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# Reproductive ecology of *Potamogeton pectinatus* L. (= *Stuckenia pectinata* (L.) Börner) in relation to its spread and abundance in freshwater ecosystems of the Kashmir Valley, India

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**Abstract:** The introduction and spread of various weed species in aquatic ecosystems is one of the major contemporary ecological concerns. Control and management of these weed species warrant detailed studies on reproductive ecology that aid in identification of key pathways, processes and factors that will help in devising management strategies. It is in this context that studies of the reproductive ecology of *Potamogeton pectinatus* L. (= *Stuckenia pectinata* (L.) Börner) were undertaken, with emphasis on identifying the modes of reproductive strategies that the species employs to achieve widespread occurrence in Kashmir Himalayan freshwater ecosystems. The species is a troublesome weed in water bodies, irrigational channels and drinking water reservoirs of Kashmir Himalaya. The species inhabits water bodies with different flow conditions. Detailed investigations revealed that the species employs several clonal (tubers, rhizomes, nodal plantlets) and sexual (fruits) modes of reproduction. Sexual fruits, tubers and nodal plantlets are the most important reproductive propagules in standing-water habitats, while in running-water habitats propagation is through tubers and rhizomes. In addition, plant fragments aid in the spread of this species. Thus, a highly flexible reproductive strategy is one of the key factors that contribute to the rapid spread of the species across a wide range of habitats in Kashmir Himalaya.

**Key words:** Ecological concerns; management; reproductive strategies, weed.

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## Introduction

Aquatic angiosperms, in particular, operate mixed reproductive strategies involving sexual and clonal reproduction, and disperse by both seeds and vegetative propagules (Cook 1985, 1987; Eckert 2002; Grace 1993; Honney & Bossayt 2005). Tradeoffs between sexual and clonal reproduction have been demonstrated in many species, and have been found to be influenced by plant size (Gardner & Mangel 1999; Worley & Harder 1996), competition (Rautiainen *et al.* 2004), nutrient levels (Lui *et al.* 2009), successional stages (Sun *et al.* 2001; Weppler & Stocklin 2005), and population age (Piquot *et al.* 1998; Weppler *et al.* 2006). Though the relative importance of sexual vs clonal reproduction may vary widely across species, few studies have quantified intraspecific variation in

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their relative importance (Dorken & Eckert 2001; McKee & Richards 1996) and fewer still have identified ecological and/or genetic causes (Barrett 1980a, b; Eckert *et al.* 1999; Eckert *et al.* 2000; Piquot *et al.* 1998) or consequences of reproductive variation (Aspinwall & Christian 1992; Dorken & Eckert 2001). The extent of clonal vs sexual reproduction within a population, in turn, affects genet persistence, mating patterns, and genotypic diversity (Barrett *et al.* 1993; Eriksson 1993; Grace 1993; Pan & Price 2002; Silander 1985; Gunarathne & Perera, 2016). Assessing the relative importance of sexual vs clonal propagules among populations can thus provide insight into the demographic and evolutionary processes underlying successful colonization and spread of aquatic vascular plants (Okada *et al.* 2009). Moreover, information on the spatial pattern of reproduction and dispersal of sexual and clonal propagules can lead to the design of effective strategies for managing aquatic plants (Davies & Sheley 2007). One such notorious aquatic weed is sago pondweed or fennel pondweed [*Potamogeton pectinatus* L. (= *Stuckenia pectinata* (L.) Börner], of the family Potamogetonaceae, a perennial aquatic macrophyte with a wide distribution (Kantrud 1990; Wiegleb 1988; Wiegleb & Kaplan 1998). It grows abundantly within the area of its distribution (Anderson 1978; Van Wijk 1988; Kantrud, 1990), and in many countries it is a troublesome aquatic weed (Kantrud, 1990; Pieterse & Murphy 1990;). Van Wijk (1988, 1989 a,b) and Kantrud (1990) elaborately investigated the ecology and reproductive strategies of this species, and Pilon *et al.* (2003) and Santamaria and Garcia (2004) investigated the effect of latitude on the induction of tuberisation in the species. In the field, tubers of *P. pectinatus*s were found to germinate at temperatures as low as 5.5 °C after winter stratification (Van Wijk 1983). Hay *et al.* (2000, 2008) reported that *Potamogeton* fruits survive desiccation; however, very little is known about reproductive ecology despite the widespread distribution of *P. pectinatus,* particularly with respect to flow condition. It is against this back-drop that the present study has been carried out. *Potamogeton pectinatus* reproduces both sexually and asexually. Being an aggressive colonizer in a wide array of ecological circumstances, the species grows abundantly in almost all freshwater ecosystems in the Kashmir Himalaya, including lakes, ponds, rivers, streams, canals and water reservoirs. The species was examined in an *ex-situ* growth experiment, to assess flexibility in reproductive strategies with respect to flow condition. *In- vitro* studies on fruit germination and tuber sprouting were carried out to evaluate the range of environmental conditions for these propagules, and their reproductive potential.

The luxuriant growth of *P. pectinatus* has serious ecological and economic implications, such as degradation of water quality, reduction of the flow of water in irrigation channels, and choking of the outlet of water bodies, resulting in sedimentation and eutrophication of these prized ecosystems. We hypothesized that multiple, habitat-specific modes of reproduction (particularly with respect to flow) of *P. pectinatus* are the underlying reason of its widespread occurrence in different aquatic habitats of Kashmir Himalaya. Knowledge about habitat-specific reproductive strategies and life-history patterns, including types of propagules and their time of formation and germination/sprouting, is very important for long-term management of this aggressive weed. The present study addressed the following questions:

a) What are the different types of reproductive strategies operating in *P. pectinatus*?
b) Are the reproductive strategies habitat-specific?
   An *ex-situ* experiment was undertaken to assess the flexibility of these strategies and traits with respect to flow.
c) What are the conditions that promote fruit germination and tuber sprouting in this species?
d) To what extent does the efficiency of these reproductive strategies enable the species to grow under different hydraulic conditions?

## Materials and methods

### *Study sites*

The present study was carried out in four aquatic habitats, namely Dal Lake, Anchar Lake, Aarpath Rivulet, and Nambal Stream. The geographical location of the selected sites and their characteristic features are summarized in Table 1. The habitats are located in the northern fringe of the Indian subcontinent, and are surrounded by a girdling chain of the Himalaya Mountains, namely PirPanjal in the south and the great Himalayan range in the south to northeast (Fig. 1). The Kashmir Valley has a network of glaciated streams, rivulets and rivers as well as alpine, sub-alpine and valley lakes which supports a rich diversity of aquatic vegetation.

