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Article

PATTERNS OF REPRODUCTIVE AND SEED DISPERSAL AND ECOLOGICAL SIGNIFICANCE OF THE CLONAL SPRING EPHEMEROID PLANT *Carex physodes* IN THE GURBANTUGGUT DESERT

Padrões de Reprodução e Dispersão de Sementes e Importância Ecológica da Planta Clonal Efêmera ***Carex physodes*** *no Deserto de Gurbantunggut*

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ABSTRACT - *Carex physodes* is an ephemeral species in the cold desert of Gurbantunggut in Northwest China. It has both asexual and sexual reproductive patterns. The primary aims of this study were to characterize the reproduction systems and identify the role of fruit dispersal in the sexual reproduction of *C. physodes*. Aboveground and underground biomass, root-shoot ratio, inflorescence biomass, fruit-set of *C. physodes* were measured and dispersal of perigynia and achenes in the natural habitat and indoor condition were studied. The underground biomass of *C. physodes* was approximately 10 times more than the aboveground biomass. The most parts of aboveground biomass is allocated to the inflorescence, which suggests that *C. physodes* allocates most biomass to the reproductive part. *C. physodes* produces perigynium with a pericarp containing one achene. The perigynia disperse at a much greater distance than achenes at both 1 and 4 m s^{-1} wind velocity, and the floating time of perigynia in water was much longer than that of achenes. Perigynia can hold more water and adher soil much more easily than achenes, which suggests that perigynia are suitable for wind dispersal, and they also adapt to spread at a long distance by occasionally rainfall. However, achenes may remain near the mother plants and only disperse at short distances. *C. physodes* is morphologically and physiologically adapted to the cold desert environment via a combination of characters associated with the rhizomatous and perigynium. This adaption may increase the opportunity of survival and expansion of population of *C. physodes*.

Keywords: *Carex physodes*, reproduction,dispersal pattern, perigynium

RESUMO - Carex physodes é uma espécie efêmera no deserto frio de Gurbantunggut, no noroeste da China, que possui padrões reprodutivos tanto sexuais como assexuais. Os objetivos principais deste estudo foram caracterizar os sistemas de reprodução e identificar o papel da dispersão dos frutos na reprodução sexual de ***C. physodes****. Foram medidas a biomassa aérea e de raízes, a razão raiz-parte aérea, a biomassa de inflorescência e a frutificação de* ***C. physodes*** *e estudada a dispersão de estames perigínicos e aquênios em habitat natural e ambiente interno. A biomassa das raízes de* ***C. physodes*** *foi aproximadamente dez vezes maior do que a biomassa aérea. A maior parte da biomassa aérea é alocada para a inflorescência, o que sugere que* ***C. physodes*** *aloca a maioria da biomassa para a parte reprodutiva. Ela produz estames perigínicos com pericarpo contendo um aquênio. Os estames perigínicos se dispersam a uma distância muito maior do que os aquênios na velocidade do vento de 1 e 4 m* s^{-1}*, e o tempo de flutuação dos estames perigínicos*

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na água foi muito maior que o dos aquênios. Os estames perigínicos podem reter mais água e aderir ao solo muito mais facilmente do que os aquênios, o que sugere que esses estames são apropriados para dispersão por vento; além disso, estão adaptados para dispersão por grande distância quando ocorrem chuvas ocasionais. No entanto, os aquênios podem permanecer perto das plantas-mãe e dispersar-se apenas por distâncias curtas. ***C. physodes*** *é adaptada morfológica e fisiologicamente ao ambiente do deserto frio por meio de uma combinação de caracteres associados aos rizomas e aos estames perigínicos. Essa adaptação pode aumentar a oportunidade de sobrevivência e expansão da população de* ***C. physodes****.*

Palavras-chave: *Carex physodes*, reprodução, padrão de dispersão, estames perigínicos.

