

# Polyploidy and aneuploidy of seed plants from the Qinghai–Tibetan Plateau and their biological implications

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**Abstract** The Qinghai–Tibetan Plateau is biologically diverse, with 9556 species of vascular plants in the 2,500,000 km<sup>2</sup> plateau area. We focused on seed plants from the Qinghai–Tibetan Plateau. A total of 9321 species in the Qinghai–Tibetan Plateau were recorded. Sixty-one of these genera are Chinese endemics. Our results suggested that the flora of the Qinghai–Tibetan Plateau was characterized by relatively few polyploids, and aneuploidy was also considered as relatively rare. We inferred that aneuploidy may be affected by environmental factors and the addition or loss of centromeres. Furthermore, the highest frequency of polyploids was found among perennial herbs. Annuals had low polyploidy, and perennials had high polyploidy. Species richness was correlated with the incidence of polyploids, environmental conditions, and reproductive isolation.

**Keywords** Aneuploidy · Endemic genera · Life form · Polyploids · Qinghai–Tibetan Plateau

## Introduction

The Qinghai–Tibetan Plateau is the highest mountain and plateau region in the world, with an area of approximately 2,500,000 km<sup>2</sup> and an average altitude greater than 4000 m a. s. l. (Zheng 1996). The region accounts for 26.8% of the total area of China. Approximately 9556 species of vascular plants have been recorded in this region (Wu 2008). In addition, approximately 8000 species of flowering plants have been recorded from the Hengduan Mountains on the eastern edge of the Plateau (Li and Li 1993; Wang et al. 1993, 1994), which is recognized as the world's richest and most diverse floristic temperate region (Boufford and van-Dyck 1999).

The Qinghai–Tibetan Plateau was formed by recent tectonic uplift that began approximately 50 million years (mya) and continued to occur. This uplift caused large-scale changes in air circulation, climatic zones, large river drainages, and vegetation. Climate is a major factor influencing the distribution of polyploidy (Packer 1969), and the heritable increase in genome copy number is a central feature of plant diversification (Lutz 1907; Stebbins 1951; Grant 1981).

Polyploid taxa have very diverse evolutionary histories, but many researchers have suggested that they are more adaptable to disturbed or novel niches than their diploid progenitors (Ehrendorfer 1980; Grant 1981; Stebbins 1985; Morton 1993; Otto and Whitton 2000; Levin 2004). There have been multiple estimates of the percentage of polyploidy in vascular plants (e.g., Muntzing 1936; Darlington 1937; Stebbins 1951; Grant 1963; Goldblatt 1980; Lewis

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1980; Masterson 1994). Recent genomic analyses have indicated that an early polyploidization event may have predated the radiation of flowering plants (Bowers et al. 2003), implying that all angiosperms are paleopolyploids.

In the Chinese flora, Wang (1989) reported 321 endemic genera (representing 88 families and 751 species) and 10 endemic families. Wu (1991) divided the genera of Chinese seed plants into 15 areal types, including 239 endemic genera in 67 families. Angiosperms became endemic in one of two ways: autochthonous neo-endemics mostly originated in the late Tertiary, whereas other endemics represent relict genera that once occupied huge areas in the northern hemisphere during the Tertiary or late Cretaceous. These endemics originated from Arctic, Paleotropical, and Tethys Tertiary floristic elements (and blends of these elements). Endemism occurred when several dispersal routes, such as the North Atlantic land bridge and the Bering land bridge, closed during the Tertiary; endemism also resulted from climate changes and glaciation in the late Tertiary and Quaternary. Therefore, the late Tertiary was the starting point of the extant endemism of the Chinese flora (Wu et al. 2007). In gymnosperms, all endemic genera are relics of the Arctic Tertiary flora, and their evolutionary origins can be traced back to the Cretaceous, the Jurassic, or even earlier (Wu et al. 2007).