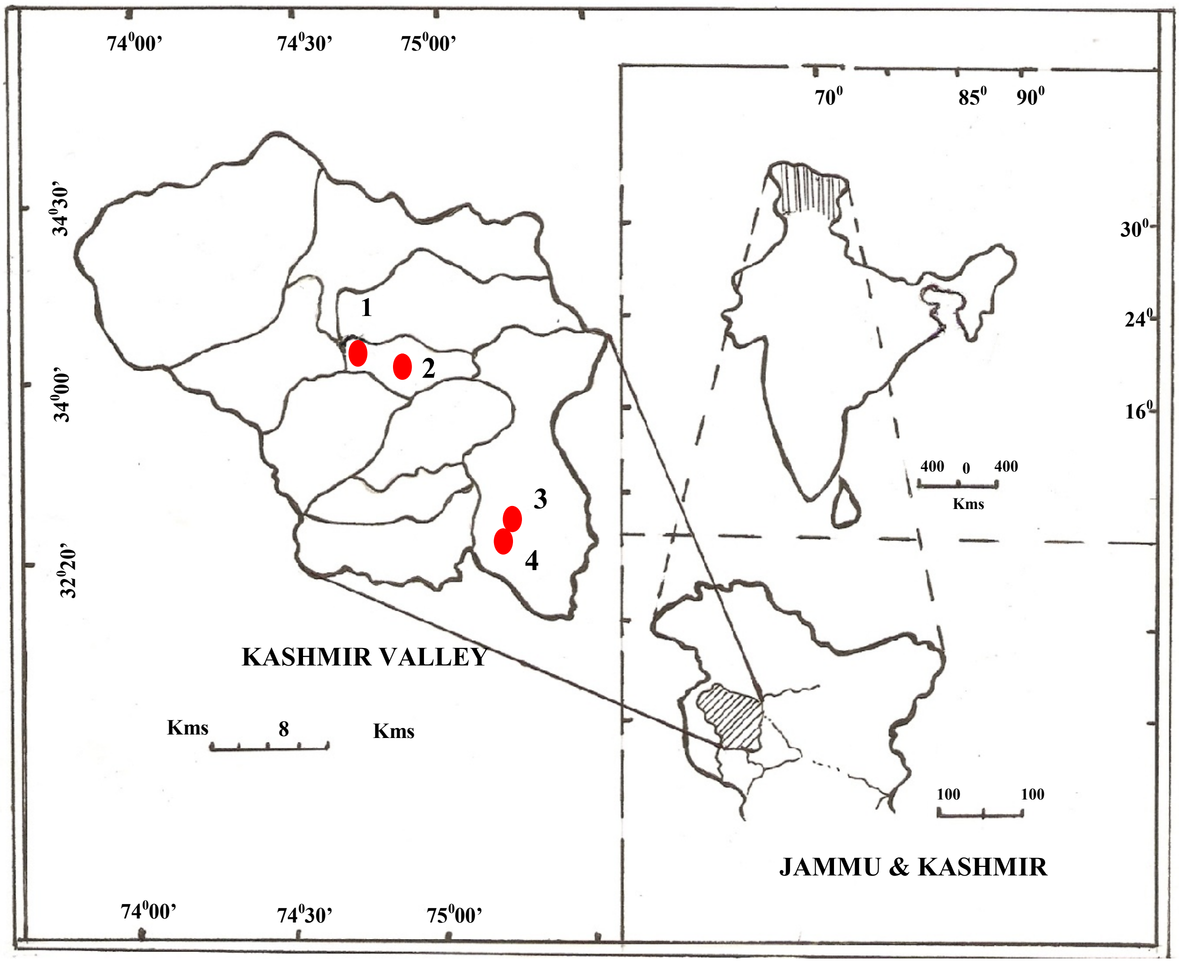


**Fig. 1.** Map of Kashmir Himalaya showing study sites (1 = Anchar Lake; 2 = Dal Lake; 3 = Aarpat Rivulet; 4 = Nambal Stream).

The sites sampled can be grouped into two sets, according to the overall current conditions:

A. Standing waters: Anchar Lake (AL) and Dal Lake (DL).

B. Running waters: Aarpath Rivulet (ARRA) and Nambal Stream (NBSA).

The water flow of the running-water study sites was measured during peak growth period (June-July) by the float and cross-section method following Kuusisto (1996), with Nambal Stream having a flow of 277l $s^{-1}$ and Arpath Rivulet 884 l $s^{-1}$.

## *Life history and traits*

Thirty two fully developed individuals (each a complete clonal unit consisting of ramets connected by rhizomes) were tagged and sampled at each selected sampling site (sampling site was 200 - 400 m long and 15 - 20 m wide depending on the water body, but with similar environmental conditions). These individuals were randomly collected from 10 $m^2$ quadrats (8 quadrats at each site, approximately 20 metres apart) and from each quadrat 4 clonal units (individuals) were sampled; in each quadrat, the clonal units were sampled as far as possible from each other, in order to sample all the clonal units of a given site under similar conditions, while minimizing the risk of sampling ramets from the same individual. These individuals were tagged and examined throughout the growing season [twice a week for 10 months i.e. from March to December every year (2005 - 2009)] to study the life-history pattern (sprouting, vegetative growth, flowering, fruitingperiods and senescence), reproductive traits (number of spikes, flower number and fruit number per individual), number of tubers per ramet (both axillary and rhizome tubers), and number of nodal plantlets from all the selected sites. The number of vegetative propagules per individual, the timing of

**Table 1.** Salient features of some aquatic sources of *Potamogeton pectinatus* in Kashmir valley J & K - India.

| Site (District) | Salient features of the water body | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Nature | Location | Altitude (m.a.s.l.) | Latitude (north) | Longitude (east) | Area (sq. km) | Maximum depth (m) | Runnig/standing waters | Nature of substratum |
| Anchar lake (Srinagar) | Urban valley lake | 12 km NW of Srinagar | 1595 | 34° 08'25" | 74°.46'12" | 6 | 4.5 | standing water | Muddy |
| Dal lake (Srinagar) | Urban valley lake | 3 km of Srinagar | 1595 | 34° 04'59" | 74° 50'29" | 11.5 | 6 | standing water | Muddy |
| Aarpath rivulet of Brakapora (Anantnag) | Rivulet | 56 km SE of Srinagar | 1600 | 33° 43'09" | 75° 11'04" | - | 2.0 | running waters | Hard stony |
| Nambal rivulet of Barakapora (Anantnag) | Stream | 55 km SE of Srinagar | 1605 | 33° .42'40" | 75° 11'36" | - | 1.25 | running waters | Hard stony |

their formation, and the timing of different phenophases were also recorded from all the collection sites throughout the growing season. To workout the resource allocation, the individuals collected were washed in tap water and dried using blotting paper at the end of the growing season. The ramets were divided into individual parts (shoots, rhizomes and roots, spikes, fruits, and tubers), and oven-dried at 80 °C for 48 hours (Kawano & Masuda 1980); the dry mass of each component was determined using an electronic balance. The dry mass of the different plant parts was compared with total dry mass to calculate the resource allocation.

