

**Winter to autumn phenophasic shift in flowering is economically productive, evolutionarily progressive, and environmentally well cued partial retrieval in *Pithecellobium dulce* (Roxb.) Benth. of semi-arid climate**

**ABSTRACT**

**Background:** *Pithecellobium dulce* is a multipurpose legume tree species of high ecological significance. Several reports indicate existence of huge genetic diversity within the natural population of the species. Various morphological parameters have been used to assess intra species genetic diversity, however, there is no report available so far on diversities in reproductive phenology of *P. dulce* of semi-arid or arid climate.

**Methods:** The present paper is based on assessment of diversity in flowering phenophases through construction of phenological calendar incorporating temporally observable morpho-phenotypic descriptors for reproductive behaviour of individual trees comprising natural population of the species at designated study sites during a period of three years. The study was carried out during September, 2015 and March, 2019 at Ajmer, Rajasthan, India. Data were periodically obtained and statistically analysed.

**Results:** Majority of trees of flowering stage (89.94%) exhibited normal or winter blooms in which flowering was initiated in almost synchronised manner during December; 10.05% of normal blooming trees inconsistently showed additional early or autumn blooms during either September or October or November; 2.58% of trees exhibited early blooms in which flowering was consistently initiated in the month of September in addition to normal blooms. The overall production and availability of fresh fruits in early-cum-normal episodic blooming trees were greater as compared to only normal blooming trees. Though, the numerical fruit productivity in winter blooms was superior to autumn, the pomometric characteristics were inferior in former in early-cum-normal episodic blooming trees.

**Conclusion:** Evidently, the present work explores agronomically valuable variants of *P. dulce* and also reports causes of appearance of persistent fruits and sporadic *in-situ* germination of seeds. Based on above findings, the present paper also makes evolutionary predictions that how a shift in flowering phenology of *P. dulce* as exhibited by the elite variants could have long-term implications for reshaping of future landscapes of semi-arid or arid climate. Conclusively, the phenophasic variants could serve as candidate plus trees that deserve out of the season floral management and clonal propagation, thereby the species may get a fillip to status up gradation from minor fruits to major fruit category.

**Keywords:** Phenology; *Pithecellobium dulce*; genetic diversity; fruit persistence; semi-arid

## 40 1. INTRODUCTION

41 *Pithecellobium dulce* (Roxb.) Benth. belongs to the sub-family Mimosoideae of family  
42 Fabaceae. The species is native to the tropical America (Mexico, USA, Argentina, Bolivia, Brazil,  
43 Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Surinam, Uruguay and Venezuela), but  
44 has now become naturalized in India, China, Cambodia, Malaysia, Myanmar, Philippines, Puerto  
45 Rico, Sudan, Tanzania, Thailand, Vietnam and cultivated there as economic and ornamental trees [1,  
46 2]. In India, *P. dulce* is present throughout the country except Jammu and Kashmir, Himachal  
47 Pradesh, Sikkim, Arunachal Pradesh, Assam, Nagaland, Meghalaya, Manipur, Tripura and Mizoram  
48 [3]. The species have wide ecological amplitude with respect to soil types and annual rainfall, in India  
49 it grows well in semi-arid regions characterized by mean monthly temperatures ranging from 7 to 8°C  
50 in January to 40 to 42°C in May and June. It is generally considered heat and drought resistant tree  
51 world over [4]. *P. dulce* is a medium-sized fast growing tree commonly attaining a height up to 10-15  
52 metres. Branching pattern is irregular and leaves are bi-pinnate with thin spines in pairs at the base of  
53 leaves that range from 2 to 15 mm in length. The growth of new leaves coincides with the loss of old  
54 leaves which give the tree an evergreen appearance. Inflorescences are panicles that differentiate  
55 axillarily or terminally from the leafy branches of the tree. Flowers are borne on short panicles 10 to  
56 20 cm in length, often as terminal compound inflorescences. Each panicle is composed of 20 to 30  
57 floral units potentially capable of fertilization. Individual flowers are greenish-white, sessile present in  
58 small stalked heads consisting of 10-15 floral buds; calyx and corolla small, single thread like tubular  
59 pistil longer than stamens, pink in colour with capitate stigma; and stamens are fifty in numbers that  
60 give hairy appearance. Because of nitrogen fixing ability and high ecological values, *P. dulce* trees  
61 are often planted on waste land for reclamation, shelter belt plants and roadside ornamentals [5,6].  
62 They are extensively planted for production of protein rich live stock fodder and fuel wood in Asia,  
63 Latin America and Africa [7,8,9]. *P. dulce* has been designated as minor fruit trees and considered  
64 one of the most suitable trees for alley cropping. Fruits are plump, constricted between the seeds,  
65 spirally coiled and spongy white arils surround 5 to 12 shiny black seeds within the pod. Arils are  
66 sweet and acidic in taste so consumed by birds which also disperse seeds in the process of eating  
67 [10]. The seed contains 20% oil which is used in soap industries, refined seed oil is edible. Flowers  
68 attract honey bees and significantly contribute to honey making. Trees have great potential for rearing  
69 lac insects. In addition to ecological significance of trees and economic values of fruits, *P. dulce* has  
70 been reported to possess many pharmacological properties and clinical applications that include *inter*  
71 *alia* Pitheduloside extracted from the plant are anti-inflammatory, anti-microbial, anti-tubercular,  
72 spermicidal, protease inhibitor, anti venom and abortifacient [11,12]. In folklore, *P. dulce* is being used  
73 to cure leprosy, venereal diseases, peptic ulcers, sores, toothache, convulsions, dyspepsia and  
74 dysentery [13]. Leaf extract has been used to relieve pain, convulsions, indigestion and diabetes. Arils  
75 are being used in preparation of beverages. Extracts of fruits, seeds, leaves, and bark have been  
76 demonstrated to possess antioxidant properties potentially capable of curing ulcers, cancers and  
77 gastrointestinal ailments [14,15,16,17,18]. In view of vast utilities of *P. dulce*, it is pertinent to explore,  
78 identify, and select the variations with superior agronomic traits from the population. Reports are