INTRODUCTION

Reproduction is one of the key life history traits with effects on fitness (Ye et al., 2006; Liu and Chen, 2009). Many flowering plants produce both sexual and asexual offsprings, and they have different probabilities in their fitness characteristics (Bengtsson and Ceplitis, 2000). The rate of offspring production directly affects the fitness of an organism, hence it should be negatively correlated with other fitness components as postulated by life history theory (Stearns, 1992; Akhavan et al., 2016). As a result of limited resource availability, allocation to one activity such as vegetative reproduction is expected to reduce resources devoted to other activities. Hence, increased expenditure on clonal spreading may affect not only population density but also the rate of nutrient absorption, and all of the above may reduce the rate of growth or generative reproduction.

Ephemeral plants are an important component of vegetation in desert ecosystems. They appear immediately after snow melt or spring rain (Zhang and Chen, 2002). The life cycles of ephemeral plants lasts for only 3 months, and their aboveground parts perish at the end of the growing season, but new individuals can be produced in the next spring from underground live buds or seeds (Abudureheman et al., 2014). The reproduction phenology of spring ephemeral plants appears to represent a specific adaptation to the short period of high availability of resources (i.e. light, water and nutrients) (Hughes, 1992). Reproductive allocation of ephemeral plants is much higher than most annual and perennial plants; they adjust their reproductive output through flower and seed production (Olejniczak, 2001).

Carex is a globally distributed genus with more than 2,000 species of herbaceous perennials (Frodin, 2004). The habitats of *Carex* species are as diverse as the genus and range from dry open savannas and rain forests to wet meadows, deciduous and coniferous forests and Arctic tundra (Chant, 1993; Leck and Schütz, 2005). Some species occur in deserts (Schütz, 2000), and they have specialized dispersal patterns that adapt to dry conditions (Price and Marshall, 1999). Seed dispersal is important for avoiding competition in order for seeds to reach safe sites, which affects recruitment（pattern） and space-time patterns, and changes in plant diversity and distribution at both local and regional scales (Vormisto et al., 2004; Muller-Landau and Hardesty, 2005). Patterns of seed dispersal are determined by the dispersal-related fruit traits and seed characteristics (Alcantara and Rey, 2003). *Carex* species are characterized by a high proportion of species with buoyant achenes, which means an inflated perigynium, a corky pericarp and achenes with narrow edges. Hydrochory is particularly widespread in the genus *Carex* and many species are capable of floating for more than 100 days (Poschlod, 1990). However, there is little information about seed dispersal of *Carex* species in arid environments. Ellner and Schmida (1981) found that the seeds of most species in Israeli deserts have no dispersal structures, and that is the result of natural selection of seeds to remain near the mother plant. Thomson et al. (2011) suggested that unassisted and wind-dispersed seeds are the most common in desert species in India and only few species are animal-dispersed. For the genus of *Carex*, seed (achene) dispersal is especially not documented for the desert sedge (Busch, 2001; Janyszek et al., 2008; Abudureheman et al., 2014, 2016).

Carex physodes is a ephemeroid rhizomatous sedge, is 15-35 cm tall, and occurs just after snow melt. The perigynia quickly ripen within 40 to 60 days and the aboveground parts perish, but their underground organs remain alive and produce new individuals from underground buds or achenes in the next spring. Rhizome emitting subterranean stolons covered by fibrous scales. The stem is erect or ascending, greyish green. Flowering and fruiting occur from April to May. The plant has compact inflorescences with androgynous flowers. Infructescence contains inflated perigynium around the achenes (Figure 1; refer to Abudureheman et al., 2016). In the Gurbantunggut Desert of Xinjiang in China, this species is only distributed on mobile semi-fixed or fixed sand dunes (Liu, 1985) and often forms a single dominant species population (Wang et al., 2004). During the spring, *C. physodes* appears in dense abundance, distributed in various geomorphic positions with a preference for the top of the dune. Thus, *C. physodes* can be used to fix and stabilize sand in the spring, which is characterized by strong winds and sandstorms (Wang et al. 2003, 2004). However, only quantitative characteristics and achene germination are studied for this species (Abudureheman et al., 2014, 2016). As a clonal species, the study of the relationship between sexual and asexual-reproduction and dispersal pattern is essential to understand the reproduction strategy and ecological adaptation of *C. physodes.* Therefore, the objectives of this study were to quantify biomass allocation of the reproductive part and identify the dispersal abilities of the dispersal unit (perigynium), in order to illustrate the adaptation strategy and the regulatory mechanism of this species in the desert environment.

