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Changes in reproductive phenology and sex ratio of *Trewia nudiflora* Linn. growing in sal forest of north-eastern Uttar Pradesh, India

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Abstract: *Trewia nudiflora* Linn. (Euphorbiaceae) is a fast growing multipurpose dioecious tree which grows mostly at moist places under fairly high light environment within the forest vegetation of north-eastern Uttar Pradesh. The effect of moisture regime on the quantitative and temporal pattern of flowering was significantly evident. The reproductive activities started comparatively earlier and continued for shorter period on trees growing at upland compared to those at relatively lowland sites. Further, the trees growing at high soil moisture sites showed greater numbers of inflorescences, flowers and fruits (in case of female individuals) compared to those growing at sites with average soil moisture. The sex ratio (i.e. the number of male to female trees) of the species along with different phenophases round the year was examined at eight sites having different light and soil moisture regimes. In fully exposed and average soil moisture conditions, the sex ratio was clearly male-biased, while it was female-biased under high soil moisture regimes. Under partially shaded environment, the sex ratio was quite close to unity but under shaded environment, it was clearly male-biased, irrespective of soil moisture regimes. In a given light environment, the tendency towards female-biased sex ratio increased with increase in soil moisture status. The lowering of light regime, however, adversely affected the femaleness and increased the male-biased sex ratio. It indicates that the female-biased sex ratio of *Trewia nudiflora* is probably selected in response to greater soil moisture and high light environment to ensure the production and maturation of large fleshy fruits with no chance of their desiccation or hindrance against seed dispersal.

Resumen: *Trewia nudiflora* Linn. (Euphorbiaceae) es un árbol dioico multipropósito de crecimiento rápido que crece principalmente en lugares húmedos, en condiciones de iluminación relativamente altas en la vegetación forestal del noreste de Uttar Pradesh. El efecto del régimen de humedad sobre el patrón cuantitativo y temporal de floración fue significativamente evidente. Las actividades reproductivas comenzaron comparativamente temprano y continuaron por periodos más cortos en los árboles que crecían en las tierras altas que en los de sitios de tierras relativamente bajas. Además, los árboles que crecían en sitios con humedad del suelo alta mostraron inflorescencias, flores y frutos (en el caso de individuos femeninos) más numerosos que los que crecían en sitios con una humedad del suelo promedio. La proporción de sexos (i.e., el número de árboles macho respecto al de árboles hembra) de la especie y las diferentes fenofases en todo el año fueron examinadas en ocho sitios con diferentes regímenes de luz y de humedad del suelo. En condiciones completamente expuestas y con humedad del suelo promedio, la proporción sexual estuvo claramente sesgada hacia los machos, mientras que el sesgo fue hacia las hembras bajo regímenes de alta humedad del suelo. En un ambiente con sombra parcial, la proporción de sexos fue muy cercana a 1 pero en el ambiente sombreado tuvo un claro sesgo hacia los machos, independientemente de los regímenes de humedad. En un cierto ambiente lumínico, la tendencia hacia una proporción sexual con sesgo femenino aumentó con el incremento en el estatus de la humedad del suelo. La disminución del régimen lumínico, sin embargo, afectó de forma negativa

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el carácter femenino e incrementó la proporción sexual sesgada hacia los machos. Esto indica que la proporción sexual con sesgo femenino de *Trewia nudiflora* probablemente sea seleccionada en respuesta a una mayor humedad del suelo y un ambiente de luz alta para asegurar la producción y maduración de los frutos grandes y carnosos sin que haya ninguna probabilidad de su desecación u obstáculos para la dispersión de sus semillas.