79 available on genetic diversity in *Pithecellobium elegans* [19], as well as selections of agronomically  
80 desirable genotypic variants of *P. dulce* from natural population with large pods containing small  
81 seeds and sweet less astringent arils, and variegated plants with green and white leaves. They are  
82 being clonally propagated and grown in gardens in Thailand, Philippines, and Hawaii [20,21]. Quite  
83 recently, Goyal et al., 2014 [22], have made assessment of genetic diversity in *P. dulce* germplasm of  
84 Rajasthan state using RAPD and ISSR markers. Their findings indicate a high level of morphological  
85 and genetic diversity in *P. dulce*. Their selections were based on the phenotypic assessment of  
86 various characters viz., branching habit, branching pattern, canopy size, number of primary branches,  
87 colour of bark, height of tree, leaf shape, number of flowers per inflorescence, pod size, number of  
88 seeds per fruit, leaf size and percent seed germination. There has been no report so far on the  
89 diversity in flowering and fruiting phenology of the species. Therefore, the present paper attempts to  
90 identify agronomically advantageous variations in flowering-fruiting phenophases of *P. dulce* growing  
91 in semi-arid climate of Ajmer (RIE campus, Nag Pahar hillocks and along Ajmer-Pushkar road side)  
92 with prime objective to enhance production and prolong the availability of fruits respectively.  
93 Ecological phenomena of persistence of fruits throughout the year and sporadic *in situ* germination of  
94 seeds under specific environmental conditions have also been studied. Undoubtedly, such exploration  
95 and selections would help plant breeders to design appropriate strategies for multiplication and  
96 conservation of the elite variants or germplasm and also pave the way for further genetic  
97 improvement of cultivars. Additionally, these phenophasic variants could serve as potential candidate  
98 plus trees for out of the season floral management through biotechnical interventions. If successfully  
99 employed the species may get a fillip to status up gradation from minor fruits to major fruit category.  
100 Nevertheless, the greater understanding of diversity in reproductive strategies of *P. dulce* in  
101 conjunction with time and environmental dynamics would provide better insights into predictive  
102 evolutionary processes that might impact on future reshaping of semi-arid or arid landscapes.

103

## 104 **2. MATERIALS AND METHODS**

105 Three study sites of naturally growing populations of *P. dulce* were identified within 10-15  
106 kilometres range at Ajmer, Rajasthan, India. Study sites: RIE campus, Nag Pahar hillocks and Ajmer-  
107 Pushkar road side barren land were marked as site – I, II and III respectively. Phytosociological  
108 survey was initially conducted at all study sites to identify and enlist species of tree communities,  
109 species of *Pithecellobium* and numbers of individuals of *P. dulce* during August-September, 2015 at  
110 all study sites. Periodical observations were made during August 2015 and December 2018 to collect  
111 data on phenology of *P. dulce* with particular focus on flowering and fruiting events to explore diversity  
112 in phenophases with respect to onset and completion of flower initiation, flowering continuum, fruit  
113 initiation, fruit maturation and fruit ripening. Annual records of number of trees with persistent fruits  
114 and number of persistent fruits per trees were also maintained for all study sites during the period  
115 under study. Phenological observations on flowering frequencies of all tree species constituting the  
116 plant community of the habitat under study were also made to classify four levels of species: continual  
117 species, episodic or sub-annual species, annual species, and supra-annual species.

118 Data pertaining to comparative account of two blooms, viz., early or autumn and normal or  
119 winter with respect to number of branches bearing flowers, position of inflorescence on trees, number  
120 of inflorescences per branch, number of floral units per inflorescence, number of fruits per  
121 inflorescence, number of seeds per pod, average length and diameter of fruits, and degree of  
122 synchrony in flowering of elite variants were separately maintained and statistically analysed and  
123 presented in tabular forms. Data recording on flowers necessitates elaboration on structure of  
124 inflorescences to conceptualize experimental use of floral units equivalent to flowers potentially  
125 capable of fertilization. Inflorescences are panicles that differentiate axillarily or terminally from the  
126 leafy branches. Each panicle produces small clusters of 2 to 5 heads all along its length of 10-20 cm,  
127 at the distance of 1.0 cm in spiral manner. Clustered heads originate from a single point  
128 asynchronously. Each head consists of about 10 to 20 small floral buds connected to the point of  
129 origin through a stalk. All buds of a head open synchronically, therefore, anthesis is of long duration  
130 when about fifty of hair like stamens in a flower grows further along with long thread like single pink  
131 coloured pistil. So, clustered flowers give hairy appearance with fragrance and extra floral nectaries  
132 attract honey bees and other insect pollinators. If all floral buds of all clustered heads of each  
133 inflorescence are counted before anthesis, about 3000-4000 flowers should have been produced in  
134 each inflorescence. However, fruit setting in each inflorescence never exceeded 10-15 in our  
135 observations thereby making the fruit to flower ratio as low as 0.003. Hence, the huge numbers of  
136 flowers per inflorescence posed a big challenge in experimental data recording for numbers of flowers  
137 per inflorescence. To overcome such obstacle, we examined many samples of inflorescences from  
138 different blooms as well as trees and found that majority of floral buds constituting an inflorescence  
139 are not functional in reproduction because of absence of pistils in flowers, improper orientation of  
140 stigmas, partially drying up of long tubular pistills, non-opening and drying up of many floral buds. Data  
141 on numbers of functional flowers capable of fertilization was obtained after long observation on  
142 numbers of floral heads showing anthesis per day or a week, duration of anthesis and blossoming till  
143 fruit setting. Therefore, floral units in observation table correspond to numbers of functional flowers  
144 capable of reproduction per inflorescence. Data were also utilised in construction of flowering-fruiting  
145 phenophasic calendar of *P. dulce* for specified population during the study period. Vaucher  
146 specimens and seeds of agronomically advantageous flowering-fruiting phenophasic variants or  
147 genotypes were deposited in herbaria of Botany Department of RIE, Ajmer.

148

### 149 **3. RESULTS AND DISCUSSION**

#### 150 **3.1 Diversities in flowering-fruiting phenophases in natural population of *P. dulce***

151 Species of tropical plant communities vary considerably with respect to flowering onset  
152 timings viz., winter, spring, summer or autumn; frequency of flowering, several times in a year, or  
153 once in several years; and duration of flowering from a few days to the whole year. Thus the onset  
154 timing, duration, and frequency of flowering define reproductive phenological patterns of species  
155 which interact with each other in order to display spectacular diversities in flowering patterns what we  
156 observe in nature [23,24,25,26]. Furthermore, phenological patterns in tropical trees particularly

