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SHORT RESEARCH PAPER

Altitudinal variations in flower and bulbil production of an alpine perennial, *Polygonum viviparum* L. (Polygonaceae)

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ABSTRACT

Two opposite views exist regarding sexual *versus* asexual reproductive performance of *Polygonum viviparum*. One suggests that increasing altitude favors flower production, while the other suggests that increasing altitude increases bulbil production. In this study, we present an investigation of the reproductive performance of 13 populations of *P. viviparum* on the Qinghai–Tibet Plateau (QTP). Our results show that, with increasing altitude, the height of inflorescence and total number of flowers and bulbils decrease significantly, but there is no significant effect on bulbil and flower number. In addition, there is a weak correlation between the proportion of flowers per population and altitude in our study sites due to the exception population 12, which is in a disturbed habitat. We conclude that more resources might be allocated to flowers in populations at higher altitudes, indicating the importance of sexual reproduction over asexual reproduction in alpine plants of QTP.

INTRODUCTION

The Qinghai–Tibet Plateau (QTP) is the largest and highest plateau in the world, with an average altitude of about 4000 m a.s.l. and an area of approximate 2.5×10^6 km^2 (Zheng 1996). The southeast part of this plateau, the Hengduan Mountains, and adjacent areas comprise one of 25 global biodiversity hotspots (Myers *et al.* 2000). One of only two such hotspots in the northern hemisphere, it is renowned for its phyletic radiation and concomitant high levels of endemism (Ying *et al.* 1993). In addition, the Hengduan Mountains comprise a series of spectacular north–south ridges, alternating with deep valleys and altitudes ranging from 2000 to 6000 m a.s.l. (Li *et al.* 1995). The unique geomorphological configuration, complex topography, and diverse climate combine to make the QTP an area of worldwide importance for the evolution and adaptation of montane species, especially for endemic and highly specialized species. Comparisons of the reproductive ecology of different altitudinal populations enhance our understanding of reproductive adaptations to alpine environments. However, at present, little is known about the reproductive strategies of alpine plants inhabiting the QTP.

In alpine ecosystems, the limited opportunities for outcross pollination due to reduced insect diversity and activity, and the short growing season may favor evolution of self-pollination in plants (Körner 2003). Asexual reproduction provides a solution to limited outcross pollination opportunities in harsh alpine environments. Asexual reproduction can occur via stolons, runners, rhizomes, tubers, buds on bulbs and corms, layering of stems, agamospermy, or bulbils (Price & Marshall 1999). Among these diverse types of asexual reproduction, bulbils are unique because they are produced on the inflorescence, usually accompanied by flowers. Asexual reproduction via bulbils has been found in several families, including Polygonaceae, Liliaceae, and Saxifragaceae (Ronsheim & Bever 1987; Molau 1992; Bauert 1993). *Polygonum viviparum* L., a small viviparous perennial, is circumpolar and common in alpine and arctic areas (Callaghan & Emanuelsson 1985; Hultén & Fries 1986). Inflorescences of *P. viviparum* usually bear flowers in the upper part and bulbils in the lower part, thus enabling it to reproduce via both sexual and asexual reproduction. This makes *P. viviparum* an ideal plant to investigate the relationship between modes of reproduction.

The trade-off between flower number and bulbil number on a single inflorescence of *P. viviparum* has been described in different areas, but two opposing views exist regarding the relationship of these adaptations to increasing altitude: increased flower production (Law *et al.* 1983) *versus* increased bulbil production (Bauert 1993). These two opposing viewpoints suggest the importance of sexual or asexual reproduction at high altitudes, respectively. However, these previous studies on the reproductive performance of *P. viviparum* were carried out outside the QTP and in populations below 3000 m. Therefore, in this study, we present an investigation in the QTP on flower and bulbil production of *P. viviparum* in 13 populations, all of which are situated above 3000 m, to further investigate the relationship between sexual and asexual reproduction in high-altitude plant populations. Furthermore, we compared data from Law *et al.* (1983) and Bauert (1993) with our own data to understand the reproductive strategy of this plant over a broader geographical and altitudinal range. The objectives of the study were to examine: (i) variations in proportions of bulbils and flowers of *P. viviparum* along an altitudinal gradient in the QTP, and (ii) reproductive performance of this species in the QTP.