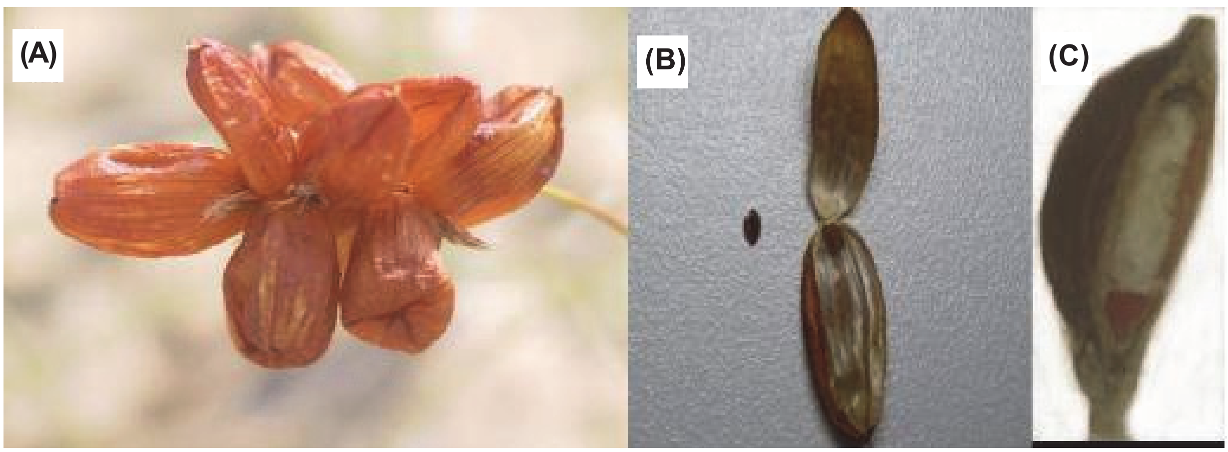

Figure 1 - *Carex physodes*. Infructescence showing an inflated perigynium around each achenes (A); Achene removed from perigynium (left) and perigynium opened to show achene (right) (B); Embryo and endosperm (C).

MATERIALS AND METHODS

Site description

The Gurbantunggut Desert is located at the center of the Junggar Basin in Xinjiang, which is the second largest desert in China, with an area of 48,800 km^2 (Hu et al., 1962). The mean annual temperature is 6-10 °C, and the maximum temperature rises above 40 °C in July. The minimum temperature is -40 °C and snow accumulates to a depth of 20 cm in the winter. Mean humidity is about 50-60%. The mean annual precipitation is approximately 79.5 mm, and 29% of the rain falls in April and May (Zhang and Chen, 2002). The mean potential annual evaporation is 2607.0 mm (Zhang et al., 2006), which is 20-30 times greater than precipitation. It belongs to the typical inland arid zone. Mean temperature and precipitation were 13.6 °C and 24.7 mm in April, respectively, and 19.4 °C and 19.1 mm in May, respectively (Climatological data from the Cainan Oil Station of the Gurbantunggut Desert for years 2006-2012). Precipitation in winter and spring creates a favorable condition for the growth of ephemeral plants (Wang et al., 2004).