157 flowering and fruiting are determined through interactions between short-term environmental events  
158 and evolutionary forces. Alternatively, flowering phenology is both under genetic control and is plastic  
159 to environment, that means changes in climatic conditions may trigger the expression of phenotypic  
160 responses currently hidden [27]. Different geographic locations comprise their own edaphic and  
161 climatic conditions such as soil nutrients (level of N in soil), variation in rainfall, changes in  
162 atmospheric temperature, photoperiod, irradiance and sporadic environmental events that serve to  
163 provide environmental cues in triggering floral phenological events in tropical plants  
164 [28,29,30,31,32,33,34,35,36,37,38,39,40]. Newstrom et al., 1994 [41], and Engel et al., 2005 [42],  
165 have described four levels of flowering frequency: continual species that continuously flower  
166 throughout the year, episodic species that flower more than once a year, annual species that flower  
167 once a year, and supra-annual species that flower less frequently than once a year. Based on above  
168 classification, *Cordia crenata*, *Commiphora wightii*, *Manilkara zapota*, and some varieties of *Morus*  
169 *alba* constitute the continual species; about 60% of the population of *Prosopis cineraria*, *Acacia*  
170 *nilotica*, and few individuals of *Pithecellobium dulce*, *Psidium guajava*, *Cordia dichotoma*, *Azadirichta*  
171 *indica*, *Grewia asiatica* constitute sub-annual or episodic species; while some cultivars of *Mangifera*  
172 *indica*, *Bamboos*, and *Agave americana* constitute supra-annual species; whereas remaining majority  
173 of plants constitute annual species as observed in the habitat under study. Similar observations on  
174 frequency of flowering in above mentioned species growing in different habitats have also been  
175 reported by [43,44,45,46,47,48]. *P. dulce* generally flowers and fruits between December to May and  
176 February to August respectively in its native habitat [2]. In Indian tropical deciduous forests, *P. dulce*  
177 flowering occurs in January and February and fruiting in April and June respectively [49]. However, a  
178 bit altered flowering and fruiting phenologies have been observed in Philippines and West Java where  
179 they flower in October-November and April-June respectively. While fruiting at these two locations  
180 occurs in January-February and July to August respectively [1]. In Puerto Rico fruiting has been  
181 observed throughout the year [2]. Therefore, *P. dulce* exhibits three levels of reproductive  
182 phenological patterns based on annual flowering frequency as annual flowering at most of the  
183 geographic locations world over, continual flowering in Puerto Rico and episodic flowering by some  
184 individuals at semi-arid habitat under study. In present study at Ajmer, India, intra species flowering-  
185 fruiting phenology at three designated study sites – I, II, III have been consistently observed during  
186 September, 2015 and December, 2018 for flower initiation, fruit initiation, maturation and ripening of  
187 fruits. About 90% of flowering individuals of natural population exhibited almost synchronous  
188 behaviour for onset of flowering during winter whereas, approximately 10% of them showed  
189 alterations. Out of 10% alterations, 7.47% alterations were not consistent with respect to floral  
190 initiation timings, 2.58% alterations were consistently observed throughout the study duration (Table 1  
191 & 2).

192 In other words, these individuals exhibited offseason flowering, i.e.; two blooms, viz., autumn  
193 and winter occur consecutively in same tree thereby the flowering and fruiting durations are prolonged  
194 (Fig. 1- A & B). They belong to the episodic or sub-annual species level based on flowering  
195 frequency as described by Newstrom et al., 1994 [41]. Similar phenophasic change in flowering of  
196 *Prosopis cineraria* or Khejari has been reported by Krishnan et al., 2015, in Indian Thar desert [47].

197 On account of prolonged flowering and fruiting in *P. dulce*, the overall quantitative and qualitative  
198 productivity and time duration of availability of fruits are greater in early-cum-twice blooming trees as  
199 compared to normal and single blooming trees (Fig. 3&4). However, early formed fruits during  
200 December and January are highly vulnerable to frugivores since very few other trees with fruits are  
201 available in vicinity as observed in the habitat under study. Table-3 provides comparative account of  
202 flowering and fruiting in autumn and winter blooms of early and twice flowering individuals of *P. dulce*.  
203 It is evident that winter or normal bloom is superior to autumn or early bloom with respect to numbers  
204 of inflorescences, flowers and fruits, also winter bloom is more synchronous as compared to autumn  
205 blooms in flower initiation timing, blossoming period and fruit-setting, notwithstanding that fruits  
206 produced through autumn blooms are more robust with respect to length, diameter, and number of  
207 seeds (Fig. 1-D & Fig. 4). Rodriguez et al., 2016 [50] has reported similar observations that during  
208 flowering off-peak, episodic variants flowering for shorter periods with even less synchronicity  
209 proportionally set more fruits since they were less affected by fluctuations in biotic and abiotic factors.  
210 During the three years study period, about 17% of trees of the population of *P. dulce* remained in non-  
211 flowering state. They were not the same trees rather different trees did not flower either first or second  
212 or third year. However, about 34% of all non flowering trees showed late flowering with onset timings  
213 either in February or March. We consistently observed flowering abnormalities in most of these trees  
214 since they produced a very low number and much smaller size of inflorescences. Their flowering  
215 durations and fruit setting were also very low probably because of non availability of resources such  
216 as water, high level of air pollution or very old age of trees. Data have not been included in this paper  
217 since they serve separate topic of research. In view of the natural episodic flowering in *P. dulce*, the  
218 species is a potential candidate tree that deserve out-of-season management of flowering to avoid  
219 detrimental harsh weather conditions of April, May, and June that hamper fruit development of normal  
220 or winter blooms through biotechnical engineering in flowering phenology. Phenological engineering  
221 of reproductive behaviour of fruit trees through biotechnological interventions involving exogenous  
222 applications of plant growth regulators and adoption of appropriate agronomic practices such as  
223 pruning, trimming, and chopping of branches have been successfully employed to induce off-season  
224 flowering for enhanced fruit yield in mango [51], lychee [52], longan [53], custard apple [54], apple &  
225 sweet cherry [55], and guava [46,56,57]. It would not only increase the fruit yield rather prolong  
226 availability of fruits to take advantage of market opportunities. Genetic improvement of tree species  
227 through conventional selection methods of plant breeding is highly laborious and time consuming. As  
228 suggested by Narayan, biotechnological *in vitro* cultures and propagation techniques can circumvent  
229 the bottlenecks through by passing the unwanted juvenile phase of tree species as performance  
230 trouble-shooter. Therefore, phenologically plus trees such as *P. dulce* need to be put under prioritised  
231 objectives of *in vitro* propagation technology in addition to endemic, threatened, endangered, and elite  
232 germplasm not only to multiply and genetically modify them but also to maintain *in vitro* biodiversity  
233 [58,59,60].