MATERIAL AND METHODS

Study species

Polygonum viviparum L. (Polygonaceae) is a viviparous plant with broad distribution in arctic and alpine areas in the northern hemisphere (Law *et al.* 1983; Callaghan & Emanuelsson 1985; Bauert 1993; Wookey *et al.* 1994; Diggle 1997, 2002; Diggle *et al.* 2002). At an early stage of growth, a rhizome is formed and continues to grow without branching for as long as the plant survives, a period which may exceed 26 years (Callaghan & Collins 1981). *Polygonum viviparum* can reproduce sexually via seeds (Law *et al.* 1983) and asexually via bulbils (Callaghan 1973; Engell 1973, 1978), although seeds are rarely observed in the field due to a low rate of fertilization and embryo/fruit abortion (Diggle *et al.* 2002).

Sample sites and methods

Our investigations were carried out in July 2007, on 13 populations of *P. viviparum* in Yunnan and Qinghai Provinces (Table 1). The altitude of the selected locations ranged from 3290 to 4810 m a.s.l., and all populations were in undisturbed natural habitats except population 12, which is in a tourism site. In each population, roughly 100 randomly selected inflorescences, separated by at least 10 m to guarantee that they were from different plants were collected. The height of each inflorescence was measured before collection, and bulbils and flowers per inflorescence were collected and counted. The proportion of flowers per inflorescence was calculated as (flower number)/(total number of flowers and bulbils).

Data analysis

Five variables were tested for each inflorescence: inflorescence height, flower number, bulbil number, total number of flowers and bulbils, and proportion of flowers to bulbils.

One-way ANOVA and *post hoc* LSD were used to analyse the differences in inflorescence height, flower number, bubil number, and proportion of flowers to bulbils among populations. We used two-tailed Pearson correlation coefficients to examine: (i) altitudinal trends of means per population in inflorescence height, total number of flowers and bulbils, and proportion of flowers, and (ii) the trade-off between flower number and bulbil number in all sampled individuals of the 13 populations. Statistical analyses were performed using SPSS version 13.0 (SPSS 2004).

RESULTS

Significant differences were found among the 13 populations in inflorescence height ($F = 183.1$, $P < 0.001$), bulbil number ($F = 48.7$, $P < 0.001$), flower number

Table 1. Location and habitat type of sampled populations of *Polygonum viviparum*.

location of sampled population	habitat type	longitude	latitude	altitude (m)
Yulong Snow Mountain, Yunnan	alpine scrubby meadow	E99°38′	N27°54′	3290
Tianbao Mountain, Yunnan	alpine scrubby meadow	E99°50′	N27°34′	3434
Tianbao Mountain, Yunnan	alpine scrubby meadow	E99°52′	N27°36′	3794
Baima Snow Mountain, Yunnan	alpine meadow	E98°59′	N28°24′	3890
Baima Snow Mountain, Yunnan	alpine meadow	E98°59′	N28°25′	3957
Baima Snow Mountain, Yunnan	alpine meadow	E98°59′	N28°25′	3994
Baima Snow Mountain, Yunnan	alpine meadow	E98°59′	N28°25′	4090
Baima Snow Mountain, Yunnan	alpine meadow	E98°58′	N28°22′	4347
Yeniugou, Qinghai	alpine meadow	E87°57′	N34°22′	4441
Baima Snow Mountain, Yunnan	alpine scrubby meadow	E99°00′	N28°24′	4469
Gaduojuwu, Qinghai	alpine scrubby meadow	E96°36′	N33°47′	4492
Niutoubei, Qinghai	alpine meadow (disturbed)	E97°31′	N34°54′	4606
Bayankala Mountain, Qinghai	alpine meadow	E97°39′	N34°07′	4810