## In vitro *fruit germination*

For germination studies, the fruits of the species were randomly collected from the selected sites and washed with 0.1 % mercuric chloride for 5 - 7 minutes, followed by washing 4 - 5 times with distilled water. The fruits were then subjected to different physical and chemical treatments for 45 days. The physical treatments included 60 days' wet chilling, and surgical exposure of embryo; the chemical treatments consisted of treatment of fruits with different concentrations of $GA_3$, or concentrated sulphuric acid, for different time durations (2, 5, 10, 20, 30, 40 and 50 minutes). All the experiments were conducted in incubation cabinets with temperature, light and humidity controlled (Table 2). Cool white fluorescent 18-W tubes (Philips India Ltd. Mohali, India) provided irradiance (400 - 700 nm) of ~400 μ mol $m^{-2}$ $S^{-1}$. For the treatment solutions, deionized water and analytical grade chemicals were used. Treatments were applied to 15 fruits placed in a closed glass petri-dish on Whatman No. 1 filter paper moistened with 15 ml of the treatment solution in question or distilled water (control). Fruits planned for dark treatment were moistened under green light and then quickly wrapped in aluminium foil to reduce the chances of inadvertent exposure to light. The whole experiment was set up with five replicates. The plumule (which emerges first in *Potamogeton*) was used as the indicator of germination, and total germination in each unit was recorded at the end of the experiment.

## In vitro *tuber sprouting*

The effects of environmental conditions on the sprouting of asexually produced tubers were studied *in vitro*. The tubers were set to sprout under different temperature regimes (10, 15, 20, 25, 30 °C), varying light exposures (light and dark), and under four different moisture treatments (5 cm, 10 cm above sediment, at field capacity and at half the field capacity) (Table 3). To test the effect of sediment on tuber sprouting,

**Table 2.** Effect of various treatments on germination of fruits of different ages of *Potamogetan pectinatus* under alternate light and dark (L) and continuous dark (D) conditions at 25 °C.

| Treatment | Year | Light regimes | Percent fruit germination (Mean ± SE) |
|---|---|---|---|
| 60 days wet chilling | $E_0$ | L | 6.14 ± 1.83 |
| | | D | NFG |
| | $E_1$, $E_2$, $E_3$ | L | NFG |
| | | D | NFG |
| Surgical exposure of embryo (cut of epi-, meso- and endo-carp) | $E_0$ | L | 48.93 ± 1.83 |
| | | D | 33.03 ± 1.83 |
| | $E_1$ | L | 34.92 ± 1.83 |
| | | D | 28.78 ± 1.83 |
| | $E_2$ | L | 21.14 ± 1.83 |
| | | D | 12.28 ± 1.83 |
| | $E_3$ | L | NFG |
| | | D | NFG |
| Cut of fruit wall +1.5milimolar (mM)$GA_3$ | $E_0$ | L | 54.78 ± 1.83 |
| | | D | 35.21 ± 1.83 |
| | $E_1$ | L | 33.00 ± 1.83 |
| | | D | 28.78 ± 1.83 |
| | $E_2$ | L | 21.14 ± 1.83 |
| | | D | 12.28 ± 1.83 |
| | $E_3$ | L | NFG |
| | | D | NFG |
| Cut of fruit wall +1mM of $GA_3$ | $E_0$ | L | 52.77 ± 1.83 |
| | | D | 35.01 ± 1.83 |
| | $E_1$ | L | 35.01 ± 1.83 |
| | | D | 26.57 ± 1.83 |
| | $E_2$ | L | 18.43 ± 1.83 |
| | | D | 12.28 ± 1.83 |
| | $E_3$ | L | NFG |
| | | D | NFG |

E0 = Fresh fruit; E1 = 1 year old fruit; E2 = 2 year old fruit; E3 = 3 year old fruit; NFGF = No fruit germination.
Note: The fruit in which fruit wall was not cut, did not germinate at all when treated with different concentrations of $GA_3$, and concentrated sulphuric acid for different time durations, nor did the untreated (control) fruits germinate.

containers with and without sediment were exposed to five different temperature regimes (10, 15, 20, 25, 30 °C) and two different moisture conditions (water maintained at 5 and 10 cm). Ten replicate glass containers were set up for each treatment combination (Table 4). Each of the containers with sediment received 500 g (dry weight).

Five propagules from each site were placed in each container. Different moisture levels were maintained daily by adding the necessary quantity of distilled water. The amount of water to be added to the containers with sediments had been estimated before the start of the experiment by using Buckner's funnel. All containers were kept for thirty days in growth chambers with automatic temperature and light controls. Tubers intended for dark treatment were moistened under green light and then wrapped quickly in aluminium foil; but tubers in alternating light and dark treatments (12 hours light and 12 hours dark) were not covered with aluminium foil. Light was provided by four cool white fluorescent 18 W tubes (Phillips India Limited), providing a light intensity of 1,015

**Table 3.** Effect of moisture content and temperature on sprouting of tubers under alternate light and dark (L) and continuous dark (D) conditions.

| Treatment | Temperature °C | Light regimes | Percent tuber sprouting (Mean±SE) |
|---|---|---|---|
| Flooded water level 5 cm above sediment | 10 | L | NTS |
| | | D | NTS |
| | 15 | L | 46.92 ± 5.45 |
| | | D | 46.92 ± 5.45 |
| | 20 | L | 81.14 ± 5.41 |
| | | D | 59.21 ± 5.41 |
| | 25 | L | 90.00 ± 5.41 |
| | | D | 68.06 ± 5.41 |
| | 30 | L | 26.57 ± 5.41 |
| | | D | 17.71 ± 5.41 |
| Flooded water level 10 cm above sediment | 10 | L | NTS |
| | | D | NTS |
| | 15 | L | 46.92 ± 5.41 |
| | | D | 43.07 ± 5.41 |
| | 20 | L | 90.00 ± 5.41 |
| | | D | 63.43 ± 5.41 |
| | 25 | L | 90.00 ± 5.41 |
| | | D | 72.28 ± 5.41 |
| | 30 | L | 39.23 ± 5.41 |
| | | D | 21.93 ± 5.41 |
| At field capacity | 10 | L | NTS |
| | | D | NTS |
| | 15 | L | 35.01 ± 5.41 |
| | | D | 30.79 ± 5.41 |
| | 20 | L | 51.14 ± 5.41 |
| | | D | 47.29 ± 5.41 |
| | 25 | L | 63.84 ± 5.41 |
| | | D | 46.29 ± 5.41 |
| | 30 | L | 17.71 ± 5.41 |
| | | D | 8.85 ± 5.41 |
| At half the field capacity | | NTS | |

NTS = No tuber sprouting.

lumens per sq. metre. Total sprouting was recorded at the end of the experiment in respect of all the treatments.