Although the chromosome numbers of many species from the Qinghai–Tibetan Plateau have been reported, they have not been statistically analyzed in detail. This study addressed the following questions about the flora of the Qinghai–Tibetan Plateau: (1) How many species have reported chromosome numbers? (2) What percentage of species in each genus has reported chromosome numbers, and does the frequency of polyploids correlate with life form, life span, or ploidy level? (3) Is species richness significantly correlated to the incidence of polyploidy, environmental conditions, and/or reproductive strategy? According to Wu (1991)'s areal types of Chinese genera of seed plants, we analyze in situ levels of plant polyploidization.

## Materials and methods

This study focused on seed plants from the Qinghai–Tibetan Plateau. We assembled a chromosome count database from the portion of the Index of Plant Chromosome Numbers (IPCN) that was available in digital form (Goldblatt and Johnson 1979); all chromosome numbers have been previously published. Taxa with three or more basic nuclear chromosome sets were regarded as polyploids (Bennett 2004). Aneuploidy was considered as the presence of an abnormal number of chromosomes in a cell, which originated during cell division when the chromosomes did not separate properly between the two cells (Griffiths et al.

2000). Taxa were classified into five groups according to life form and further classified as either diploid or polyploid. These groups were trees (DT: diploid trees; PT: polyploid trees), shrubs (DS: diploid shrubs; PS: polyploid shrubs), herbs (DH: diploid herbs; PH: polyploid herbs), woody lianas (DWL: diploid woody lianas; PWL: polyploid woody lianas), and herbaceous lianas (DHL: diploid herbaceous lianas; PHL: polyploid herbaceous lianas).

## Results

The plant taxa from the Qinghai–Tibetan Plateau are summarized in Table 1. This total includes 9246 species and infraspecific taxa in 1415 genera and 172 families of angiosperms, and 75 species and infraspecific taxa in 17 genera and 8 families of gymnosperms. The overall frequency of polyploids was 10.50% (969/9321); the frequency in angiosperms was 10.40% (962/9246), and the frequency in gymnosperms was 9.33% (7/75).

Chromosome counts were available for 2611 species in 870 genera 130 families in angiosperms, and for 39 species in 13 genera 6 families in gymnosperms. Of those chromosome counts, 1688 species in 621 genera 103 families in angiosperms and 27 species in 9 genera 5 families in gymnosperms were identified in the Qinghai–Tibetan Plateau. Thus, 5.39% (502/9321) of the plants from the Qinghai–Tibetan Plateau were polyploids; this percentage included 5.42% (501/9246) of angiosperms and 1.33% (1/75) of gymnosperms. Aneuploidy occurred within 49 genera 33 families. The frequency of aneuploidy in each genus is summarized in Fig. 1. Twenty genera contained all aneuploids, eight genera comprised 50–75% aneuploids, and 21 genera had 2.70–38.46% aneuploids.