Resumo: A *Trewia nudiflora* Linn. (Euphorbiaceae) é uma árvore dioica polivalente de crescimento rápido, que vegeta principalmente em lugares húmidos sob ambiente de luz bastante elevado no interior da vegetação da floresta do nordeste do Uttar Pradesh. O efeito do regime de humidade no padrão quantitativo e temporal da floração foi significativamente evidente. As atividades reprodutivas começaram relativamente cedo e continuaram por um período mais curto nas árvores que crescem em terras altas em comparação com aquelas em locais a relativamente baixa altitude. Além disso, as árvores que crescem em locais de elevada humidade do solo mostraram maior número de inflorescências, flores e frutos (no caso de indivíduos do sexo feminino) quando comparadas com as que crescem em locais com humidade média de solo. A razão sexual da espécie (ou seja, a razão entre o número de árvores masculinas e as árvores femininas), juntamente com as diferentes fenofases ao longo do ano foi analisada em oito locais com diferentes regimes de luz e humidade do solo. Em condições totalmente expostas com humidades médias do solo, a razão de sexo era claramente desviada para espécimes masculinos, enquanto que sob regimes alta humidade do solo se verificava ser superior o número de exemplares femininos. Sob ambiente parcialmente sombreado, a razão de sexo era muito próximo da unidade, mas em ambiente sombreado, o sexo masculino era claramente superior, independentemente dos regimes de humidade do solo. Num determinado ambiente de luz, a tendência para a razão de sexo apresentar maior número de espécimes femininos cresceu com o aumento do status de humidade do solo. A redução do regime de luz, no entanto, prejudicou a feminilidade e aumentou a razão de sexo tendentemente masculino. Isto indica que a razão sexual tendentemente feminina da *Trewia nudiflora* ocorre provavelmente em resposta à maior humidade do solo e ambiente de alta luminosidade para garantir a produção e maturação dos grandes frutos carnudos, sem chance da sua dessecação ou impedimento para a dispersão de sementes.

Key words: Dioecy, light and soil moisture regimes, phenology, sex ratio, *Trewia nudiflora*.

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Introduction

Tropical floras show high incidence of dioecy as compared to temperate ones and the increase in the frequency of dioecy is correlated with an increase in plants' size (Bawa 1980). About six percent of angiosperm species are estimated to be dioecious (Renner & Ricklefs 1995) and their sex ratio varies in response to habitat condition, age state and plant size (Nicotra 1998). The sex ratio is reported to be altered by such environmental conditions as light regime, soil moisture and nutrients (Bierzychudek & Eckhart 1988; Iglesias & Bell 1989). The dioecious species of Indian forests however, are little explored as regard to sex ratio variations (Aluri *et al*. 1997). Sexual reproduction in dioecious trees requires a vector to transfer pollen between conspecifics, and, therefore, reproductive success of the species in such trees is subject to many ecological constraints and phenological attributes. Reproductive phenology deals with the occurrence of flowering and fruiting events, and its investigation in case of tropical trees would be important for biodiversity conservation efforts in the tropics. The reproductive events in tropical trees are not self regulatory and often depend on vegetative phenology and environmental periodicity. A set of reproductive traits may critically regulate the reproductive success (Rathcke & Lecey 1985; Shukla & Ramakrishanan 1982). Flowering phenology determines utilization of seasonally available resources such as light and

moisture by plants (David *et al*. 2012; Gunarathne & Perera 2014; Murali & Sukumar 1994), which in turn determines the availability of resources for frugivorous animals. The timing and duration of flowering and fruiting are crucial in understanding forest regeneration dynamics as the pronounced seasonality affects the reproductive output and performances such as seed production, germination, survival and seedling growth (Augspurger 1981). A few observations on the variations in reproductive phenology and sex ratio of *Mallotus philippensis* in relation to prevailing light regimes were made within different sal forest communities of the north-eastern Uttar Pradesh (Pathak & Shukla 2004; Shukla & Pandey 1991). Such information is basic to the understanding of biological processes and functioning of the forest ecosystem.

Trewia nudiflora Linn. (Euphorbiaceae) is a fast growing early successional dioecious tree whose natural regeneration is quite frequent in the moist and coarse textured soil. The seedlings of the species are, however, sensitive to drought and usually get killed at the exposed upland sites (Troup 1921). The light and moisture regimes are the two major factors of forest environment playing an important roles in the relative abundance and distribution of male and female individuals. This paper reports the observations on the reproductive phenology and sex ratio variation in relation to abiotic factors (light and soil moisture regimes) in *T. nudiflora* growing in moist semi-evergreen tropical forests of north-eastern Uttar Pradesh, India. The information on important abiotic factors that affect the sex ratio and reproductive phenology of the species have application in forest management and tree improvement programmes.