Three sites in the Gurbantunggut Desert were selected (site 1 at 44°592’823” N, 88°232’ 203” E; site 2 at 45°002’783” N, 88°222’943” E; site 3 at 44°572’023” N, 88°222’853” E). Mature fruits and achenes were collected from the natural population in May, 2011, and stored at ambient conditions in the laboratory (18-25 °C, 15-20% RH) in paper bags until used.

Aboveground and underground biomass allocation

To understand the biomass allocation characteristics of this species to the reproductive part and clonal part, the aboveground and underground biomass allocation is measured. In each sand dune, a 5 m x 20 m scale was established. Five 0.5 m x 0.5 m quadrats from each sand dune were conducted. The aboveground and underground parts of each ramet from each quadrat of each sand dune were harvested at 15th of May and their biomass was determined after drying in an oven at 85 ^{o}C for 24 h.

Fruit-set

To identify the biomass allocation patterns to sexual reproduction part, the flowers of inflorescence of 50 ramets from each sand dune were randomly selected and the number of flowers was counted. At the beginning of perigynium development, the number of perigynia of each infructescence was counted. The fruit-set was calculated as: mean number of mature perigynium/mean number of flowers (Winfree et al., 2009).

Color, shape, size and mass of perigynium and achene

To understand the morphology of the perigynium and the achene, the color and shape of perigynia (diapersal unit) and achenes were observed, and 50 perigynium and achenes were randomly chosen and measured for size (length and width) by using SF2000 digital calipers and five replications of 100 perigynium and achenes were weighed for mass by using a Sartorius BS210S electronic balance (0.0001 g) in June, 2011.

The hydration and dehydration of perigynia and achenes

The hydration and the dehydration tests were conducted to study the role of inflated perigynia. Perigynia and achenes were placed in 9 cm diameter Petri dishes on filter paper moistened with distilled water at room temperature, using three replicates (100 perigynium and achenes for each). They were weighed to the nearest 0.0001 g by using a digital analytical balance after 0 h, 1 h, 2 h, 4 h, 6 h, 12 h. Then, they were weighed every 24 h until there was no further increase in mass. The surface water of each perigynium and achene was dried in each weighting, and then the perigynia and achanes were returned to moist filter paper in Petri dishes (Funes and Venier, 2006). Further, the perigynia and achenes in each Petri dish were naturally dried at air temperature and then weighted every 0.5 h for 4 h. After that, they were weighted every 1 h interval to their initial mass. The amount of absorbed/dehydrated water was determined as the actual increase/decrease in the weight of perigynia and achenes and then converted to percentage. Percentage increase/decrease in the mass of perigynia and achenes was calculated using the following formula (Hidayati, 2000):

$$\text{Percentage increase/decrease in mass (\%)} = W_i\text{-}W_d/W_d x100$$

where W_i and W_d = imbibed/dehydrate and initial mass of perigynia or achenes, respectively.

Dispersal characteristics

In the windy desert, the morphological features of dispersal units have a significant effect on anemophilous dispersal. In July, 2011, the effect of vesicular pericarp on the dispersal ability of perigynia was determined by the following procedures: (a) Dispersal of the perigynia in the field. Thirty plants randomly marked in natural populations and all perigynia of per plant were stained with painting stain when the perigynium ripened. Record were made of the beginning and end of dispersal time of perigynia in each plant. (b) To measure the fall rate of perigynia and achenes, a tube 120 cm tall and 15 cm wide was used. One hundred perigynia and achenes were released individually from the top of the tube, and the time required for them to fall from the release point to the bottom of the tube was measured with a digital stopwatch. Fall rate (cm s^{-1}) was calculated over this height (Gravuer et al., 2003). (c) 100 perigynium and achenes, which were parallel to the flat perigynium/achene-landing surface, were exposed for 60 s to a constant stream of air produced by an electric fan. The perigynia and achenes were released from the front of the fan at a height of 30 cm and exposed to wind velocities of 1 and 4 m s^{-1}, and the distances they traveled were measured to 0.001 m (Telenius and Torstensson, 1989). (d) In the natural environment, surface runoff formed by precipitation has certain influence on the dispersal of perigynia in surface soil. In order to confirm the effect of vesicular pericarp on perigynium dispersal at surface runoff, the water floating characteristics of perigynium and achenes was studied comparatively at the lab. The perigynia and achenes (30 dispersal units in each) were placed in 5 containers of 10 cm in diameter and 20 cm in depth, filled with 600 mL tap water. The sedimentation coefficient of perigynium in each container was recorded every 12 h for 10 d and there was a 4 d interval after that until the whole perigynia were sedimented. For achenes, it was recorded every 4 h on the 1st d and 24 h after that (Mamut et al., 2014).