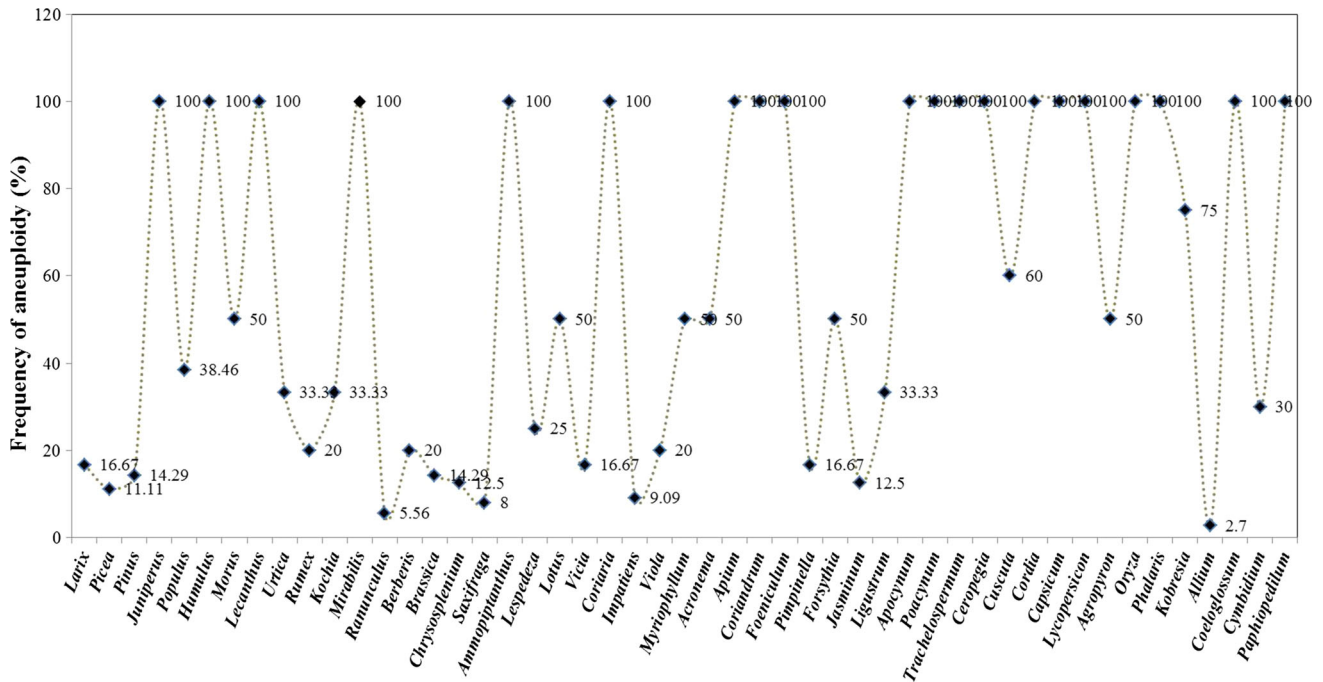
## Polyploidy and species richness

Among the 9321 species from the Qinghai–Tibetan Plateau, 777 were trees, 1726 were shrubs, 6626 were herbs, 107 were woody lianas, and 85 were herbaceous lianas. The taxa with reported chromosome numbers are summarized in Fig. 2. Perennial diploid herbs were more numerous than other forms (Fig. 3). The analysis of diploid and polyploid species according to their life forms (Fig. 4) showed that diploid taxa were significantly more numerous than polyploids. The highest frequency of polyploids was found among perennial herbs (6.68%, 623/9321), followed by shrubs (0.80%, 75/9321) and trees (0.65%, 61/9321), whereas the lowest frequency occurred in woody lianas (0.06%, 6/9321).

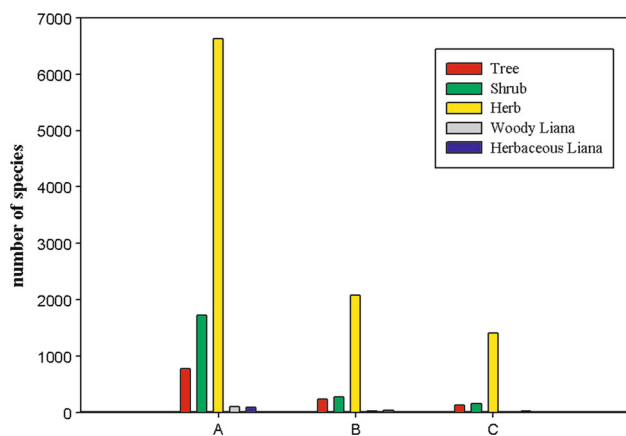
The proportion of polyploid taxa in each life form was 8.74% in herbs, 0.77% in shrubs, 0.60% in trees, 0.12% in herbaceous lianas, and 0.064% in woody lianas. The

**Table 1** Frequency of polyploids in plant species from the Qinghai–Tibetan Plateau

Type	Number of species		Percent polyploids		
	Gymnosperm	Angiosperm	Gymnosperm	Angiosperm	Gymnosperm and Angiosperm
Total number of species	75	9246			
Number of species with reported chromosome number	39	2611	9.33%	10.40%	10.50%
Number of species with reported chromosome number from the Qinghai–Tibetan Plateau	27	1688	1.33%	5.42%	5.39%