234

235 **3.2 Flowering-phenophasic shift to autumn could be an evolutionary event towards**  
236 **better establishment of *P. dulce* under semi arid or arid climate**

237 In spite of quantitative inferiority of autumn blooms of *P. dulce* with respect to morphological  
238 descriptors of reproductive behaviour (extent of flowering and fruiting) as compared to winter blooms,  
239 pomometric characteristics of autumn bloom fruits were observed to be impressive as depicted  
240 through graphical representations in fig. 4. Robust growth of autumn bloom fruits could be attributed  
241 to abiotic and biotic components of the prevailing environmental complex. Favourable abiotic  
242 environmental conditions of winter with respect to mild temperature, bright sun light, low or mild wind  
243 velocity, adequate moisture level in soil and plant body, and low rate of evapo-transpiration in  
244 conjunction with biotic factors such as availability of highly specialised pollinators- bees, sun birds and  
245 bulbuls that concentrate on *P. dulce* since very few flowering trees were present in vicinity; provided  
246 congenial conditions for fruit setting and development. However, concentration of frugivores was also  
247 observed which proved to be highly detrimental to developing fruits that warranted special protection  
248 to them. Moreover, brief winter shower coupled with greater monthly mean temperature during winter  
249 months were growth promoting for fruits of autumn blooms whereas, same conditions were growth  
250 retarding for flowering in winter blooms as noticed during 2016-17. In view of above observations in  
251 the light of research findings by [24,61,62] that species that flower several times a year or episodically  
252 as exhibited by some variants in present study should be more abundant than either annually or  
253 supra-annually flowering species. They postulated that multiple clutches may have been selected to  
254 reduce reproductive failure from fluctuating populations of pollinators. Therefore, the following  
255 evolutionary predictions of future reproductive success of episodically flowering variants of *P. dulce*  
256 may prove true in course of time for the habitat of semi-arid climate currently dominated by Acacia  
257 species. A shift in flowering phenophase from winter to autumn may perhaps be the first evolutionary  
258 step of the species towards better perpetuation and establishment to the semi arid or arid climate  
259 characterized by low rainfall, high temperature, dryness of air, intense sun light and high velocity wind  
260 for most of the period in a year. According to Elberling et al., 2001 [63], and Anderson and Hill, 2002  
261 [64] findings that in out crossing insect pollinated plants, flowering during harsh seasons (winter or  
262 early spring-December, January and February) may decrease reproduction compared with flowering  
263 during favourable periods. In consonance with their findings we noticed a long lag phase in  
264 reproductive processes after induction of flowering during December in winter blooms till mid  
265 February when pollination and fruit setting started because of increase in number of pollinators,  
266 whereas, pollination and fruit setting immediately begins with floral induction in case of autumn  
267 blooms of *P. dulce* (Table 2). Currently, fruit maturation and ripening period of winter or normal  
268 bloom, viz., April-June period is extremely harsh, hence detrimental to aril and fruit development.  
269 Despite good tastes, nutritious and high medicinal values of fruits, *P. dulce* has not gone up beyond  
270 the level of minor or underutilized fruits. Harsh climatic conditions of summer in semi-arid or arid  
271 regions adversely affect fruit development in wild habitats. Many fruits because of poor development  
272 of aril in the absence of adequate moisture level in plant body and high atmospheric temperature get  
273 dry up and become hard, in some cases that persist throughout the year attached with the parent  
274 trees (Fig. 1- E, F). Similar findings have been reported by Mohandass et al., 2018, for woody tree  
275 species of tropical seasonal forest in China [65]. Low atmospheric humidity triggers splitting of pods  
276 and subsequent shrinkage (Fig. 1-C). Dryness induced leaf fall in May and June render top fruiting

277 branches leafless thereby exposing the fruits to frugivores that indiscriminately chop off developing or  
278 immature fruits. It would also aid to spirally coiled hanging fruits pose resistance to the high velocity  
279 wind during extreme summer and get easily detached from the trees (Fig. 2-B). Consequently, overall  
280 fruit yield is drastically reduced and fruit to flower ratio is very poor. Gradual shift of reproductive  
281 events of winter bloom towards autumn bloom through internal genetic mechanisms in response to  
282 evolutionary forces to be perceptive to new environmental cues of adequate moisture level in plant  
283 body, decreasing day length, and mild temperature regime as happens during autumn (September-  
284 October) to trigger flowering phenophase. In course of time, if natural population of *P. dulce* acquire  
285 such characteristics and flowering and fruiting phenophases completely shift from winter blooms to  
286 autumn blooms, all reproductive events of the species including fruit dehiscence and seed dispersal  
287 ought to be completed by the end of March, thereby a complete avoidance of harsh weather  
288 conditions of April, May and June months of semi-arid and arid climate may occur. Under new  
289 phenophase, January, February and March months would be a period of fruit development,  
290 maturation and ripening. Congenial climatic conditions of spring would provide favourable conditions  
291 for proper fruit development in *P. dulce*. Undoubtedly, the overall productivity in terms of quantity and  
292 quality of fruits would be enhanced. *P. dulce* would be able to compete with other species in attracting  
293 varieties of frugivores thereby wide seed dispersal would ensure enhanced multiplication and better  
294 establishment of the species in semi-arid or arid climate. Encinas-Viso, 2014 [66]; Lavabre et al.,  
295 2016 [67], and Garcia, 2018 [68] have also emphasised on importance of frugivore diversity in  
296 reproductive success of tree species. The phenological shift in flowering is outcomes of interactions  
297 between pollinators and other biotic and abiotic factors that led to evolution of long duration flowering  
298 in *P. dulce*, which is exclusively pollinated by insects, therefore, in agreement with Elzinga, 2007 [69],  
299 and Munguia-Rosas, 2011 [70], it would be appropriate to state that insect pollinated plants flower for  
300 longer durations as compared to abiotically pollinated plants (Fig. 2-A).

301

### 302 **3.3 Persistence of fruits and sporadic in situ germination of seeds under specific** 303 **environmental conditions**

304 Flowering trees naturally shed their fruits when they are fully developed and ripened. Fruit  
305 ripening in many tropical trees is completed within few months, however, some trees such as *Cassia*  
306 *fistula*, *Thespecia populnea* shed their fruits after one or two years of fruit inception since their fruit  
307 development and ripening processes are highly prolonged. Fruits remain attached with the parent  
308 plant for more than one year and two generation fruits with distinct developmental stages could be  
309 viewed at any point of time unless older generation fruits are mechanically detached from the trees.  
310 Fruit persistence in *P. dulce* primarily seems sheer mechanical and environmental phenomena,  
311 however, the influence of biotic factors cannot be ruled out. Least number of trees about 16.20% of  
312 site-I (Man managed ecosystem) showed persistent fruits during the period of study, whereas, a  
313 greater percentage of trees (51.32 and 58.82) of sites-II and III exhibited persistent fruits. These two  
314 sites were apparently deficient in soil moisture content during the period of fruit development,  
315 however, number of persistent fruits per tree were maximum at site- I (RIE campus), and site- II (Nag