Methods of study

A survey of forest stands and adjoining areas of Gorakhpur Forest Division (between 27° 05′ and 27° 40′ N latitudes and 83° 30′ and 84° E longitudes at an elevation of 95 m), Uttar Pradesh, India, was made to identify sample plots containing trees of *T. nudiflora*, for the study of its sex-ratio and reproductive phenology in different environments. A total of eight plots were identified at six different locations (Fig. 1). The details of location and area of sample plots, their habitat conditions (light and moisture regimes) and the number of individuals of *Trewia* are given in Table 1. All the individuals of male and female trees including juveniles of *T. nudiflora* (a total of 512 individuals) were counted in each of the eight sample plots. The sex ratio, expressed as the ratio of number of male individuals to female individuals, was calculated for each sample plots excluding juveniles. A total of 310 individuals with varying diameter range (10 - 75 cm) were identified at different locations in and around the sample plots. The maturity stages of trees were categorized into five different stem diameter (dbh) classes (10 - 25, 26 - 40, 41 - 55, 56 - 70 and > 70 cm). The light regimes and moisture conditions were measured for each of the 310 reproductively mature individuals. The light intensity in the vicinity of each individual was measured by illuminometer (Kyoritsu 5200, Japan) at mid sunny days in the month of November. Average percent soil moisture in upper depth (0 - 10 cm) near each individual was measured as mean of three samples per individual. The occurrences of trees were grouped under three light regimes, open (> 2400 lux), partial shade (~ 1600 lux) and shade (< 800 lux). Individuals occurring in each of these light regimes were further sorted out into two soil moisture levels, low (30 - 40 %) and high moisture site (> 50 %). The sex ratio was determined for each set of conditions on the basis of count of male and female flowering individuals during Feb-March. The sex ratio was also analyzed for the whole *T. nudifolia* population at each of the six different sites to observe sex ratio variation as related to site conditions across the regional landscape.

The span of different life activities or phenophases like leafing, budding, flowering, fruit maturation and fall and the seed germination were observed round the year. For these observations, three mature (23 ± 4.2 cm dbh) and three over mature (42 ± 5.7 cm dbh) trees of both sexes at upland and relatively lowland sites in fully exposed conditions were selected. The peaking of any phenological activity was taken as the time period during which more than 50 % of the individuals were undergoing that phenophase. The phenodiagrams were drawn for both the male and female trees growing on upland as well as lowland sites. The phenometrical analysis was done to assess the effect of site conditions on the number of different reproductive units (inflorescence, flowers and fruits). The sampling of reproductive units was made in heirarchial order starting from twigs, small branches, large branches, and major branches to tree as a whole.