Statistical analysis

All data analyses were performed with SPSS version 16.0 (SPSS Inc, Chicago, Illinois, USA), and all data were expressed as mean±SE. Data were analyzed for normality and homogeneity of variance prior to analysis to fulfill requirements of one-way ANOVA. One-way ANOVA was used to analyze the difference between flowering rate, aboveground and underground biomasses, fruit (perigynium)-set patterns and the effects of the pericarp on the dispersal distance of the perigynia. Duncan's test was performed for multiple comparison to determine significant ($p<0.05$) differences among levels of each treatment. When the transformed data were still not homogenous, differences were determined by the Tamhane's T2 test. Statistical tests were conducted at $p=0.05$ (Sokal and Rohlf, 1995).

RESULTS AND DISCUSSION

Aboveground and underground biomass allocation and fruit-set

This species allocated more biomass in the underground part 422.07 (SE=107.07) mg, and there was approximately 10 times more underground biomass than aboveground biomass 36.27 (SE=3.86) mg. The root-shoot ratio was 10.84 (SE=0.63), and inflorescence biomass 28.23 (SE=4.53) mg occupied a large percentage of aboveground biomass. Flower numbers were 8.65 (SE=0.81) and fruit set was 75.47 (SE=2.61)%.

Color, shape, size and mass of perigynia and achenes

The perigynia are globose or elongate, conical or cylindrical, brown or scarious, with length of 11.95 (SE=2.29) mm, width of 6.49 (SE=1.24) mm, thickness of 4.13 (SE=1.09) mm. The weight of 100 perigynia was 0.70 (SE=0.08) g. Each perigynium contains one achene. Achenes are spherical, bi-convex and light brown in color. The length of the achene was 3.58 (SE=0.45) mm, width was 1.81 (SE=0.25) mm, thickness was 1.21 (SE=0.12) mm and 100 achene mass was 0.25 (SE=0.002) g (Figure 1).

The absorption and dehydration dynamics of perigynia and achenes

Perigynium absorb water more quickly than achenes, and the imbibition rate was over 137.54% within 1h, and it reached 890.04% in 120h (Figure 2A). By contrast, achenes absorb water slightly and the imbibition rate reached 24.51% after 120h (Figure 2B). Dehydration of perigynia and achenes was faster than absorption, and they dehydrated to their initial weight after 4 h and 6 h, respectively. It was shown the coat of achenes and the pericarp of perigynia had no significant differences in maintaining water.

Natural dispersal characteristics of perigynia of *C. physodes*

In natural habitat, *C. physodes* flowers in April and perigynia ripen in mid-May, and it (the perigynia) disperses until mid-August.