### *Transplantation experiment*

To assess the plasticity of the reproductive strategies, a transplantation experiment in common hydraulic conditions was carried out. Five tubers (of equal size) originating from the four above-mentioned habitats (in five replicates) i.e. 100 tubers in all, were transplanted into 37.5 × 30 × 30 cm aluminium containers (a total of 20 containers) each containing 3 kg of sediment (wet mass). The sediment used for all the transplantations was collected from a single water body in order to provide uniform conditions. For the same reason, tap water was used to fill the containers and maintain the water level at 25 cm above the sediment. The containers were kept at Kashmir University Botanical Garden (KUBG) for 6 months (1st April - 30th September) with proper

**Table 4**. Effect of temperature and sediment under alternate light and dark conditions on tuber sprouting.

| Treatment | Temperature °C | With sediment/without sediment | Percent tuber sprouting (mean ± SE) |
|---|---|---|---|
| Flooded 5 cm depth of water under alternate light and dark | 10 | S | NTS |
| | | W | NTS |
| | 15 | S | 54.99 ± 5.54 |
| | | W | 50.77 ± 5.54 |
| | 20 | S | 72.28 ± 5.54 |
| | | W | 63.43 ± 5.54 |
| | 25 | S | 90.00 ± 5.41 |
| | | W | 81.14 ± 5.41 |
| | 30 | S | 30.79 ± 5.54 |
| | | W | 26.57 ± 5.54 |
| Flooded 10 cm depth of water, under alternate light and dark | 10 | S | NTS |
| | | W | NTS |
| | 15 | S | 68.06 ± 5.54 |
| | | W | 59.21 ± 5.54 |
| | 20 | S | 81.14 ± 5.54 |
| | | W | 81.14 ± 5.54 |
| | 25 | S | 90.00 ± 5.54 |
| | | W | 81.14 ± 5.54 |
| | 30 | S | 35.01 ± 5.54 |
| | | W | 30.79 ± 5.54 |

NTS = No tuber sprouting
S = with sediment; W = without sediment

care. Quantitative data on reproductive traits (spike length, number of spikes, flower number and fruit number per individual) and resource allocation were recorded at the end of the experiment.

### *Reproductive potential and spread of tubers*

The reproductive potential and spread of tubers were estimated by placing five germinated tubers (in five replicates) in 50 x 60 x 37.5 cm trays containing 3 kg (dry mass) of sediment, and the water level was maintained at 20 cm above the sediment. The trays were kept at Kashmir University Botanical Garden (KUBG) for six months (1st March - 30th September), with regular monitoring. During this period, the temperature ranged between 3.6 and 33.6 °C, and the photoperiod between 12 hrs 20 minutes and 14 hr 55 minutes. At the end of the experiment, the sprouted tubers with primary and secondary plantlets, meristematic branches and rhizomes (Fig. 2) were collected and analyzed for repro-ductive potential and spread. The characters studied included the total number of plantlets produced, the number of meristematic branches formed, the spacer length and newly formed tubers, if any.

### *Statistical analyses*

The variation in reproductive traits in standing- and running-water habitats and across standing and running waters were analysed by one-way ANOVA. Tukey tests were carried out to determine post-hoc differences between treatment means. All the statistical analyses were performed using SPSS (12) software.

## Results

*Potamogeton pectinatus* is a herbaceous, submerged plant; it is cosmopolitan,with a rhizome which is robust, terete, and perennial; the stem is sparingly to richly branched, slender and terete; the leaves are filiform to narrowly linear, entire, sessile, 3 - 20 cm long and 0.1 - 0.4 cm broad, bright green to olive green in colour; stipules are prominent, 2 - 5 cm long, adnate to the leaf at the