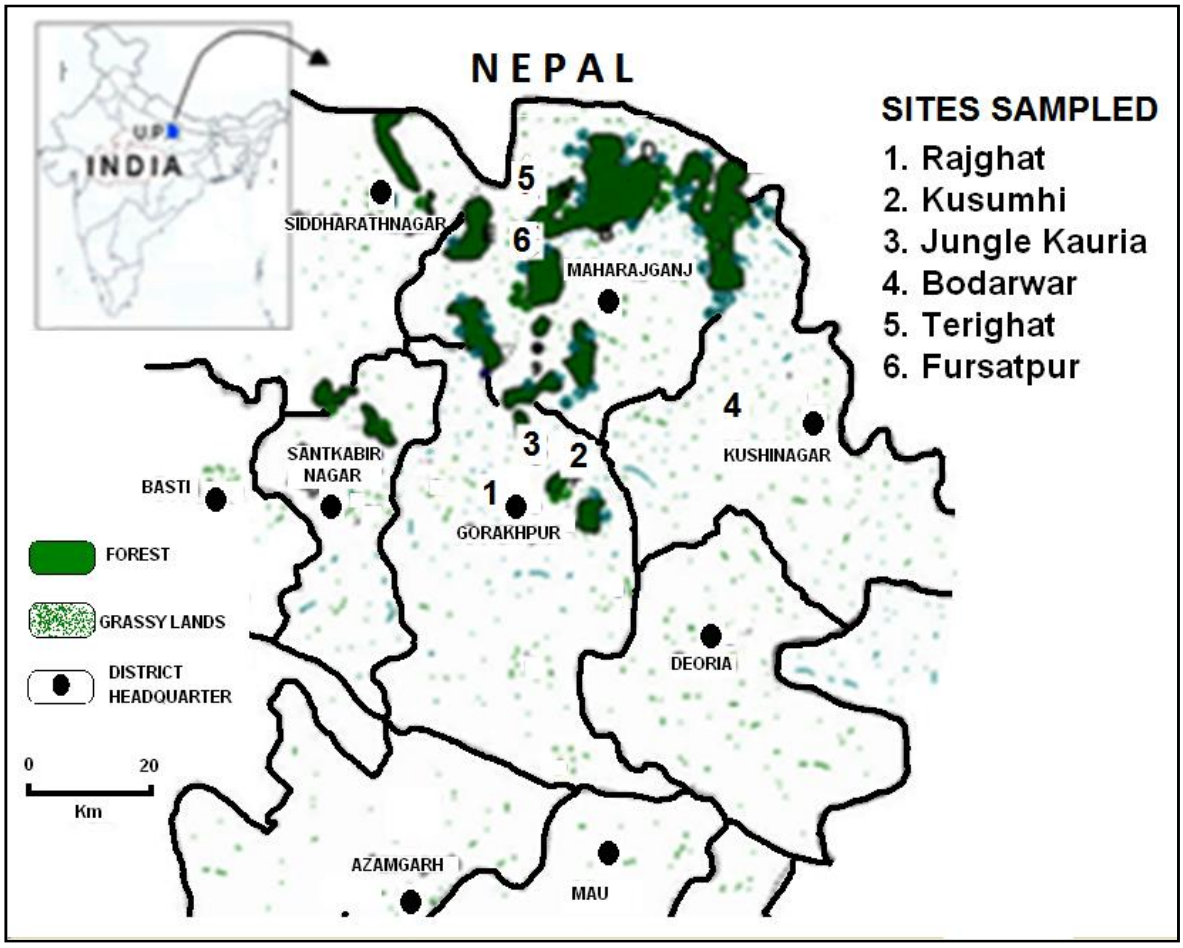

Fig. 1. Map showing the sites (1 - 6) of observed trees of *Trewia nudiflora* within north-eastern U.P.

Table 1. Details of locations, habitat conditions (light and moisture), plot area and total number of individuals per plot.

Locations	Plot Number	Moisture condition	Light condition	Area /plot (m^2)	Total number of *Trewia* individuals
Kusmhi Forest	1	Average moist (30-40 %)	Partial shade (~1600 lux)	1250	71
Kusmhi Forest	2	Moist rich (> 50 %)	Partial shade	1250	59
Rajghat	3	Average moist	Open (> 2400 lux)	500	57
Jungle Kaudia	4	Moisture rich	Open	500	54
Boderwar	5	Average moist	Open	2500	60
Terighat	6	Average moist	Partial shade	2500	73
Terighat	7	Moisture rich	Partial shade	500	55
Fursatpur	8	Average moist	Open	2500	83

Table 2. The values of sex ratio (no. of male individuals/ female individuals) for three lowland and five upland populations of *Trewia nudiflora*.

Locations	Plot number	Plot condition	Area (m^2)	Total no. of individuals	% Number			Sex ratio	χ^2 value
					Male	Female	Juvenile		
Kusmhi Forest	1	Upland	1250	71	22.5	18.3	59.2	1.23	0.31
Kusmhi Forest	2	Lowland	1250	59	20.3	27.1	52.6	0.75	0.57
Rajghat (River dam)	3	Upland	500	57	42.1	29.8	28.1	1.41	1.20
Jungle Kaudia	4	Lowland	500	54	27.8	37.0	35.2	0.75	0.71
Boderwar	5	Upland	2500	60	55.0	21.7	23.3	2.54	8.70*
Terighat	6	Upland	2500	73	26.0	17.8	56.2	1.46	1.13
Terighat	7	Lowland	500	55	23.6	29.1	47.3	0.81	0.31
Fursatpur	8	Upland	2500	83	48.2	28.9	22.9	1.67	4.00**

The values are significant at 1 % probability* level and 5 % probability** levels.