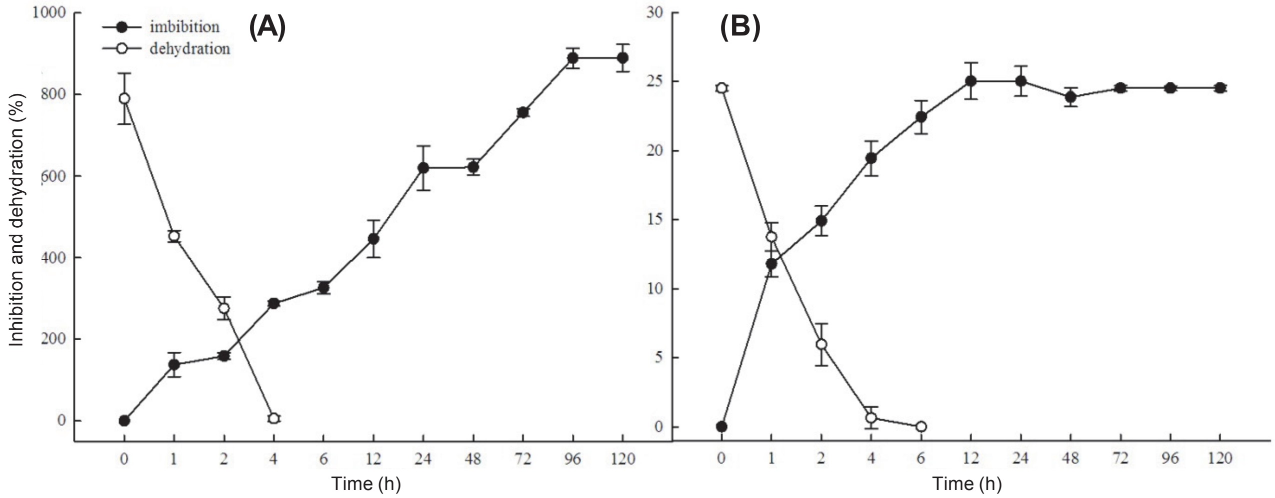

Figure 2 - Imbibition and dehydration curve of fruits (perigynium) (A) and seeds (achene) (B) of *Carex physodes*.

The effects of the pericarp on the dispersal of perigynia under wind velocity

The perigynia and achenes differed significantly in landing time, fall rate and dispersal distance (Table 1; P<0.001), and the perigynia take a longer time than achenes to fall a specific distance. This suggested that the dispersal ability of perigynia will be much greater than those of achenes. The dispersal distances of perigynium in a parallel stream of air were usually considerably greater than those of achenes at wind speeds at both 1 and 4 m s^{-1} (Table 1).

Table 1 **-** Effects of wind speed on dispersal distance of the fruits (perigynium) and seeds (achene) for *Carex physodes*

Rate of descent	Fruit (perigynium)	Achene	*F-value*	*P-value*
Fall time (s)	0.75±0.01 a	0.40±0.01 b	461.72	<0.001
Fall rate (cm s^{-1})	48.14±1.15 a	109.88±2.27 b	430.21	<0.001
Dispersal distance (cm) - 1m s^{-1}	9.44±0.30 a	5.65±0.44 b	577.80	<0.001
Dispersal distance (cm) - 4 m s^{-1}	50.07±1.18 a	16.43±0.36 b	738.54	<0.001

Note: Different letters within a row indicate significant differences (One-Way ANOVA, P=0.05).

The effects of pericarp on dispersal of perigynia in water

The lab experiment results showed that the achenes remained afloat for 264 h; however, the perigynia floated<10% for 9d, and then fell quickly, and they remained afloat after 38 d (Figure 3).

Species prioritize to allocate resources to organs that maximize their own survival and fitness (Poorter and Nagel, 2000). In the desert ecosystem, water (limited resource) availability is both unpredictable and highly variable. Ecological theories for the expression of phenotypic plasticity predict that plants from competitive environments should increase allocation for clonal propagation to escape harsh environmental conditions (Grime and Mackey, 2002). This study found that the underground biomass of *C. physodes* was approximately 10 times higher than that of aboveground biomass, and ramet production seems to be the most efficient way of achieving high reproductive success; thus, vegetative reproduction by means of rhizomes is responsible for establishment of the population in the dune habitat. There is a trend for overall water loss through transpiration and increase in the absorptive surface area exposed to the sandy habitat by clonal integration (Xie et al., 2007). This suggests that environmental selective forces result in modification of reproductive strategies of clonal species (Silvertown and Doust, 1993; Li et al., 2005).

