences in flowering time between the cytotypes reduced the frequency of pollinator movement between cytotypes in mixed populations from 49% (if mating is random) to 2% of the total pollinator flights.

The taxonomy of *Chamerion angustifolium* has undergone modest changes in the last 50 years (Baum & al., 1994). Intraspecifically, numerous classifications have been proposed and biologists have differed in the taxa they recognized. Based on an assessment of "morphological discontinuities" from 2,000 herbarium specimens from around the world, and 95 chromosome counts, Mosquin (1966) proposed two subspecies, which correspond to diploid and polyploid cytotypes. *Chamerion angustifolium* subsp. *angustifolium* represents the diploid cytotype ($2n = 2x = 36$) and is characterized by glabrous abaxial leaf midribs, triporate pollen, and relatively narrow and short leaves. It occurs at northern latitudes in North America, Europe, and east-central Asia. *Chamerion angustifolium* subsp. *circumvagum* (Mosquin) Hoch encompasses both tetraploids ($2n = 4x = 72$) and hexaploids ($2n = 6x = 108$) and has glabrous to very pubescent leaf midribs, triporate and quadriporate pollen, and wider and longer leaves. The data available on morphology, ecology, and gene flow provide a strong argument for recognition of diploids and tetraploids as separate species. Appropriate treatment of the hexaploids, which are allopatric to the tetraploids, is less clear due to the general lack of information.

***Heuchera.* —** Autotetraploids in *Heuchera grossulariifolia* Rydb. were discovered through a survey of natural populations using isozyme electrophoresis. Individual plants that exhibited three or four alleles at a locus were observed, and chromosome counts revealed that

these plants were tetraploid ($2n = 28$) (Wolf & al., 1990). Subsequent studies documented the distributions of the cytotypes (Fig. 4) and revealed that the tetraploid had formed more than once (Wolf & al., 1990; Segraves & al., 1999). Genetic studies demonstrated tetrasomic segregation in the tetraploid and a very high genetic similarity between diploid and autotetraploid populations (Wolf & al., 1989, 1990; Segraves & al., 1999).

Heuchera grossulariifolia is endemic to the northern Rocky Mountains of the United States (Fig. 4) with disjunct populations in the Columbia River Gorge of Oregon. Some populations are exclusively tetraploid, whereas others are diploid, and some mixed populations occur in Idaho. These mixed populations usually constitute a relatively narrow zone of overlap between diploid and tetraploid populations. Triploids are also encountered in the field, albeit rarely; artificial crosses between diploids and autotetraploids also yield some triploids (C.C. Fernandez & J.N. Thompson, in prep.).

In some regions, such as the Salmon River of Idaho, the diploids and tetraploids differ in morphology, with tetraploid plants often having shorter inflorescences; they also differ in floral morphology (Segraves & Thompson, 1999) and flowering time. Recent multi-year studies have shown evidence of selection for phenotypic divergence between diploids and tetraploids in this zone of sympatry (Nuismer & Cunningham, 2005). In other regions, such as the upper Selway River of Idaho, diploid and tetraploid plants are morphologically indistinguishable (reviewed in Thompson & al., 2004).

Polyploidy in *H. grossulariifolia* is associated with a major difference in pollinator visitation. In the area of sympatry along the Salmon River, the majority of floral visits are by bees, but the proportion of visits to each ploidal level differs greatly (Segraves & Thompson, 1999). For example, *Lasioglossum* bees comprised about 25% of the visits to diploids but only 10% of the visits to tetraploids, whereas *Bombus centralis* queens visited the tetraploids more frequently, and workers visited the diploids more frequently. Similarly, pollinators on the upper Selway River distinguish between diploid and tetraploid plants, even though plants of different ploidy are morphologically indistinguishable in that region (K. Merg & J.N. Thompson, in prep.).

Herbivores also distinguish between diploid and tetraploid *H. grossulariifolia*. Multi-year studies have shown that *Greya politella* moths oviposit more commonly in tetraploid plants, whereas congeneric *Greya piperella* moths and *Eupithecia misturata* moths oviposit more commonly in diploid plants in habitats where the plants occur sympatrically (Nuismer & Thompson, 2001). Hence, diploid and tetraploid plants have different ecological niches within these biological communities in their interactions with pollinators and herbivores.