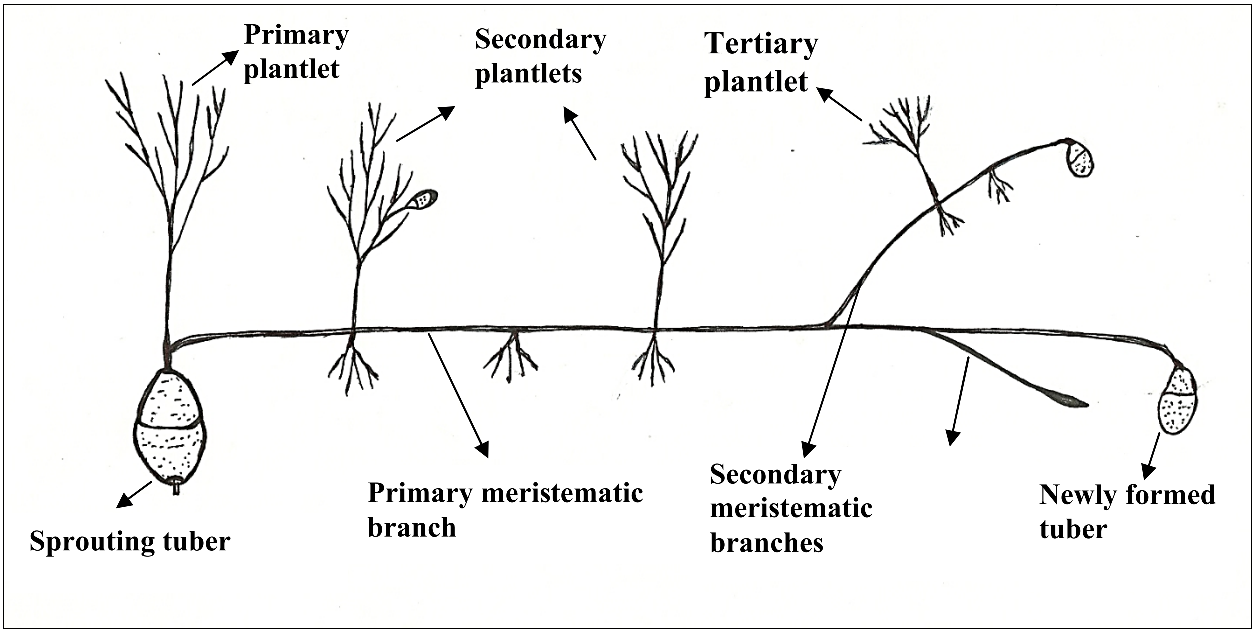


**Fig. 2.** Role of tubers in the spatial spread of *P. pectinatus.*

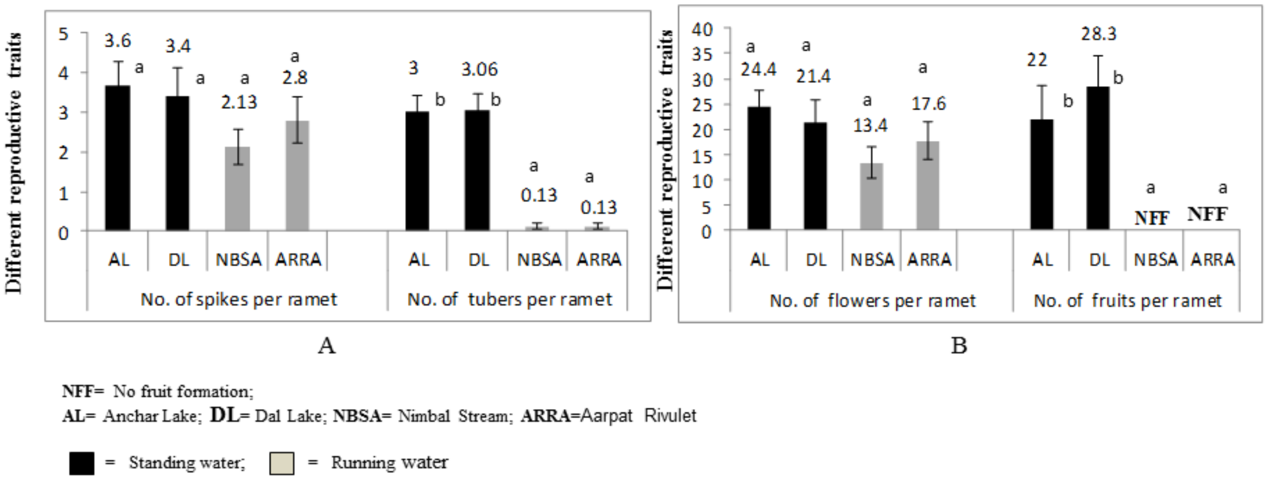


**Fig. 3 (A, B).** Comparison of different reproductive traits in standing- and running-water habitats. [One-way ANOVA analysis; different letters 'a' and 'b' indicate that the means are significantly different (Tukey test: $P < 0.05$)].

base to form a sheath wider than the stem, greenish to whitish in colour, the free portion less than the length of the sheath; the peduncles are 2 - 15 cm long; the spikes are 2 - 6 cm long, with 5 - 12 flowers arranged in 3 - 5 whorls; the spikes are contiguous at first, later becoming moniliform; the flower is 2 mm in diameter, with orbicular perianth lobes 1 mm long, 1.5 - 2 mm broad; the fruit is obliquely obovate, narrow at the base, rounded on the dorsal side; without a dorsal keel but obscure lateral keels, 0.3 - 0.5 mm long.

### *Life history pattern*

*Potamogeton pectinatus* grows luxuriantly in almost all the aquatic habitats of Kashmir Valley. The species initiates its life cycle, from March to early April, by germination of fruits and sprouting of tubers, producing plantlets. These juvenile plantlets grow vigorously from April to May, and produce spikes from the middle of May. Concomitantly, they also produce tubers (both axillary and rhizome tubers).

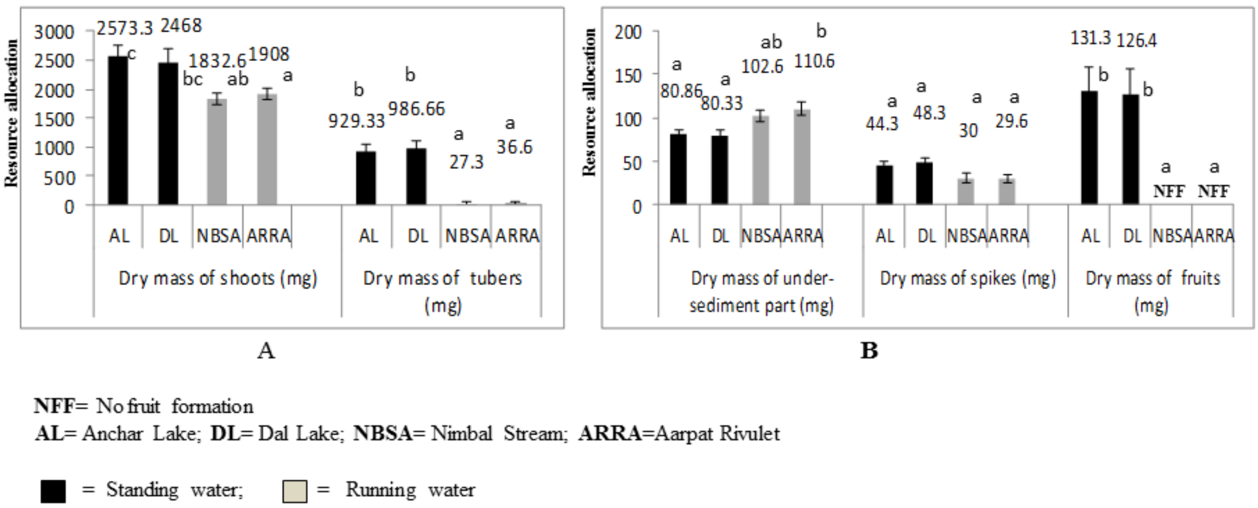


**Fig. 4 (A, B).** Comparison of resource allocation to different plant parts in standing- and running-water habitats. [One-way ANOVA analysis; different letters 'a', 'b' and 'c' indicate means are significantly different (Tukey test: $P < 0.05$)].

### *Sexual and asexual traits*

Significant differences ($P < 0.05$) were observed in sexual and asexual traits between running and standing waters (Fig. 3). The number of spikes, flowers, fruits and tubers per ramet were significantly less in running water than in standing-water habitats. The allocation of dry mass to different plant parts also differed. In standing water, a higher dry mass (relative to total mother dry mass) was allocated to shoots, followed by tubers and fruits, and was least to under-sedimentparts; however, the opposite was true in running water. The under-sediment part in running-water habitats had the higher resource allocation, and hence had a higher dry mass, as compared with standing-water sites (Fig. 4). The dry-mass allocation in running-water habitats was higher to shoots, followed by the under-sediment part and tubers; fruit was not formed in such habitats because of pollination failure.

### *Sexual reproduction*

Each flower in *P. pectinatus* produces 0 - 4 fruits. The flowers are borne in spikes with acropetal flower development. The flowers are quadrimerous with four reddish green tepals, four androecia adnate to opposite tepals, and four apocarpous gynoecia. The number of flowers per ramet was 13.93 ± 3.00 (Nambal Stream) and 24.40 ± 3.36 (Anchar Lake) while the number of fruits produced in standing-water habitats was recorded to be 22.00 ± 6.51 to 28.33 ± 6.12; no fruit were produced in running-water habitats (Fig. 3) because there was no pollination in moving water and the flowing water washes off most of the pollen grains.