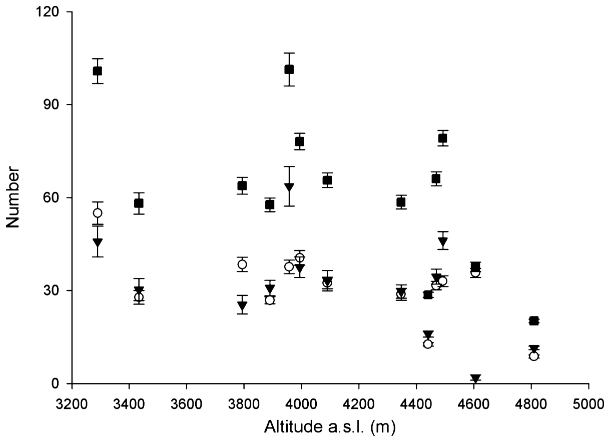

Fig. 1. Variations in the means of bulbil numbers (open circles, One-way ANOVA: F = 48.7, $P < 0.001$; two-tailed Pearson correlation: $r = -0.624$, $P = 0.23$), flower number (filled triangles, F = 30.9, $P < 0.001$; $r = -0.483$, $P = 0.095$), and total number of flowers and bulbils (filled squares, F = 98.3, $P < 0.001$; $r = -0.617$, $P = 0.025$) per population of *Polygonum viviparum* along the altitudinal gradient.

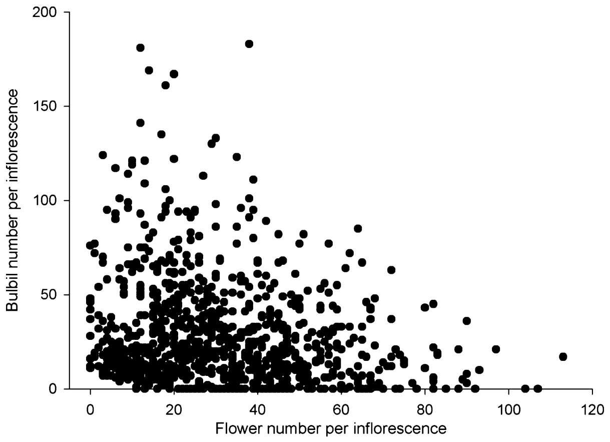

Fig. 2. Scatter diagram of the number of flowers and of bulbils per inflorescence in *Polygonum viviparum* in the 13 populations (two-tailed Pearson correlation, $r = -0.129$, $P < 0.001$).

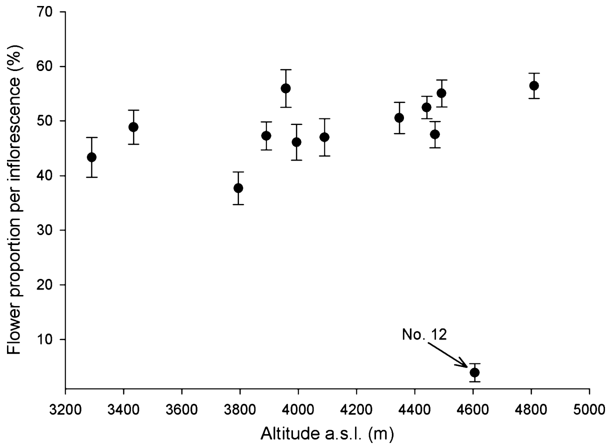

Fig. 3. Variation in the means of the proportion of flowers (flower number/total number of flowers and bulbils) per population of *Polygonum viviparum* along an altitudinal gradients (two-tailed Pearson correlation, $r = -0.07$, $P = 0.819$).

(F = 30.9, $P < 0.001$), total number of flowers and bulbils (F = 98.3, $P < 0.001$), and proportion of flowers to bulbils (F = 22.2, $P < 0.001$) (Fig. 1). With increasing altitude, inflorescence height ($r = -0.808$, $P = 0.001$), bulbil number ($r = -0.624$, $P = 0.23$), flower number ($r = -0.483$, $P = 0.095$), and the total number of flowers and bulbils ($r = -0.617$, $P = 0.025$) decreased (Fig. 1), but only the total number of flowers and bulbils decreased significantly.

There was a significant negative correlation between flower number and bulbil number when all inflorescences were pooled among populations (Fig. 2). Comparing the 13 populations, there was a negative, but not significant, correlation between altitude and proportion of flowers to bulbils per inflorescence (Fig. 3). However, population 12 is an outlier, and when this population was excluded, the correlation between altitude and flowers/bulbils was significantly positive ($r = 0.606$, $P = 0.037$).