**Fig. 1** Frequency of aneuploidy in the plant genera of the Qinghai–Tibetan Plateau

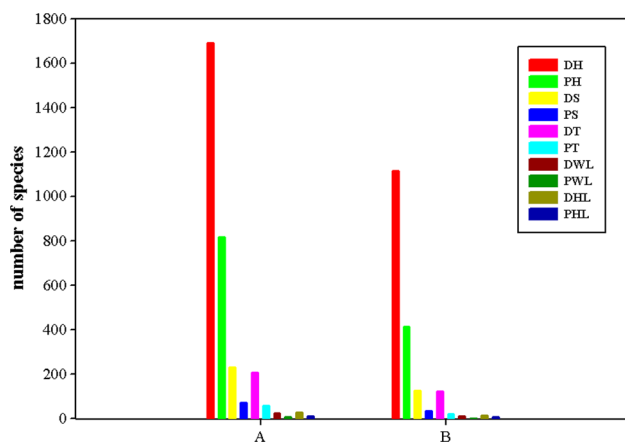


**Fig. 2** Life forms of plant species with reported chromosome numbers. *A* total number of species; *B* number of species with reported chromosome number; *C* number of species with reported chromosome number collecting from the Qinghai–Tibetan Plateau

proportion of polyploid taxa in each life form in the Qinghai–Tibetan Plateau was 4.44% in herbs, 0.35% in shrubs, 0.21% in trees, 0.08% in herbaceous lianas, and 0.01% in woody lianas (Fig. 4).

### Endemic genera of seed plants from the Qinghai–Tibetan Plateau

The frequency of polyploids in situ (species distributed in the Qinghai–Tibetan Plateau) was 36.73% (259/969). According to Wu (1991)’s areal types of Chinese genera of seed plants, we focused on Chinese endemic genera. In our study, 134 species (representing 30 families and 61 genera) were Chinese endemics. Because of the large number of species examined, the data are summarized at the family level (Table 2).

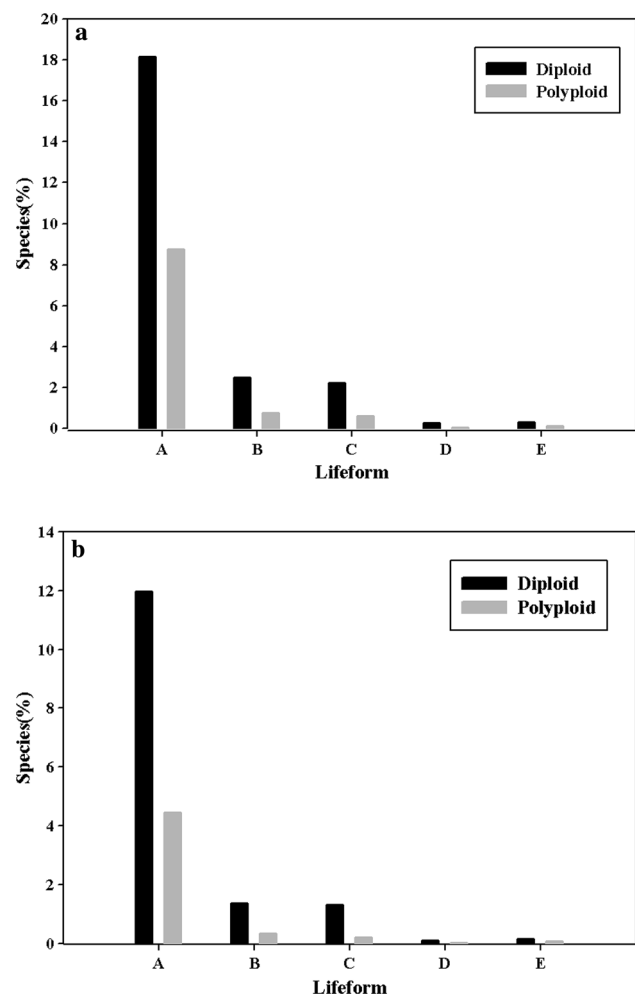


**Fig. 3** Life form and ploidy of species with reported chromosome numbers. **A** number of species with reported chromosome number; **B** number of species with reported chromosome number collecting from the Qinghai–Tibetan Plateau. *DH* diploid herbs, *PH* polyploid herbs, *DS* diploid shrubs, *PS* polyploid shrubs, *DT* diploid trees, *PT* polyploid trees, *DWL* diploid woody lianas, *PWL* polyploid woody lianas, *DHL* diploid herbaceous lianas, *PHL* polyploid herbaceous lianas