### *Vegetative/clonal propagation*

The present study revealed that in *P. pectinatus* clonal propagation was accomplished through different types of clonal growth organs (CGO) including tubers (both rhizome and axillary), nodal plantlets that are produced by rhizomes, meristematic branches (stolons), or plant fragments fresh or one year old. The various modes of vegetative reproduction were habitat-specific. Tubers constitute the most important type of propagule in lentic-water habitats, in addition to meristematic branches and plant fragments from a parent plant, while in lotic-water habitats rhizomes were the most important.

The rhizomes regenerated from decaying rhizomes of the previous year, which gave rise to new plantlets. Meristematic branches were produced by the stem or from the rhizome, and gave rise to new plantlets at their alternate nodes. The present study also revealed that rhizome tubers (hypogeogenous tubers) were very rarely produced in running-water habitats, and no axillary tubers (epigeogenous tubers) were formed there. Tubers are globose structures, either single, double or in chains, brown to creamish in colour with 1 - 5 horn-like structures which upon sprouting give rise to new plantlets.

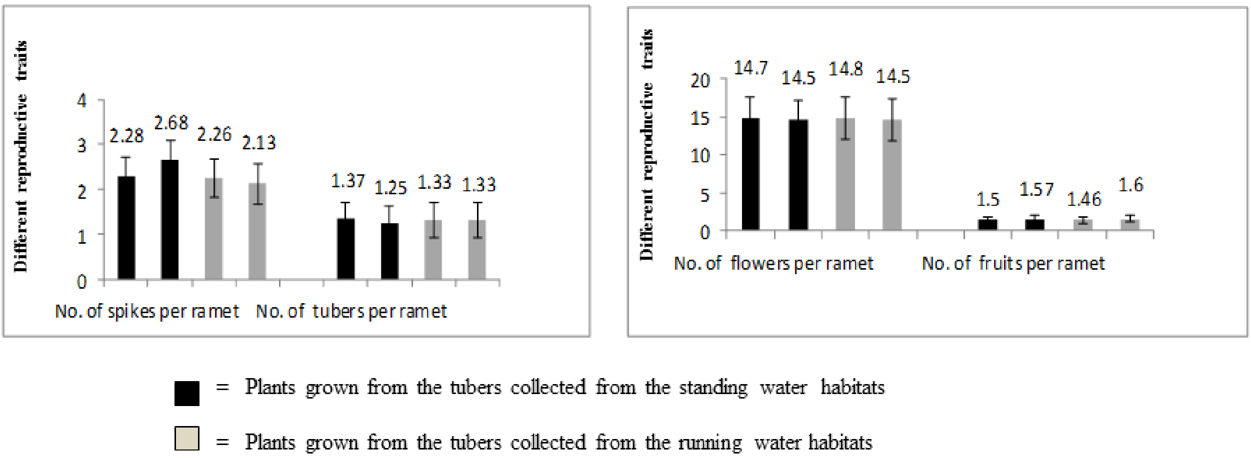


**Fig. 5 (A, B).** Comparison of different reproductive traits when tubers from standing- and running-water habitats were grown under similar flow conditions [One way ANOVA; none of the differences shown is significant (Tukey test: $P > 0.05$)].

### *Fruit germination*

The effects of different concentrations of $GA_3$, treatment with concentrated sulphuric acid, incision/cut of the fruit wall (surgical exposure of the embryo), wet chilling, or removal of epi-mesocarp on fruit germination of *P. pectinatus* incubated under alternating light and dark condition (12 hour light and 12 hour dark), or continuous dark conditions at 25 °C is shown in Table 2. Surgical exposure of the embryo promoted fruit germination. Treatment with different concentrations of $GA_3$ after fruit-wall removal did not further increase fruit germination significantly; but the rate of germination was increased. The fruits germinated rapidly and more in number in alternating light and dark than in continuous darkness. Wet chilling of fruits improves their germination. Fruits in which the fruit wall was not cut did not germinate at all, either with or withoutthe various chemical treatments tested. Age of the fruit had a significant effect on fruit germination. Freshly collected fruits germinated rapidly and in greater numbers as compared to those one year old; two - year-old fruits germinated, but those three years old failed to do so throughout (Table 2).

One can conclude that, with increase in age, the fruits lost their viability, which lasted for 2 years; light promoted fruit germination.

### *Tuber sprouting*

The effects of temperature and moisture conditions on tuber sprouting under alternating light and dark (12 hrs light and 12 hrs dark), and continuous dark conditions are presented in Table 3, and the effects of temperature and sediment in Table 4. The optimum temperature for tuber sprouting was 20 - 25 °C; considerable sprouting of tubers occurred at 15 °C; below 15 °C the sprouting was very low; no sprouting was recorded at 10 °C. Above 25 °C, sprouting started to decline, and it was inhibited above 30 °C. The data also show that flooded conditions enhanced tuber sprouting; no tuber sprouting was recorded when sediments were at half their field capacity. The sediment did not have any role in tuber sprouting since a good percentage of tuber sprouting was recorded in treatments without sediment (Table 4). Under alternating light and darkness, tubers sprouted rapidly and in greater numbers than in complete darkness.

### *Reproductive potential of tubers*

The primary meristematic branches from the tubers gave rise to secondary plantlets at their nodes; the first plantlets were always produced at the second node, whereas secondary meristematic branches were produced at the third or fourth node. The secondary meristematic branches produced tertiary plantlets at their nodes, and also gave rise to tertiary meristematic branches (Fig. 2). The primary, secondary and tertiary meristematic branches were produced in all possible directions, and spread upto 30 - 40 cm (clonal integration). The plantlets produced at these branches were spaced at various distances. A tuber produced 7.60 ± 0.45 plantlets and 2.40 ±