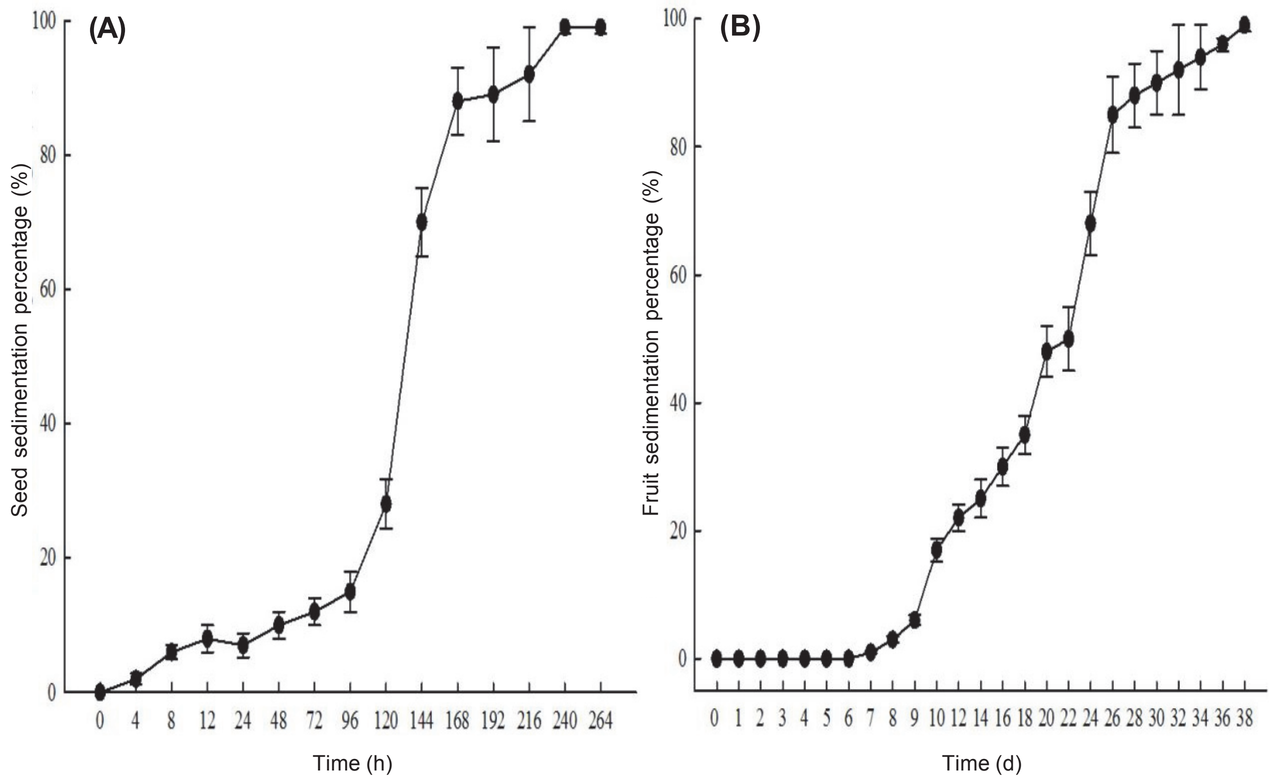

Figure 3 - Flotation dynamics of seeds (achene) (A) and fruits (perigynium) (B) of *Carex physodes* on still water.

Seed production is thought to be more nutrient-demanding than vegetative reproduction (Harper, 1977). As the amount of nutrients is more critical in seeds, their cost will increase faster than the cost of ramets when nutrient availability is low (Olejniczak, 2001). Thus, the model of Olejniczak (2001) predicts a relatively higher rate of ramet production in nutrient-poor soils. Although *C. physodes* allocate a great amount of biomass to the underground part because it has high root-shoot value, this species also has high fruit-set, suggesting that *C. physodes* allocates almost all biomass to reproduction.