316 Pahar hillocks) on account of dense tree top canopies and structural barriers to high velocity wind  
317 through buildings and hill stones at site-I and II respectively. Sites-I&II showed the maximum number  
318 of persistent fruits per tree since trees were sparsely scattered and directly subjected to intense sun  
319 light and many of them were heavily infested with horned tree hoppers (Table-1). Studies on mode of  
320 persistence of fruits in *P. dulce* reveal that those fruits whose developmental pace is slow due to low  
321 level of moisture content and spirally coiled fruits get entangled with the spines or small branches that  
322 remain under the cover of dense leaves (Fig. 1-E&F). Drying up of such fruits is slow and fruit stalk is  
323 protected from frugivores while some parts of pods are eaten away, such fruits remain attached with  
324 the parent trees for one or two years (Fig. 1-F&G). These persistent fruits slowly split into two halves  
325 exposing their seeds which in most of the cases serve as microhabitat for breeding of insects such as  
326 horned plant hoppers, butter flies and plant spiders which serve as pollinators for *P. dulce* as well as  
327 neighbouring plants. Some of the persistent fruits sporadically showed *in situ* germination of seeds  
328 under high humid conditions during rainy season, July and August (Fig. 2-C). About 7-10% of  
329 persistent fruits were observed to exhibit *in-situ* germination of seeds in trees at sites-I and II probably  
330 due to high humidity and shade conditions maintained through underneath decaying thick leaf debris  
331 and stagnant wind around persistent fruits on account of structural barriers posed by buildings and  
332 hillocks respectively; no *in situ* germination of seeds was observed at site-III where trees are exposed  
333 in open space along the road side (Table 1). *In situ* germination of seeds in *P. dulce* is unique in the  
334 sense they do not involve hormonal elicitation secreted through maternal fruit tissues since extremely  
335 low numbers of persistent fruits under sporadic conditions exhibit such germination behaviour.  
336 Therefore, it cannot be equated with either vivipary or crypto-vivipary. *In situ* germination behaviour  
337 has been seen in those persistent fruits of *P. dulce* that get entangled with small branches and  
338 possess some viable seeds. During hot and windy summer small cracks develop on the walls of the  
339 pods which help in deposition of fine dust particles over the dried arils as well as empty spaces within  
340 the cavities of fruits. Rain water easily percolates into the fruit cavities through the cracks during July  
341 and August. Hygroscopic arils along with fine dust particles form thin substrata within the cavities of  
342 pods which retain water for a week thereby helping seeds to absorb water and quickly germinate  
343 within the pods since *P. dulce* shows orthodox seed storage behaviour and have wide range of  
344 tolerance in germination with respect to temperature and light conditions, even very thin substratum  
345 can support germination when seeds are oriented with sideward facing hilum as reported by Vargas-  
346 Figueroa et al. 2015 [71]; and Guimaraes et al. 2016 [72]; on the basis of their seed germination  
347 studies. However, some of the germinating seeds have been observed to be dropped on to the soil  
348 and further grow. Moreover, many seedlings derived from those seeds are abnormally coiled being  
349 confined within the walls of fruits (Fig. 2-C). Persistence of fruits is wide spread phenomena in *P.*  
350 *dulce* particularly in semi-arid or arid climate, which commence in response to interactions between  
351 abiotic and biotic factors. When drastic changes in atmospheric temperature and humidity are  
352 perceived, horned tree hoppers, *Leptocentrus taurus* migrate from exposed branches of deciduous  
353 trees to the evergreen branches of *P. dulce* to get reprieve and shelter. They have been frequently  
354 observed sucking fruit sap, thereby rendering them highly vulnerable which gradually dry up under  
355 high temperature of summer. Being dehydrated, fruits no longer attract frugivores, thus they remain

356 attached with the parent trees for several months in the bunch of dried partially eaten fruits by  
 357 frugivores particularly parrots and bulbuls. Similar observations have also been reported by Tang et  
 358 al. 2005 [73]. Hence, it cannot be regarded as a phenological event of reproductive process, however,  
 359 it could serve as bio-indicator of high temperature and low humidity. Conversely, low temperature of  
 360 winter is an essential prerequisite for floral induction in *P. dulce*, thus most of the trees of population  
 361 respond to the low temperature (5-8°C) during December and exhibit floral induction in a  
 362 synchronised manner. Therefore, data records on flowering phenology and persistence of fruits for a  
 363 long period could accurately portray plant responses to climate change. Similar views have been  
 364 expressed by Tooke and Battey 2010 [74], Siegmund et al. 2016 [75], and Wadgyamar et al. 2018 [76]  
 365 in their research findings. It would not be surprising to know that how some Japanese climatologists  
 366 have reconstructed climatic calendar of changes in spring time temperature in Kyoto, Japan for a  
 367 period of 732 years since 9<sup>th</sup> Century on the basis of historical flowering phenological data series of  
 368 Cherry tree, *Prunus jamasakura* [77].

369

370 Table 1. Distribution, number of trees with persistent fruits and average number of *in-situ*  
 371 germination in persistent fruits of *P. dulce* at three study sites during September 2015 –  
 372 December 2018.

373

Study sites	Duration	No. of tree species	No. of species of <i>P. dulce</i>	No. of individuals of <i>P. dulce</i>	No. of trees with persistent fruits	No. of persistent fruits/tree Mean ± SE	% of persistent fruits showing <i>in-situ</i> germination
Site-I	2015-16	76	1	105	18	3.33 ± 0.442	8.34
	2016-17	75	1	95	14	4.5 ± 0.626	9.52
	2017-18	75	1	90	15	6.26 ± 0.407	9.58
Site-II	2015-16	26	1	31	15	4.26 ± 0.589	9.38
	2016-17	24	1	25	12	4.16 ± 0.548	10.01
	2017-18	21	1	20	12	4.5 ± 0.657	7.4
Site-III	2015-16	21	1	19	11	1.63 ± 0.278	-
	2016-17	20	1	17	10	1.6 ± 0.266	-
	2017-18	17	1	15	9	1.66 ± 0.235	-

374

Table 2. Phenological calendar depicting month-wise flowering-fruitlet phenophases of individual trees of *P.dulce* natural population during September 2015 – December 2018 at three study sites.