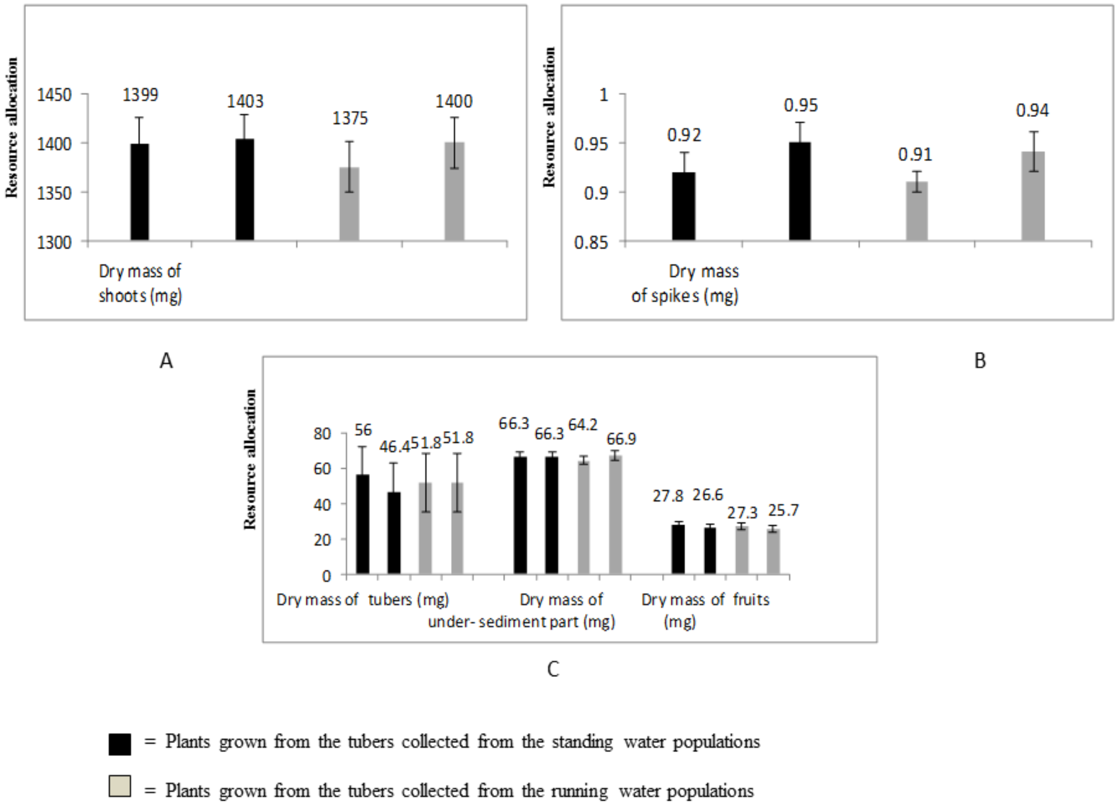


**Fig. 6 (A, B, C).** Comparison of resource allocation to different plant parts when tubers from standing- and running-water habitats were grown under similar flow conditions [One way ANOVA; none of the differences shown is significant (Tukey test: $P > 0.05$)].

0.27 meristematic branches; the average space between the plantlets was 4.59 ± 0.17 cm. Tubers were also produced at the end of the rhizome.

### *Transplantation experiments*

When tubers collected from different habitats (standing and running waters) were grown under similar conditions,.morphological and reproductive traits did not differ significantly ($P \geq 0.05$) (Fig. 5). The plants grown from tubers from running water and those from standing water showed similar reproductive traits and dry mass allocation to different plant parts; these traits did not differ significantly ($P \geq 0.05$) (Fig. 6). The study showed that the species employs habitat-specific reproductive strategies.

## Discussion

### *Life-history pattern and habitat-specific reproductive strategies*

The present study revealed that *P. pectinatus* employs habitat-specific reproductive strategy in running- and standing-water habitats. In running water the species mostly propagated by rhizomes and nodal plantlets from meristematic branches. The absence of axillary tubers and fruits in running-water habitats was possibly due to mechanical stress of flowing waters which detached and/or caused injury to juvenile tubers, and impaired pollination by washing away pollen grains from floating and submerged spikes (Ganie *et al.* 2008). The very low production of subterranean tubers in running-water habitats seemed to be attributable to hard bed and stony substrata. This is why in running-water habitats the species propagates by rhizomes and plantlets arising from nodes of meristematic branches (Ganie *et al.* 2008). This strategy, involving vegetative as well as sexual reproduction seems to maximize the fitness of the species in diverse habitats (Dong *et al.* 2006; Ganie *et al.* 2008). *Potamogeton pectinatus* presumably follows the strategy of economization of resources in the stressful environment of running waters. In addition, branches with apical meristematic tips (meristematic branches and stolons) in running waters grow horizontally along the surface of sediment, giving rise to plantlets at their nodes. These branches are well suited for such habitats, where they serve as an effective means of anchorage and survival (Grace 1993; Sosnova *et al.* 2010). On the other hand, in standing water the species reproduces both sexually by fruits and asexually by tubers. Although propagation by tubers is the primary mode of reproduction in standing-water habitats, the species also perpetuates through fruits. Tuber formation requires minimum resources to propagate, while the sexual process generates variability for adaptation in changing environments; the two help to account for the wide distribution of the species. In fact, strong vegetative regeneration, sexual reproduction, and high levels of fitness across different habitats are some of the characteristics invoked most frequently to explain the wide spread as well as the invasive nature of some species (Barrett & Colauti, 2008; Tiebre *et al.* 2007; Zhang *et al.* 2010), and the trade-off between 'reproductive' and 'clonal' strategies is regarded as a crucial determinant of successful spread (Brown & Eckert 2005; Lui *et al.* 2005).

### *Tuber sprouting*

The experimental studies showed that tuber sprouting was controlled by temperature, moisture and light. It varied significantly across different moisture levels and temperatures ($P \leq 0.001$). The sprouting of tubers was inhibited below 10 °C and above 30 °C; the optimum temperature for tuber sprouting was 20 - 25 °C (Madsen & Adams 1988; Van Wijk 1989a). Under natural conditions also, the tubers remained dormant during the cold winter of the Kashmir Valley, when the temperature of water bodies was much lower, mostly less than 5 °C; sprouting begins from mid-February and proceeds up to April when the temperature is optimal for sprouting. The requirement of light and water, as is evident from the present studies, serve as cues to facilitate recruitment and establishment of new plantlets during periods of favourable environmental conditions. The rate and overall percentage of tuber sprouting was higher under alternating light and dark conditions (12 hrs light and 12 hrs dark) as compared with continuous dark conditions. Perhaps decreases in the rate and overall percentage of tuber sprouting with increase in the depth of water bodies can be ascribed to decrease in light intensity at deeper depths (Ganie *et al.* 2008; Jain *et al.* 2003). Inhibition of tuber sprouting at half the field capacity clearly points out that moisture plays a critical role in tuber sprouting. Thus, tuber sprouting in habitats where water dries up for some period is hampered by low availability of moisture. In these habitats rhizomes and/or sexual fruits are the means of propagation. The results of tuber-sprouting experiments indicate that the dormancy of tubers of *P. pectinatus* inhabiting irrigation channels was due to the very low availability of moisture upto the last week of May, and not because the propagules were innately dormant (Spencer & Ksander 1992); they have been said to exhibit enforced dormancy (Silvertown 1982). Furthermore, the present study also shows that the presence of sediment is not obligatory for the sprouting of tubers. Tuber sprouting did not vary significantly ($P \geq 0.05$) between treatments with and without sediment (Table 4); instead, a sufficient quantity of water was necessary for their germination (Ganie *et al.* 2008; Jain *et al.* 2003). Obviously, tubers are capable of sprouting in any water body irrespective of the type of substratum.