Results

Changes in sex ratio along different sites

Out of eight plots studied, commensurate changes in sex ratio in three plots (2, 4 and 7) situated at lowland sites with greater soil moisture content were female-biased, whereas other five plots (1, 3, 5, 6 and 8) on relatively upland sites with average soil moisture showed highly male-biased sex ratios (Table 2). The bias towards maleness, however, increased from 1.23 to 2.54 along the gentle slope of upland sites from lower to higher side. Further, the sex ratio in lower diameter classes was strongly male-biased, whereas it gradually tended towards unity or even slightly female-biased in higher diameter classes. In younger ages, flowering was not as frequent in female plants as in male plants (Table 3).

The sex ratio also changed in three different light regimes with strong male bias under fully exposed conditions (having average moisture environment) and strong female bias under high moisture environment. Under partially shaded condition, the sex ratio was slightly male-biased under average moisture condition and slightly female-biased under high moisture condition. In shaded environment, however, the sex ratio was highly male-biased in both the moisture regimes (Table 4).

To observe the site related changes in sex ratio of different species populations within the region, *T. nudiflora* populations were analyzed at six different sites. As evident from Table 5, sites 1 and 6 situated at slightly lowland towards forest edge, showed female-biased sex ratio. Open upland site adjacent to Rapti river dam and relatively lowland roadside showed slightly male-biased sex ratios, which were quite close to unity. The upland *Trewia* populations along railway track and forest edge showed highly male-biased sex ratios. The average sex ratio for north-eastern region of Uttar Pradesh, however, was slightly male-biased.

Table 3. Sex ratio variation within five different diameter-class ranges of trees of *Trewia nudiflora*.

Diameter class (in cm)	Total no. of individuals	% Number of trees		Sex ratio	χ^2 value
		Male	Female		
10-25	68	66.18	33.82	1.96	7.12*
26-40	152	59.87	40.13	1.49	5.92**
41-55	50	44.00	56.00	0.79	0.72
56-70	25	52.00	48.00	1.08	0.01
≥ 71	15	46.67	53.33	0.87	0.01

The values are significant at 1% probability* level and 5% probability** level.

Phenological & phenometrical analysis

In general, the male trees started flowering earlier by fortnight and continued for longer time

Table 4. Sex ratio of *Trewia nudiflora* under three different light regimes (open, > 2400 lux; partial shade, ~1600 lux; shade, < 800 lux) and two moisture regimes (average moisture = 30 - 40 % soil moisture content and high moisture = > 50 %. soil moisture content).

Trewia Population	Open		Partial shade		Partial shade	
	Average moisture	High moisture	Average moisture	High moisture	Average moisture	High moisture
Male	73	42	22	21	13	7
Female	31	50	18	22	7	4
Sex ratio	2.35	0.84	1.22	0.95	1.86	1.75
χ^2 value	16.96*	0.70	0.40	.02	1.80	0.82

*The value is significant at 1 % probability level.

Table 5. **S**ex ratio of *Trewia nudiflora* at six different sites of north-eastern U.P.

Study sites	Site condition	Total no. of individuals	% Number			Sex ratio(male/female)	χ^2 value
			Male	Female	Juveniles		
Kusmhi forest	Partial shaded (at the forest edge)	117	20.5	25.6	53.9	0.80	0.67
Rajghat	Open (along Rapti river dam)	67	38.8	32.8	28.4	1.18	0.33
Jungle Kaudia	Open lowland (along roadside)	200	32.5	31.5	36.0	1.03	0.03
Boderwar	Open upland (along railway track)	207	44.0	31.9	24.1	1.38	3.98**
Fursatpur	Open upland (managed *Trewia* stand at forest edge)	189	51.9	27.5	20.6	1.88	0.38
Terighat	Partially shaded lowland (mixed forest)	236	25.9	28.8	45.7	0.90	14.11*

The value are significant at 1 % probability level and 5 %** probability level.