## Discussion

### Polyploids and aneuploids in the Qinghai–Tibetan Plateau

Stebbins (1951) estimated that between 30 and 35% of worldwide angiosperms were polyploid; approximately 22% of angiosperms in the Hengduan Mountains have been shown to be polyploids (Nie et al. 2005). Our data suggested that the flora of the Qinghai–Tibetan Plateau was characterized by relatively few polyploids (5.39%). The hypothesized that the Qinghai–Tibetan Plateau could have served as a refuge during the last Quaternary glaciation and that diploids were well preserved and thus little affected by glaciation, e.g., *Cremanthodium* (Liu et al. 2001), *Ligularia* (Liu 2004), *Tibetia* (Nie et al. 2002), and *Delphinium* (Yuan and Yang 2008). In our study, 9.33% of gymnosperms were estimated to be polyploids. Stebbins (1951) indicated that polyploidy was particularly uncommon among the extant gymnosperms. Khoshoo (1959) suggested that the frequency of polyploids was only 4.6% in gymnosperms, and proposed possible reasons. First, the chief causes of such rarity were the habitat stability and habitat ecospecific differentiation of all the taxa where hybridization occurred, even when the two taxa represented two distinct genera in a morphological sense. Second, polyploids from the resulting hybridization were expected to possess autopolyploid characteristics. Finally, apomixis did not occur in gymnosperms. Three additional hypotheses have also been proposed. The first was proposed by Sax (1932), who found a dominance of interstitial chiasmata at meiosis. The second was advanced by Muntzing (1933, 1936), who proposed that double fertilization in



**Fig. 4** The frequency (%) of diploids and polyploids by life form **a** Number of species with reported chromosome number. **b** Number of species with reported chromosome number collecting from the Qinghai–Tibetan Plateau. **A** herb; **B** shrub; **C** tree; **D** woody liana; **E** herbaceous liana

angiosperms preserved polyploidy. In an unpublished manuscript, the third concluded that the gymnosperm genera (except notably *Podocarpus*) were homoploid, and speciation was a matter of gene mutation and/or repatterning of chromosomes (Khoshoo 1959). Ahuja (2005) also stated that there were only a few natural polyploids in gymnosperms.

Brown (1972) suggested that evolutionary changes resulting in aneuploidy have occurred repeatedly, particularly in higher plants. Aneuploidy can be caused by four factors (Schulz-Schaeffer 1980): (1) loss of chromosomes in mitotic or meiotic cells; (2) non-disjunction of chromosomes or chromatids during mitosis or meiosis; (3) irregularities in chromosome distribution during the meiosis of polyploids with odd ploidy levels, such as in triploids and pentaploids; or (4) the occurrence of multipolar mitosis, resulting in an irregular chromosome distribution during anaphase. In our study, aneuploidy occurred