### *Reproductive potential of tubers*

The present study also showed that tubers of *P. pectinatus* make a high contribution to the spatial spread of this species. Sprouting tubers spread up to 20 - 40 cm in a season, producing vertical shoots and roots at their nodes; a single tuber is capable of establishing a large population by producing new propagules in a few years. Individuals of clonal plants consist of physically and physiologically connected ramets; the clonal integration resulting may facilitate the colonization and growth of the ramets in heterogeneous habitats with stressful conditions (Chidumayo 2006; Roiloa & Retuerto 2007), may also help individuals to survive and to recover after severe environmental change (Yu *et al.* 2008; Moola and Vasseur 2009), and facilitate the occupation of new space (Wang *et al.* 2008; Xiao *et al.* 2011).

### *Fruit germination*

The cold stratification treatments to some extent improved germination in intact fruits. Low temperature caused rupturing of the fruit wall, and thus their dormancy was overcome (Teltscherov & Henj 1973; Baskin & Baskin 1998; Hay *et al.* 2008). Under natural conditions also, the stratification treatment (more closely akin to the freezing winter temperature of the Kashmir Valley) may have a promoting effect on fruit germination. Cold stratification is an effective way of alleviating dormancy in many species, especially those from temperate regions (Baskin & Baskin 1998, 2004), which ensures that germination does not occur until the beginning of spring when water temperature is more favourable to vegetative growth of aquatic plants (Hay *et al.* 2008). The conditions most favourable for germination of *Potamogeton* fruits are temperatures of 20 - 25 °C, anaerobic conditions and light (Hay *et al.* 2008; Xiao *et al.* 2010). The species investigated here also uses these environmental conditions that ensure survival and establishment conditions for new recruits. Scarification (surgical exposure of embryo) had promotive effects on fruit germination; this is an effective way to alleviate the mechanical restriction of the fruit wall. The application of $GA_3$ to the scarified fruits did not increase the overall percentage of germination significantly but enhanced the rate of germination. $GA_3$ is most likely involved in coordinating metabolic processes that occur once seed germination has started, and not directly in breaking dormancy (Gallardo *et al.* 2002; Ogaya *et al.* 2003).

Fruit age had a significant ($P \leq 0.01$) effect on germination. The data confirmed that the fruits of this species survive desiccation (Hay *et al.* 2000, 2008). The freshly collected fruits, as well as those dry-stored for upto two years, germinated, provided the fruit wall was cut. Percent germination, however, declined with age of the fruit. These observations indicated that no after- ripening period was needed by the embryo of this species, and that fruits are an important means of propagation in habitats where water dries up for some period during the year. In wetlands that are annually dewatered, resilient aquatic plant communities maintain their presence through sexual reproduction (Liu *et al.* 2006; Weigleb & Kadano 1989). The fruit germination varied significantly ($P \leq 0.01$) between alternating dark and light, and continuous dark conditions. The ability to germinate under a range of environmental conditions is one of the reasons why *P. pectinatus* in found in various habitats, and has a wide distribution in diverse ecosystems of Kashmir Valley. Fruits aid the species in its widespread distribution, and in colonization of new aquatic and semi-aquatic habitats. Kimber *et al.* (1995) reported that seeds of aquatic macrophytes, including *Potamogeton,* have been found to playan important role in establishment of new genotypes in existing populations, dispersion of populations into new regions (Arnold *et al.* 2000; Figuerola & Green 2002; Harwell & Orth 2002), and re-establishment of populations after episodic declines (Jarvis & Moore 2008; Preen *et al.* 1995; Titus & Hoover 1991). From the genetic pattern of *P. pectinatus,* Van Wijk (1989a) deduced hat seed banks in the species provide the main means of re-establishing populations after extirpation, and of long-distance dispersal (De Vlaming & Proctor 1968; Figuerola *et al.* 2010; Guppy 1987).

*Potamogeton pectinatus* also regenerates from fragments of the mature plant, the apical part of the shoot, and from detached old (one-year-old) plant material. These plant parts also help the species in colonization of new habitats (Riis *et al.* 2009).

### *Relationship between reproductive strategies and habitat range*

The transplantation experiment showed that differences in morphological and reproductive traits (e.g. floral traits, fruit, tuber number per ramet, and dry mass allocation to different plant parts) under different flow conditions in the field are not observed under similar hydraulic conditions; they are mostly due to phenotypic plasticity and not to genetic differentiation. Plastic responses upon transplantation were also observed in different species of the genus *Potamogeton* (Ganie *et al.* 2014; Kaplan 2002, 2008). Puijalon & Bornette (2006) and Puijalon *et al.* (2008) also reported that upon transplantation under similar environmental conditions, differences in various morphological traits in several aquatic plant species with respect to flow have not been observed when compared with field observations. The maintenance of clonal multiplication under stressful conditions in *Mentha aquatica* L. counter balances the detrimental effect of flow stress on sexual reproduction (Puijalone *et al.* 2008). Moreover, high clonal multiplication under running-water conditions may be an important feature for species maintenance in habitats where recruitment by seeds or plant fragments is largely impeded by flow-induced drift (Ganie *et al.* 2008; Puijalon & Bornette 2006). Species able to colonize running water have the capacity to display high clonal multiplication under such conditions (Puijalone *et al.* 2008). The ability of an individual to tolerate multiple stresses through adjustments in morphological and reproductive traits is a major feature determining species survival and colonization, and hence the ecological range of a species (Bazzaz 1996; Chapin *et al.* 1987; Ganie *et al.* 2014; Sultan *et al.* 1998). Flexible reproductive traits contribute to the fitness of a species across a wide range of habitats.

From the present study it can be concluded that effective and habitat-specific reproductive strategies significantly contribute to the wide spread of *P. pectinatus* in freshwater ecosystems of Kashmir Himalaya. Knowledge about life-history traits such as types of propagules in different habitats, their time of formation and germination/sprouting, about reproductive potential, and favourable/unfavourable environmental conditions, is very important for the long-term management of the species. Knowledge of life-history pattern can be utilized to identify weak points in the plant's life cycle, and to exploit them for long-term management (Madsen 1993). For example, the species studied in this paper produces flowers, fruits and turions between May and August. Therefore, removal of ramets before June would control the growth and spread of the species. In *P. pectinatus* tuber production starts in the month of June; therefore, the removal of the tubers before sprouting and establishment of new recruits can prove an effective method for control of this aggressive species. Caffrey & Monahan (2006) reported that traditional control methods, which include annual treatment with dichlobenil, often followed by mechanical cutting, have been unsuccessful in providing long-term control of the weed *Myriophyllum verticillatum* L. by contrast, removal of turions yielded desirable results, allowing significant savings since there is no requirement for costly herbicides, manpower and transport.

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