DISCUSSION

Alpine environments are characterized by strong winds, high UV radiation, and low temperatures (Körner 2003) that might restrict plant growth with increasing altitude. Our study showed that the inflorescence height of *P. viviparum* declined with increasing altitude, accompanied by weak reductions in both flower number and bulbil number. This could be the result of decreased availability of resources (Körner 2003). Alternatively, decreasing height could benefit high-altitude plants by protecting them against wind and subsequent heat and water loss in the harsh environment (Gauslaa & Odasz 1990; Körner 2003). Therefore, a reduction in plant height of *P. viviparum* might decrease the negative effects of low temperature on growth and reproduction. Moreover, soil heat accumulation around plants may also have a positive effect on flower temperature, which may increase seed set and attractiveness to pollinators (Donnelly & Lortie 1998; Fabbro & Körner 2004). The reduction in plant height could also reduce animal herbivory or trampling at higher altitudes (Reekie 1998). Thus, the decline in inflorescence height of *P. viviparum* with increasing altitude might be an adaptation in harsh alpine ecosystems.

Two contrasting arguments can be used to predict either a decrease or an increase in sexual reproduction with increasing altitude. First, a decrease in sexual reproduction could be adaptive if pollination becomes increasingly unpredictable at higher altitudes. If this were the case, asexual reproduction through bulbil production would be favored, as found in *P. viviparum* by Bauert (1993). Second, asexual reproduction carries a cost of greater genetic uniformity (Mclellan *et al.* 1997) that might limit the ability of populations to adapt evolutionarily in the face of environmental uncertainty (Bell & Bliss 1980; Ronsheim & Bever 1987; Gugerli 1998). Thus, the increasing environmental uncertainty with increasing altitude might favor flower production, as found in *P. viviparum* by Law *et al.* (1983) and this study. These two possible adaptive scenarios are in conflict, because there is a trade-off between flower and bulbil production. A significant negative relationship between bulbil number and flower number on inflorescences of *P. viviparum*, was found in previous work for this species (Law *et al.* 1983; Bauert 1993). By pooling these published data and our data, we found an increasing trend to more flower production at high altitudes ($r = 0.691$, $P < 0.001$). However, the three study sites are quite different (arctic, Alps, and QTP), and bulbil production is also affected by environmental factors (Law *et al.* 1983; Bauert 1993, and references therein). Therefore, one should be cautious in drawing a conclusion of an increasing proportion of flowers to bulbils with increasing altitude without further sampling on a worldwide scale, although our results seem to support the existing data.

Our overall finding that the proportion of flowers/bulbils per inflorescence increases with altitude indicates that the advantages of sexual reproduction outweigh those of asexual reproduction at high altitudes. When including all 13 study sites, there was a non-significant trend, but excluding population 12, which had an extremely low proportion of flowers/bulbils, led to a statistically significant positive correlation. Population 12 is at a high site in the QTP (4606 m a.s.l.) in Maduo County, which has been a famous sightseeing area for the past 20 years because it is the source of the Yellow River. Sexual reproduction is more common in such disturbed habitats (Silvertown 2008), and human activities from tourism development are frequent in the summer, when *P. viviparum* is in full anthesis, and could disrupt insect pollinators in this area. Therefore, *P. viviparum* might depend more on asexual reproduction than on sexual reproduction because sexual reproduction becomes more unreliable due to long-term disturbance by human activities in this population.

Our results indicate that *P. viviparum* depends more on sexual reproduction at high altitudes, highlighting the importance of sexual reproduction in alpine plants. Nonetheless, seed production was rarely observed in *P. viviparum*, probably due to low rates of pollen viability or pollinator limitation (Diggle *et al.* 2002). However, the high level of genetic diversity in this species indicates frequent pollen flow between individuals in the QTP (Lu *et al.* 2007). Therefore, we speculate that *P. viviparum* might depend on bulbils for the maintenance of population size, but can also maintain high levels of genetic diversity when pollinators are available, as shown by the greater allocation to flowers in these high altitude populations.

After comparing 20 low-altitude species in 10 families and 30 high-altitude species in 15 families, Fabbro & Körner (2004) found that although the total aboveground biomass at higher altitudes was significantly lower than that at lower altitudes, the proportion of flowers at high altitudes was significantly higher than that at lower altitudes, suggesting the importance of outcrossing in alpine plants and its priority over growth. This is supported by our study, in which flower proportion increased with altitude. Furthermore, our results indicate the importance of sexual reproduction and its priority over asexual reproduction in *P. viviparum* at high altitudes, as also suggested by Silvertown (2008), who concluded that sexual reproduction is indispensable for plants to maintain long-term success, and that asexual reproduction is no substitute for sexual reproduction but can prolong the time a population can persist.

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