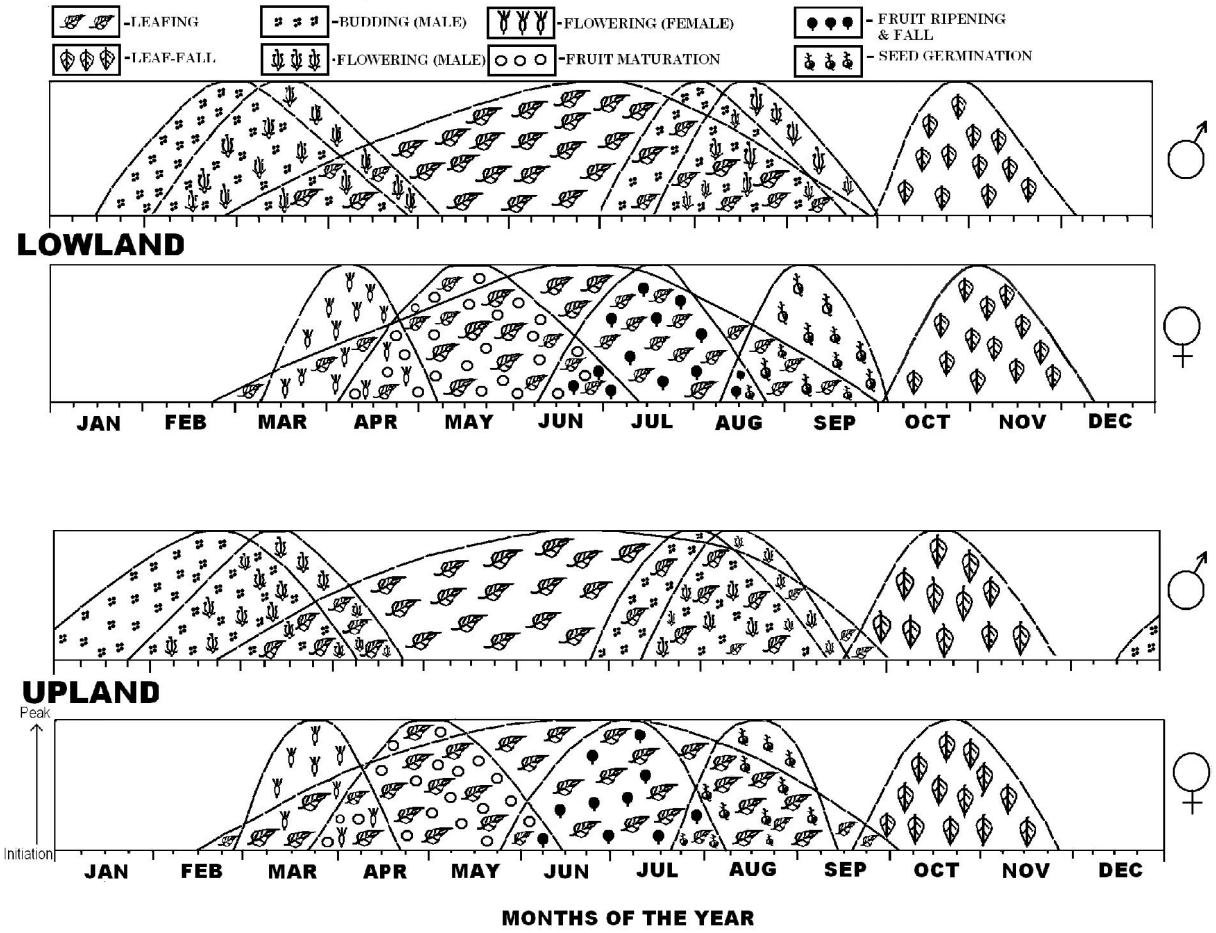

Fig. 2. Reproductive phenology of male and female trees of *Trewia nudiflora* growing under fully exposed condition at upland (average moisture) and lowland (moisture rich) sites.