**Table 2** Summary chromosome and ploidy data by plant family for Chinese endemic species

Family	Genera numbers	Species numbers	Basic number of chromosome	Frequency of polyploidy
Ginkgoaceae	1	1	12	0
Betulaceae	1	1	–	0
Ulmaceae	1	1	10	0
Polygonaceae	1	1	–	0
Caryophyllaceae	1	1	14	0
Ranunculaceae	4	4	8, 9	0
Lauraceae	2	27	12	0
Cruciferae	2	2	4–15	0.75%
Eucommiaceae	1	1	17	0
Rosaceae	3	3	7, 17	0
Leguminosae	3	7	8	0
Sapindaceae	1	1	–	0
Actinidiaceae	1	1	12	0.75%
Araliaceae	1	1	–	0
Umbelliferae	10	16	9, 10, 11	0
Diapensiaceae	1	1	–	0
Primulaceae	1	1	10	0
Gentianaceae	1	2	6	0
Asclepiadaceae	1	1	–	0
Boraginaceae	1	1	–	0
Labiatae	1	1	–	0
Solanaceae	1	1	11	0.75%
Scrophulariaceae	1	1	–	0
Gesneriaceae	2	2	17, 20	0
Adoxaceae	2	2	18	0
Compositae	10	29	9	1.49%
Gramineae	3	20	7	5.22%
Liliaceae	1	2	–	0
Orchidaceae	1	1	–	0
Velloziaceae	1	1	19	0

within 33 families and 49 genera. We inferred that aneuploidy was considered as a relatively rare event. Sanderson and Strother (1973) proposed that aneuploid reduction was seldom found at the time of its establishment, where it would presumably occur within a single population. We believe that aneuploidy may be affected by chromosome rearrangements (mostly translocations), the loss or gain of centromere, and environmental factors. The occurrence of aneuploidy as reported here may provide an opportunity to understand aneuploid evolution.

### Life form and ploidy

A total of 883 genera in the Qinghai–Tibetan Plateau have had their chromosome numbers reported. In the genus *Poa*, 13 species were polyploid perennials, and 6 species were diploids and polyploids annuals. In the genus *Bromus*, 2

species were diploid annuals, 1 species was a polyploid annual, and 3 species were polyploid perennials. In the genus *Juncus*, 1 species was a polyploid annual and 8 were polyploid perennials. In the genus *Rumex*, 1 species was a diploid annual and 3 were polyploid perennials. In the genus *Polygonum*, 4 species were diploid annuals, 6 were diploid annuals and perennials, and 4 were polyploid perennials. In the genus *Cerastium*, 2 species were polyploid annuals and biennials and 3 were polyploid perennials. In the genus *Ranunculus*, 8 species were polyploid annuals and 12 were polyploid perennials. In the genus *Sedum*, 1 species was a diploid annual and biennial, 1 was a diploid perennial, and 3 were polyploid perennials. In the genus *Senecio*, 2 species were diploid annuals, 1 was a polyploid annual, 3 were diploid perennials, and 2 were polyploid perennials. We inferred that annuals had low polyploidy and perennials had high polyploidy. Gustafsson



(1948) analyzed the relationship between life form and polyploidy of 38 genera and concluded that annuals had low basic chromosome numbers and were predominantly diploid or low-level polyploids, whereas perennials often had higher basic chromosome numbers and higher polyploidy. Our results are consistent with Gustafsson (1948)'s conclusion. Moreover, our results showed that the highest frequency of polyploids was found among perennial herbs, a smaller frequency occurred in shrubs and in trees, and the lowest frequency was found in perennial woody lianas. This supports the viewpoint that polyploidy is more common in herbs than in woody plants (Stebbins 1951).

### Endemic genera and in situ polyploidy

The Chinese seed plant flora is one of the most diverse in the world and has a substantial amount of endemism (Wang 1989). Endemic genera represent approximately 10% of all Chinese spermatophytic genera. In our study of the flora of the Qinghai–Tibetan Plateau, 61 genera were Chinese endemics, and all were included in Wu (1991)'s areal types of Chinese endemic seed plant genera. The Himalayan orogeny and uplift of the Qinghai–Tibetan Plateau may have played an important role in the formation, development, and present-day distribution of Chinese endemic genera.

Our data showed that 259 species experienced in situ polyploidization. Stebbins (1951) proposed that the development of polyploidy in plant groups could be caused by both internal (growth, reproduction, genetics) and external (new niche space) factors. Hewitt (2000) thought dramatic climatic fluctuations during the Quaternary glaciation caused many plants and animals to migrate. We suggest that these phenomena may have greatly influenced polyploidization on the Plateau.

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### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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