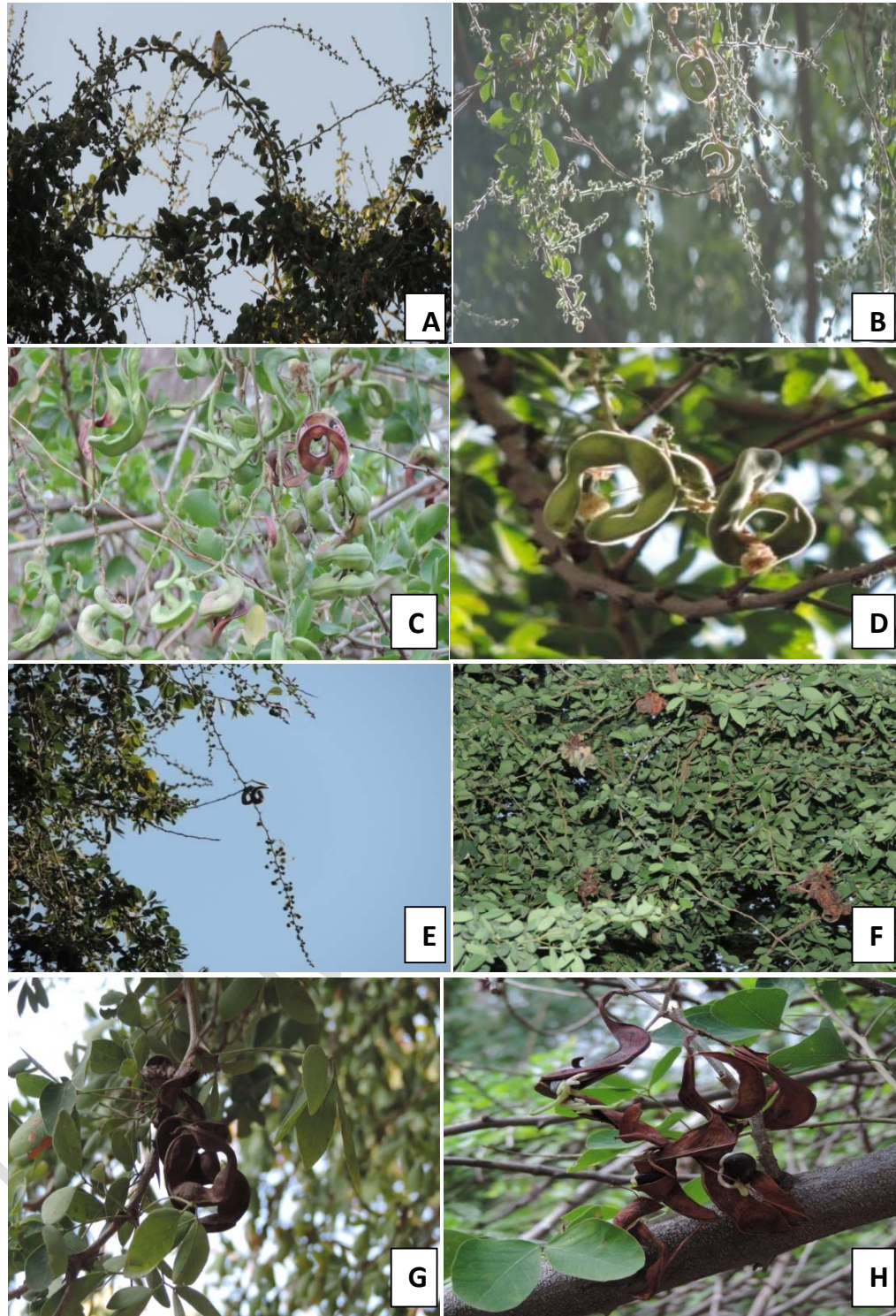
Study sites	Duration	Flowering-fruitlet phenophases of individuals	J	F	M	A	M	J	J	A	S	O	N	D
Site-I	2015-16	EFIs	Fr.m-3+2, Fc.-1, Fc-6	Fr.m-3+2, Fr.i.-1, Fc-6	Fr.r-1+2, Fr.m-1, Fr.i-6	Fr.r-1, Fr.m-6	Fr.r-6	Fr.r-6			Fi-3	Fc-3, Fi-2	Fr.i.-3, Fc.-2, Fi.-1	Fr.m-3, Fr.i.-2, Fc.-1, Fi.-6
		NFIs	Fc.-86	Fc.-85	Fr.i-82	Fr.m-78	Fr.r-75	Fr.r-70	Fr.r-10	Fr.r-5				Fi-90
	2016-17	EFIs	Fr.m-3, Fc-3+1+4	Fr.m-3, Fr.i-3+1, Fc-4	Fr.r-3, Fr.m-3+1, Fr.i-4	Fr.r-3, Fr.m-3+1+4	Fr.r-3+1+4	Fr.r-3+4	Fr.r-1+2		Fi-3	Fc-3	Fr.i-3, Fi-1	Fr.m-3, Fc-3+1, Fi-4
		NFIs	Fc-80	Fc-80	Fr.i-70	Fr.m-70	Fr.r-50	Fr.r-40	Fr.r-12	Fr.r-7				Fi-84
	2017-18	EFIs	Fr.m-3, Fr.i-2, Fc-5	Fr.r-3, Fr.m-2, Fc-5	Fr.r-3+2, Fr.i-5	Fr.r-2, Fr.m-5	Fr.m-5	Fr.r-5	Fr.r-2		Fi-3	Fc-3, Fi-2	Fr.i.-3, Fc-2	Fr.m-3, Fc-2, Fi-5
		NFIs	Fc-73	Fc-70	Fr.i-65	Fr.m-62	Fr.m-62	Fr.r-60	Fr.r-9	Fr.r-6				Fi-75
Site-II	2015-16	EFIs	Fr.m-4, Fc-2+6	Fr.m-4, Fr.i-2, Fc-6	Fr.r-4, Fr.m-2, Fr.i-6	Fr.r-4, Fr.m-2+6	Fr.r-3, Fr.m-6	Fr.r-6	Fr.r-2			Fi-4	Fc-4, Fi-2	Fr.i-4, Fc.-2, Fi-6
		NFIs	Fc-12	Fc-12	Fr.i-10	Fr.m-10	Fr.m-10	Fr.r-8	Fr.r-4	Fr.r-2				Fi-16
	2016-17	EFIs	Fc-5, Fr.i-5	Fr.m-5, Fc-5	Fr.m-5, Fr.i-5	Fr.r-5, Fr.m-5	Fr.r-1, Fr.m-5	Fr.r-4					Fi-5	Fc-5, Fi-5
		NFIs	Fc-8	Fc-8	Fr.i-7	Fr.m-7	Fr.m-5	Fr.r-3						Fi-9
	2017-18	EFIs	Fr.m-3, Fc-3	Fr.m-3, Fc-3	Fr.r-3, Fr.i-3	Fr.r-3, Fr.m-3	Fr.m-3	Fr.r-3	Fr.r-1			Fi-3	Fc-3	Fr.i-3, Fi-3
		NFIs	Fc-7	Fc-7	Fr.i-7	Fr.m-6	Fr.m-6	Fr.r-5	Fr.r-2					Fi-7
Site-III	2015-16	EFIs	Fr.m-2, Fc-2	Fr.m-2, Fc-2	Fr.r-0, Fr.i-2	Fr.m-2	Fr.m-2	Fr.r-2			Fi-2	Fc-2	Fr.i-2	Fr.m-2, Fi-2
		NFIs	Fc-12	Fc-10	Fr.i-10	Fr.m-7	Fr.m-6	Fr.r-3	Fr.r-1					Fi-13
	2016-17	EFIs	Fr.m-2, Fc-2	Fr.m-2, Fr.i-2	Fr.r-2, Fr.m-2	Fr.r-2, Fr.m-2	Fr.r-1+2	Fr.r-1				Fi-2	Fc-2	Fr.i.-2, Fi-2
		NFIs	Fc-11	Fc-10	Fr.i-10	Fr.m-10	Fr.r-9	Fr.r-9	Fr.r-3					Fi-11
2017-18	EFIs	Fr.m-1, Fc-1+2	Fr.m-1, Fr.i-1, Fc-2	Fr.r-1, Fr.m-1, Fr.i-2	Fr.r-1, Fr.m-1+2	Fr.r-1, Fr.m-2	Fr.r-2				Fi-1	Fc-1, Fi-1	Fr.i-1, Fc-1, Fi-2	