Table 6. Phenometrical comparison of fully exposed mature and over mature trees of *Trewia nudiflora* growing at upland and lowland sites. The number of various reproductive units (inflorescence, flower, and fruit) is expressed as mean ± S.D.

		Mature individuals (23 ± 4 cm)		Over mature individuals (42 ± 5 cm)	
	Reproductive units	Lowland	Upland	Lowland	Upland
Female tree	Inflorescence	2342 ± 162	1740 ± 186	3851 ± 686	3248 ± 408
	Flower	11711 ± 811	7831 ± 837	17880 ± 1706	14166 ± 656
	Fruit	7378 ± 311	5221 ± 670	10375 ± 1074	8776 ± 438
Male tree	Inflorescence	3148 ± 956	2973 ± 68	6580 ± 1781	4701 ± 631
	Flower	133268 ± 4050	121890 ± 2779	256201 ± 7542	192746 ± 2591

period as compared to female trees. The male trees flowered twice annually while female trees did so once in a year (Fig. 2). The major flowering event in male trees started during December at upland sites and during January at lowland sites and continued upto April and May respectively. Male trees also showed minor flowering during the last week of June to first week of July and continued it upto last week of September. The effect of moisture regime on the quantitative and temporal pattern of flowering was quite evident. The reproductive activities like budding, flowering, fruiting and fruit-fall started earlier and continued for comparatively shorter period on trees growing

at upland sites with average soil moisture as compared to those growing at lowland sites having high soil moisture. Each phase of reproductive activity gradually merged in the next phase well before reaching its peak. Leafing activity started during the last week of February, peaked during July-August and lasted upto August - September. The whole trees were lush green having maximum number of leaves by the month of October. The leaf fall started in the beginning of October, peaked during first-half of November which resulted into complete leaflessness by mid-December (Fig. 2).

Phenometrical analysis of reproductive units were done taking mature and over mature trees of *T. nudiflora* growing on upland and lowland sites under fully exposed condition (Table 6). The number of inflorescence and flowers on male trees was far greater as compared to that on female trees. Both the male and female trees growing at sites having higher moisture showed greater number of inflorescences, flowers and fruits as compared to those growing at sites with average soil moisture. For over mature trees also, the trend was similar and the number of reproductive units per tree was much greater as compared to mature trees.

Discussion

The average sex ratio of *T. nudiflora* for the regional forested landscape in the present study was slightly male-biased. In dioecious plants, sex ratios have traditionally been studied at the whole population level and frequently found to be male-biased (Opler & Bawa 1978; Thomas & La Frankie 1993) and less frequently to be female-biased (Crawford & Balfour 1983; Chia 2000; Shelton 2010; Ueno *et al.* 2007). Further, sex ratios have also been found to vary with factors such as water availability, light regime, stress and disturbance levels (Lloyd & Bawa 1984; Pathak & Shukla 2004), which were reflected by varied responses of sex ratio to light and moisture regimes in the present study. Deviation in sex ratio could arise by several mechanisms including differential growth or mortality of each gender and also by environmental sex changes (Charnov 1982; Charnov & Dawson 1989). In the present study, sex ratio was male-biased in uplands and in open conditions with average soil moisture, whereas it was female-biased at lowland and in open condition with higher moisture. In partially shaded condition, the sex ratio approached close to 1 at sites with high soil moisture but increased to be clearly male-biased at sites with average soil moisture. Similar observations were made by Marciniuk *et al.* (2010). Putwain & Harper (1972) suggested that niche differences between the sexes may be due in part to energy requirements of male and female plants. It has been observed that plants of several species in bright sun light turn out to be female and those in shade turn out to be male (Charnov & Bull 1977; Freeman *et al.* 1976) resulting into female-biased ratio under high light regimes and male-biased ratio under low light regime. Thus sex ratio bias may, in part, be a consequence of differential costs associated with reproduction of plants of either sex. Males avoid the physiological demands by females on fruits and seeds production and, therefore, show higher fitness in stressful microhabitat (Freeman *et al.* 1980). The occurrence of male-biased population under open and shaded environment with average moisture condition and female-biased population under exposed and high moisture conditions is consistent with resource allocation theory that reproductive success is resource-limited (Goldman & Wilson 1986). The most frequent reason for the deviation of the sex ratio from theoretical 1:1 value has been attributed to different ecological niches (Cvetkovic & Jovanovic 2007; Ortiz *et al*. 2002; Rottenberg 2000). *Trewia* trees under lower diameter classes showed clearly male-biased sex ratio which approached to one and even became female-biased in more mature plants of higher diameter classes. Thus sex ratio became increasingly less skewed with increase in maturity of *Trewia.* Skewed sex ratios in relation to tree maturity have earlier been reported by several workers (Armstrong & Irvine 1989; Lloyd & Webb 1977).