Habitat features have a significant effect on size and number of diaspores (Kelly and Sork, 2002; Azcarate et al., 2002; Franzén, 2004). Diaspore morphology strongly determines seed dispersal patterns (Wender et al., 2005). In the desert, diaspores have evolved different morphological structures that enhance their probability of escaping the harsh, variable environment as well as dispersed away from their mother plant (Venable and Lawlor, 1980; Wender et al., 2005). Leck and Schütz (2005) showed that sedges achenes vary considerably in size, and many *Carex* species produced smaller perigynia while growing in dry localities than populations of the same species that occur in wet habitats. However, compared to wetland *Carex* species, the perigyna of *C. physodes* have a much larger vesicular pericarp, which indicates a significant part of their dispersal ability, a finding that reinforces the better dispersal ability of the larger dispersal units. The perigynium of *C. physodes* has a vesicular pericarp, thus wind dispersal is the major mechanisms of dispersal in *C. physodes*. After plants of *C. physodes* complete their life cycle in late May to early June, perigynia decrease their terminal velocity and thus prolong their fall time, which increases the chance of these perigynia of being carried away from the mother plant by wind events. However, achenes are usually dispersed near the mother plants. Our lab experiments showed that the perigynia dispersed at a longer distance than achenes at both 1 and 4 m s^{-1}. They suggest that the pericarp increases the buoyancy of perigynia in the air and expands the new living space of *C. physodes*, thereby increasing the opportunity of survival and expansion of the population. Apart from the vascular pericarp, the light brown-colored perigynia are more similar to the color of the living environment and thus is advantageous in order to escape from predators (Meyer and Carlson, 2001). Thus, perigynium size and color can be interpreted as a response to habitat conditions in desert environments.

Many wind dispersal fruit can also be floating in the water (Li and Qiang, 2007). Water dispersal is particularly widespread in the genus *Carex* and many species are capable of floating for more than 100 d (Poschlod, 1990). The indoor settlement experiment showed that floating time of the perigynia of *C. physodes*is is much longer than that of the achenes, which suggests that when the runoff formed by occasional rainfall occurs in the desert, the pericarp of *C. physodes* increases dispersal distance of the perigynia. The results of the still-air experiment can be used to predict that after maturation, perigynia are dispersed further by wind than achenes. After plants of *C. physodes* have completed their annual life cycle, the pericarp of perigynia decreases their terminal velocity and thus prolongs their fall time, which increases the chance of these achenes being carried away from the mother plant by wind currents. However, achenes are usually dispersed near the mother plants, which serves to leave descendants in safe sites occupied by their parents.

When rain occurs, the pericarp rapidly and greatly absorbs water (the hydration rate of perigynium was up to 800%), which aids the achenes with moist condition, thus extending the effective period over which germination can occur. When perigynia are not removed, achenes settle in the local environment and the pericarp enables a germinating seedling to survive until the next rainfall event by slowing desiccation. The great increase in mass of these perigynia after hydration prevents them from being further dispersed by wind from favorable microhabitats (Huang and Gutterman, 2004), delays or prevents achene collection by insects, thereby avoiding achene loss (Gutterman, 1993), or promotes settlement of achenes onto the soil (Huang et al., 2000). By contrast, achenes slightly take up a smaller amount of water. Perigynia and achenes rapidly dehydrate the water and the dehydration time of perigynia and achenes are not different. Thus, on the soil surface, perigynia have no advantage over achenes.

In conclusion, *C. physodes* is suitable for wind dispersal, and adaptation to further spread by occasional rainfall in the summer and autumn. During summer and autumn, when rain occurs and the soil is moist, perigynia rapidly absorb water, which is beneficial to the adherence of perigynia to the soil surface and settling in local sites.

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