		NFIs	Fc-8	Fc-8	Fr.i-7	Fr.m-6	Fr.m-5	Fr.r-4							Fi-8
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Abbreviations: EF1 – Early Flowering Individuals; NFI – Normal Flowering Individuals; Fi – Flower Initiation; Fc – Flowering Continuum; Fr.i – Fruit Initiation; Fr.m – Fruit Maturation; Fr.r – Fruit Ripening. Inside grids, digits denote number of individual trees passing through a particular phenophase. + sign is used to denote cumulative addition of trees undergoing the same phenophase. Bold letters under EFIs denote exclusively winter or normal blooming individuals

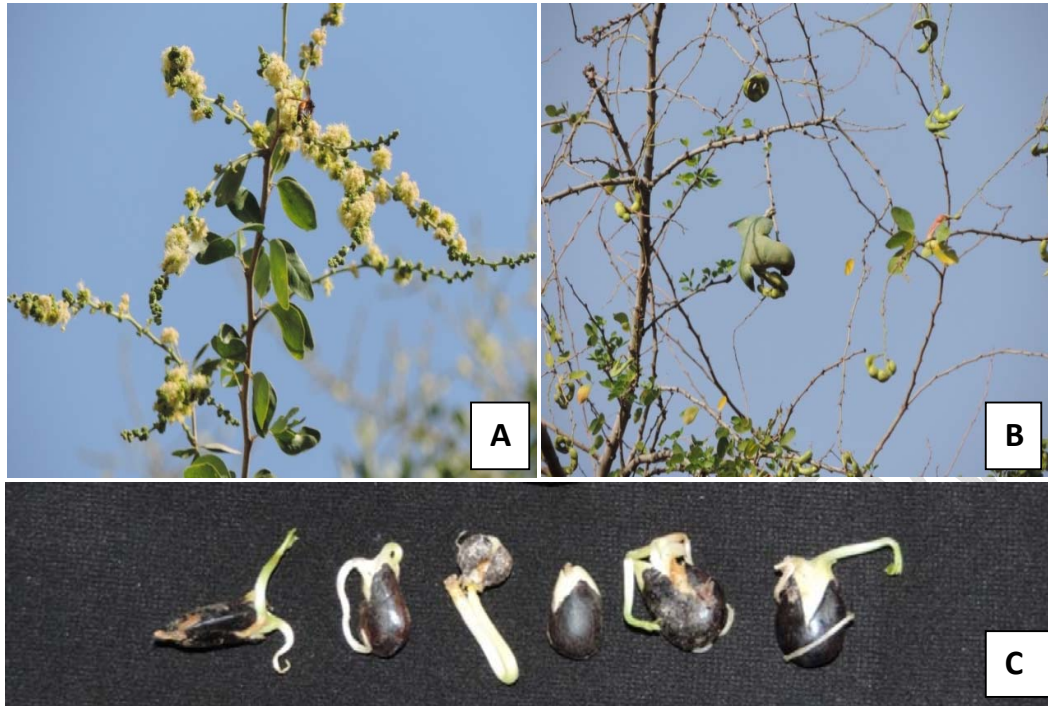
Table 3. Comparative account of morphological descriptors of flowering-fruiting in autumn and winter blooms of early-cum-normal episodic flowering individuals of *P. dulce* during three years period ( September, 2015-December, 2018 )

Trees	No. of flowering branches/tree M ± SE	Position of inflorescence on trees	No. of inflorescences /branch M ± SE	No. of floral units/inflorescence M ± SE	No. of fruits/inflorescence M ± SE	No. of seeds/pod M ± SE	Average length of fruit M ± SE (cm)	Average diameter of fruit M ± SE (cm)	Degree of synchrony in flower initiation
AUTUMN BLOOM OR EARLY FLOWERING									
1 (Site-I)	6.66±1.45	Top	7.07 ± 1.09	12.92 ± 1.17	2.16 ± 0.19	8.37 ± 0.40	11.14 ± 0.64	1.28 ± 0.06	+
2 (Site-I)	7.33±1.85	Top	6.23 ± 0.66	11.87 ± 1.87	1.94 ± 0.39	8.25 ± 0.49	11.19 ± 0.28	1.36 ± 0.12	+
3 (Site-I)	7.0±1.52	Top	7.12 ± 1.22	11.15 ± 1.83	1.98 ± 0.36	8.15 ± 0.50	10.89 ± 0.28	1.22 ± 0.05	+
WINTER BLOOM OR NORMAL FLOWERING									
1 (Site-I)	28.33±4.40	All over	9.18 ± 0.54	17.42 ± 0.93	3.04 ± 0.17	6.48 ± 0.96	7.43 ± 0.42	0.97 ± 0.06	+++
2 (Site-I)	35.0±2.88	All over	8.61 ± 0.83	15.64 ± 0.49	2.70 ± 0.16	6.98 ± 0.99	7.66 ± 0.48	0.93 ± 0.03	+++
3 (Site-I)	37.33±7.21	All over	8.18 ± 0.54	15.32 ± 0.62	2.89 ± 0.17	7.55 ± 0.97	8.50 ± 0.29	0.96 ± 0.02	+++