The distinct sexual dimorphism of *T. nudiflora* flowers suggests that changes in sex expression in the species require rather large morphological adjustments and sex-switching in response to environmental condition is quite unlikely. The male-biased ratios under lower diameter classes may be attributed to the onset of flowering event at younger age in males.

Studies from different parts of the world have shown that climatic factors are mainly responsible for vegetative and reproductive phenology at both community and species level (Frankie *et al.* 1974; Gunarathne & Perera 2014). Water stress is, however, most frequently cited as a primary factor responsible for the timing of phenological events (Singh & Singh 1992). Similar observations were

made on *T. nudiflora* where most of reproductive events occurred during the period of good soil moisture conditions. *Trewia* trees growing at upland sites showed a temporal shrinking in their phenological activities such as leaf fall, leafing, budding, flowering, fruiting and fruit-fall; the phenophases started earlier and continued for shorter period as compared to those for lowland trees.

In a forest community, the tree periodicity patterns give an idea of seasonal organization of floral and fruit resources (Frankie *et al.* 1974). In *T. nudiflora* various phenophases showed quite distinct periodicity. Maximum leaf fall occurred during the period of water stress due to low temperature during winter. The phenological events like leafing, budding and flowering occurred during warmer months of March-April before the onset of rains. Thus, the strategy of leaf replacement appears to maximize photosynthetic activity during hot and humid part of the year. Similar observations were made by Tesfaye *et al*. (2011) for seven tree species in a dry Afromontane forest in Southern Ethiopia. Fruit maturation occurs during May-July (monsoon season) when assimilation rate and soil moisture are quite high. The wet ground layer also facilitates the rottening of fleshy fruits paving the way to seed germination. Most studies of tropical fruiting phenologies report seasonalities and also reveal extreme seasonality in annual fruiting patterns among plants with fleshy-fruits in forests with distinct wet and dry seasons (Engel & Martins 2005; Howe & Smallwood 1982). It has been found that a majority of fleshy-fruit species across the globe produce fruits during rainy season (Bhat 1992; Sundarapandian *et al*. 2005). This fruiting pattern may reduce seedling mortality by dispersing seeds when soil moisture conditions are favourable for seed germination and rapid seedling growth (van Schaik *et al*. 1993). Similar correlations have been observed by Boojh & Ramakrishnan (1981) and Shukla & Ramakrishnan (1982) for a number of trees of sub-tropical evergreen montane forest of north-east India. The pattern of flowering in male trees of *T. nudiflora* showed two peaks, the major one occurred during March-April and minor one during July-August. The wet season male flowering, however, could not be attributed to any significance as no wet season female flowering was noticed. Male plant started flowering much earlier and continued for longer than females, as has also been reported for several other trees (Shukla & Pandey 1991). The number of inflorescences and flowers per male tree were far greater than that for female trees which is quite usual for the majority of dioecious species (Bawa 1980). The production of exorbitantly greater number of male flowers is regarded as an adaptation to ensure optimal distribution of pollen for each ovule (Lloyd & Webb 1977). The extent and periodicity of reproductive events in *T. nudiflora*, however, provides a significant resource base for frugivores for most part of the year.

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