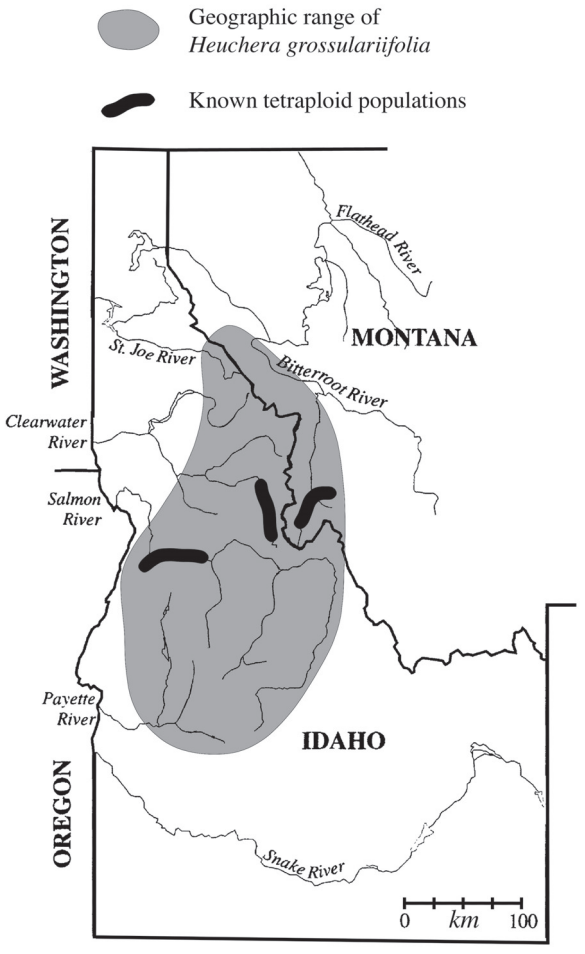

Fig. 4. Geographic distribution of *Heuchera grossulariifolia* showing the distribution of known tetraploid populations.

The diploid and autotetraploid races of *H. grossulariifolia* seem to meet the expectations for several different species concepts. As summarized by Thompson & al. (2004), "the evolution of polyploid populations has the potential to change significantly the evolutionary ecology of interactions with herbivores and pollinators." They have shown that this is the case in multiple studies of *H. grossulariifolia,* and recent work has shown clear evidence of selection for divergence of phenotypic traits in sympatry driven by these interactions with other species (Nuismer & Cunningham, 2005). Hence, the two cytotypes represent evolutionary species; they appear to be diverging evolutionary lineages, with distinct suites of herbivores and pollinators. Due to differences in geographic range, flowering phenology and pollinator behavior, they appear to be largely isolated reproductively. Hence, they appear to be functioning as separate biological species. However, the occasional presence of triploids in a few areas of sympatry and the ability to generate triploids via artificial crosses (C.C. Fernandez

& J.N. Thompson, in prep.) suggest that reproductive isolation is not complete. The diploids and tetraploids differ in inflorescence and floral morphology and hence are taxonomic species.

Vaccinium. — *Vaccinium corymbosum* L. is a woody, perennial plant that is found in coastal plains and inland bogs, pine flatwoods, and open wooded slopes in eastern North America. It is an outcrossing species, but varies widely in levels of self-fertility (Krebs & Hancock, 1989, 1990).

In the original taxonomic treatment of *Vaccinium* by Camp (1945), *V. corymbosum* was recognized as one of 15 North American polyploid species in section *Cyanococcus*. Camp identified 9 diploids ($2n = 2x = 24$), 12 tetraploids ($2n = 4x = 48$), and three hexaploids ($2n = 6x = 72$). Two distinct overall morphologies were observed, a low-growing, rhizomatous form (lowbush) and a tall-growing, crown-forming type (highbush). A considerable amount of interfertility exists among Camp's species of the same ploidy, but not between cytotypes, except through unreduced gametes that are generally rare (Luby & al., 1991; Ortiz & al., 1992; Galletta & Ballington, 1996).

Evidence for tetrasomic inheritance has been provided for tetraploid *V. corymbosum* based on isozyme and RAPD segregation data (Krebs & Hancock, 1989; Qu & Hancock, 1997). There has apparently been little chromosomal change within section *Cyanococus,* as the tetraploid hybrids formed between diploid and tetraploid species are highly fertile (Draper & al., 1982), and a hybrid between evergreen, diploid *V. darrowi* and deciduous, tetraploid *V. corymbosum* has been shown with RAPDs to be undergoing regular, tetrasomic inheritance (Qu & Hancock, 1997).