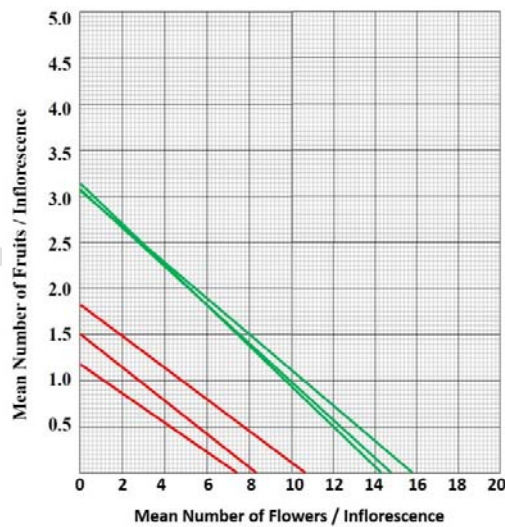
**Fig. 1 Morphological descriptors of reproductive behaviour of *Pithecellobium dulce* of semi-arid climate**

**A.** Single winter blooming tree showing synchronized floral initiation during December **B.** Early-cum-twice blooming tree showing fruits of autumn blooms along with synchronized floral initiation of winter blooms during December **C.** Shrinkage and splitting up of fruits of winter blooms during harsh summer **D.** Well developing plump fruits of autumn blooms **E.** Autumn bloom fruits entangled with winter bloom inflorescence **F.** Persistent fruits that remain attached with the parent tree throughout the year **G.** Dried persistent fruit with seeds and thin substratum within the cavity of the fruit **H.** *in situ* germination of seeds within the persistent fruit during high humid rainy season.

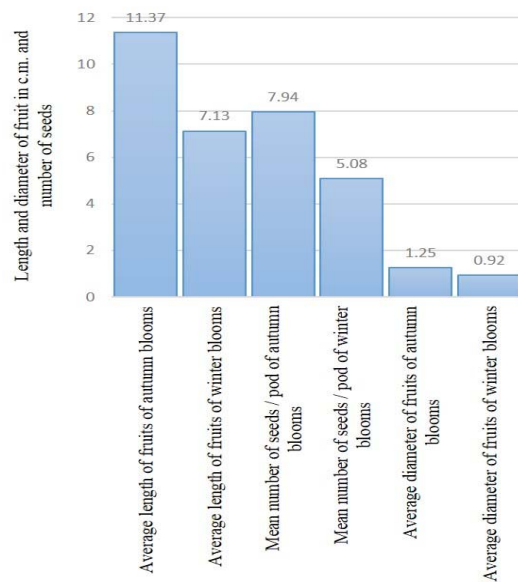


**Fig. 2 Morphological descriptors of reproductive behaviour of *Pithecellobium dulce* of semi-arid climate**

**A.** Winter bloom flowers with pollinators **B.** Dryness induced defoliation of branches with exposed fruits along with frugivores during summer months **C.** Seedling abnormalities showing constrained growth of plumules and radicles that coil around seeds during *in situ* germination within the walls of dried persistent fruits during high humid rainy days



**Fig. 3.** Graphical representation of fruit to flower ratio of winter and autumn blooms exhibited by three individual twice-flowering trees. Autumn blooms and winter blooms have been represented through red and green lines respectively.



**Fig. 4.** Histogram showing pomometric characteristics

#### 4. CONCLUSION

There are three categories of individual trees of *P. dulce* comprise its natural population of habitat under study of semi-arid climate with respect to their reproductive behaviour. Of all blooming trees, majority of them (89.94%) constitute category-I which exhibits normal or winter bloom in which flowering is initiated in almost synchronised manner during December and all reproductive activities including dehiscence of fruits are completed by June or July months every year. Category-II trees (7.47%) exhibit two blooms consecutively in a year, viz., early or autumn bloom and normal or winter bloom. However, their flowering-fruiting phenological onset timings of early or autumn blooms were inconsistent during the period of study. Category-III individuals (2.58%) of *P. dulce* exhibit agronomically advantageous flowering-fruiting phenophase, early or autumn blooms in these individuals were observed to be conspicuously consistent throughout the study duration. They exhibited very conspicuous early or autumn blooms in which flowering was initiated in the month of September in addition to normal or winter blooms. Overall productivity in terms of number of fruits in this category of trees is greater as compared to other two categories of trees. Though, the numerical value of fruit productivity of autumn blooms was inferior to winter blooms within the same tree, pomometric characteristics of former were superior. Moreover, the availability of fresh fruits in early-cum- twice blooming tree is also prolonged (February to July). Undoubtedly, Category-III variants or germplasm are horticulturally superior and more desirable that warrant their selection and clonal multiplication. It is evident through consistency in data in phenological calendar that early or autumn bloom in this category of individuals is not influenced by environmental variables alone, i.e., edaphic or climatic since they grow in a similar habitat, however, some age specific flowering was observed. They arose probably by expression of heterogeneity in seeds which differentiated through natural genetic recombination in response to evolutionary forces being operative under prevailing environmental conditions of semi-arid climate. The present paper also makes evolutionary predictions that how a shift in flowering phenology of *P. dulce* as exhibited by the elite variants or germplasm could have long-term implications for reshaping of future landscapes of semi-arid or arid climate through reproductive success, wide dissemination of seeds, consequently better establishment of the species. The concept of reproductive success as postulated in this paper is also expressed by Kudo, 2006 [78], and Elzinga et al., 2007 [69], that individual plants flowering for longer durations have several advantages over other members of the population with respect to higher out crossing rates owing to availability of diversities in pollinators, and more time for fruit development and seed maturation during favourable season as observed in case of autumn blooms of *P. dulce*. The present work identifies and selects agronomically valuable variants or germplasm of *P. dulce* through simple method of construction of phenological calendar. It also reports associated ecological phenomena of persistence of fruits serving as micro-habitat for breeding of insect pollinators and sporadic *in-situ* germination of seeds. Nevertheless, a great effort would be required in resolution of some inherent research possibilities arising with discovery of a new phenophasic variants such as innovation in designing agronomic practices or methods to enhance overall productivity of the cultivars through optimising the yield from early or autumn

blooms; development of macro and micro propagation protocols for enhanced multiplication of the elite variant or genotype; genetic modification of the cultivars through biotechnological interventions involving elite germplasm; and deciphering the molecular cascades for reception of altered environmental cues for phenological shift in flowering from normal or winter blooms to early or autumn blooms are relevant topics of scientific investigations which could further pave the way for molecular engineering of phytophenology as future area of promising research of far reaching consequences.

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