In the most recent taxonomic organization of *Vaccinium* section *Cyanococcus*, Vander Kloet (1980, 1983, 1988) joined all the highbush species into one species, *V. corymbosum*, without any race distinction based on ploidy. The ranges of the various cytotypes overlap, with the diploids and tetraploids found from northern Florida to eastern Texas and Arkansas to New York and Maine, and the hexaploids only in the southern half of this range (Fig. 5). Most recently, Luby & al. (1991) and Galletta & Ballington (1996) have argued that sufficient morphological variability and ecological separation exists to recognize individual species of diploid (*V. elliottii*), tetraploid (*V. simulatum*), and hexaploid (*V. constablaei*) highbush types; however, they still left the majority of diploids, tetraploids, and hexaploids under the umbrella *V. corymbosum*.

Vaccinium presents a more complex and less well-understood example of autopolyploidy than those described above. The polyploids appear to represent biological species; triploids are very rare between diploid and tetraploids (Dweikat & Lyrene, 1988). The polyploids can be morphologically distinguished from many diploids, but not all, making them often poor taxonomic species. The evolutionary species approach may be most appropriate for these plants. Tetraploids do not have a distinct geographic range compared to diploid *V. corymbosum*, although the cytotypes do appear to be ecologically distinct (Galletta & Ballington, 1996)

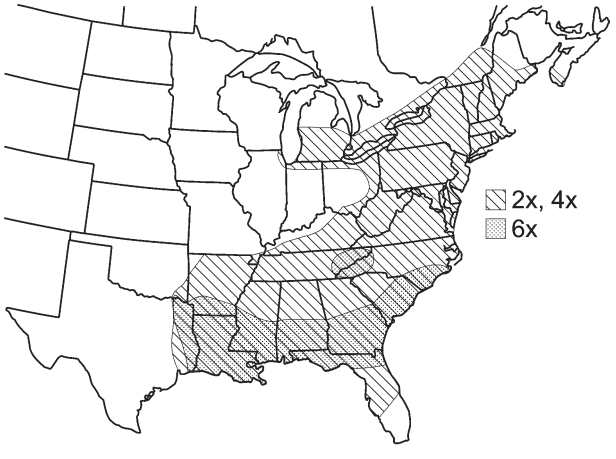

Fig. 5. Geographic distribution of diploid, tetraploid, and hexaploid cytotypes in *Vaccinium corymbosum.*

NOMENCLATURAL RECOMMENDATIONS

If we are to begin to treat autopolyploids as distinct species, there are several ways that nomenclatural changes can be implemented. A simple approach would be to attach $2x$ and $4x$, respectively, to the existing specific epithet. For example, *Tolmiea menziesii-2x* and *Tolmiea menziesii-4x* could be recognized, with the understanding that each should be considered a separate species. However, following the International Code of Botanical Nomenclature, "menziesii2x" and "menziesii4x" cannot be used as specific epithets because a scientific name has to be in the proper grammatical Latin form, and numbers cannot be included in the name; the specific epithet also would need the appropriate ending. These names could be used, however, under the PhyloCode (www.ohiou.edu/phylocode/).

A perhaps more appropriate approach is to provide a new species name for one cytotype. However, using this scheme, or any formal naming, requires research to determine the specimen to which the name is attached. That is, is the existing species name attached to a diploid or autotetraploid plant? For example, the type specimen for *Tolmiea menziesii* was collected from British Columbia, which is well within the range of the tetraploid ($2n = 28$;

Soltis, 1984). Hence the name *Tolmiea menziesii* should be applied to the tetraploid. The diploid should therefore be recognized and formally described as a distinct species (as we have done in a separate paper).

We suggest that the same basic naming method used for *Zea perennis* could be followed for other diploid/autotetraploid pairs. *Zea perennis* is a tetraploid ($2n$ = 40) that is generally accepted to be an autotetraploid derivative of a more recently discovered and described diploid ($2n$ = 20) that was named *Zea diploperennis* (Iltis & al., 1979; reviewed in Tiffin & Gaut, 2001). That is, if the type specimen goes with the tetraploid, then "diplo" could simply be added to the specific epithet to provide a new name for the diploid. Thus, in the case of *Tolmiea menziesii*, the diploid would be named *Tolmiea diplomenziesii*. This same basic approach could be followed if, in contrast, the type specimen is attached to the diploid and the tetraploid must be named. If, for example, the type for *Galax urceolata* is attributable to the diploid, then the tetraploid could be named *Galax tetraurceolata*. This could also be extended to higher ploidies that are unnamed. For example, if a hexaploid were present in *Galax*, it could be named *Galax hexaurceolata*. If this simple approach were applied to unnamed autopolyploid cytotypes that deserve recognition as separate evolutionary lineages based on available data, it would greatly simplify the naming process and would also be an easy system for taxonomists to employ.

SUMMARY AND FUTURE PROSPECTS

We maintain that the number of angiosperm species has been grossly underestimated because of the frequency of autopolyploidy and the reluctance of taxonomists to name diploids and autotetraploids as distinct species. We are not advocating a wholesale naming of diploids and autopolyploids, per the concern of Lewis (1980). However, in those instances in which careful study indicates that diploid and autopolyploid derivative(s) meet the criteria that satisfy several different species concepts, species recognition is not only appropriate, but also essential. Masking biological diversity through a "lumping" taxonomic philosophy has serious conservation implications that have been reviewed elsewhere (e.g., Soltis & Gitzendanner, 1999; Golding & Timberlake, 2003; Leadlay & Jury, 2006), although not specifically in relationship to autopolyploidy. The goals of habitat restoration are to recover the ecological function and native species composition of degraded habitats, and this may require a greater emphasis on the taxonomy and ecology of autopolyploid plant systems. For example, *Andropogon gerardii* (big bluestem) is a major component of restoration efforts in the tall grass prairie ecosystem, yet this taxonomic species is composed primarily of two cytotypes (hexaploids, 6*x*; enneaploids, 9*x*), both of which are considered to be autopolyploids (Keeler & Davis, 1999). There is evidence that the cytotypes differ in a number of ecological characteristics, and that natural selection maintains the cytotype composition of populations (Keeler & Davis, 1999). Thus, failure to recognize the cytotypes as different ecological and evolutionary entities could undermine restoration efforts.

This review has focused on the problems posed only by autopolyploids. There are also likely many cases in which allopolyploids have not been named as distinct species. However, typically allopolyploids are recognized as distinct species because they combine the attributes of their morphologically divergent parents (e.g., Clausen & al., 1945; Stebbins, 1947; Grant, 1981). However, in some cases allopolyploids have likely gone unrecognized because of similarity to one parent. For example, in *Lithophragma,* some populations referred to as *L. bolanderi* are tetraploid (with $2n$ = 28) and have clearly combined two divergent diploid ($2n$ = 14) genomes based on ITS sequence data; plastid restriction site data indicate that diploid *L. bolanderi* is consistently the maternal parent, and the second parent may be *L. glabrum* based on ITS sequence data (Kuzoff & al., 1999). The allotetraploid appears similar to *L. bolanderi*, but is larger than its parents, but until ITS sequence data were obtained, allopolyploidy had not been suspected. Pending further investigation, this allotetraploid should be named. Another noteworthy example involving an unnamed allotetraploid involves *Tragopogon miscellus* (Asteraceae). This allotetraploid has formed reciprocally from *T. dubius* and *T. pratensis*, and the switch in maternal/paternal parent results in a distinctly different inflorescence morphology (Ownbey & McCollum, 1953; reviewed in Soltis & al., 2004). Furthermore, the two allotetraploid forms of *T. miscellus* will not cross (Ownbey & McCollum, 1953). Hence, these examples meet the expectations of several species concepts. There may well be other examples (e.g., from the Arctic flora; see Brochmann & al., 2004) where allopolyploid populations of independent origin should be considered distinct species. These additional examples illustrate the complexity generated by both allopolyploids and autopolyploids.

ACKNOWLEDGMENTS

This research was funded in part by National Science Foundation grant MCB0346437, and by Assembling the Tree of Life (AToL) grant EF-0431266, as well as The University of Florida Research Foundation. We thank Dr. Guy Nesom for supplying the distribution map of *Galax*.

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