

Study on sex determination and variation in gender expression of individual trees in a population of *Cedrus deodara* (Roxb.) G. Don

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Abstract

Conifers are reported to exhibit predominantly monoecious behaviour however, numerous species and some genera show uncertainties regarding their gender expression. The factors influencing the sexual differentiation of strobili in monoecious or dioecious conifers remain poorly understood. To investigate this unpredictable phenomenon in conifers, we selected three populations representing pure stands of *Cedrus deodara* in dense temperate forests of Northern India, specifically one in Uttarakhand and two in Himachal Pradesh.

Each site was surveyed, and total 900 trees were marked as male, female, monoecious and neutral trees based on their reproductive behaviour and sexual representation. Selection criteria were based on the reproductive age of *Cedrus deodara*, as it attains maturity when it reaches a height of 19 to 20 meters. Our findings revealed that *Cedrus deodara* exhibits subdioecious behaviour, characterized by the occurrence of four basic sex forms such as male trees, female trees, monoecious trees, and neutral trees. Yearly observations from 2014 to 2016 unveiled that *Cedrus deodara* does not exhibit consistent reproductive behaviour. Instead, the species displays a fascinating pattern of alternation between dioecy and monoecy. Additionally it was also found that individual trees demonstrated change in their expression of sex during each reproductive cycle. These findings underscore the complexity of sex determination and reproductive plasticity in *Cedrus deodara*. This research paved the way for future investigations into the factors influencing sex expression and reproductive behaviour in conifers and will contribute to our broader knowledge of plant sexuality and plant evolution.

1. Introduction

The expression of gender and sex in plants is a highly intricate process that has been the focus of numerous research studies, which are still ongoing today. Both angiosperms and gymnosperms have been studied in relation to their gender expression. Plants can be classified as male, female, hermaphroditic, or monoecious, depending on their reproductive characteristics. However, gender or sex in plants is not a straight forward categorization, but rather a quantitative trait that is influenced by a variety of internal and external factors. These factors include complex mating strategies, environmental factors and the reproductive biology of the plants. As a result, categorizing plants based on gender or sex can be limited and may not fully capture the complexity of their reproductive biology. (Lloyd.,1980).

To comprehend the ecology of long-lived trees and the pressures that influence their fitness, a thorough investigation of their reproductive patterns is important (Harper.,1977). While there is less research on the life cycle of trees, particularly gymnosperms those grow in undisturbed forests, there is convincing literature available on the seed masting phenomenon that occurs in many angiosperms and some gymnosperms, particularly tree species in temperate forests (Harper., 1977; Silvertown., 1980; Ogden., 1985; Norton & Kelly., 1988). Examining gender expression patterns in plants has aided evolutionary biologists in comprehending and assessing the mechanisms behind plant breeding systems and their assessment. Gender expression is vital in determining the genetic contribution of plants as either male or female (Lloyd., 1979). Various factors, such as size, growth rate, mortality, light, and nutrient resources, can impact the ontogenic sex change in plant species (Heslop-Harrison., 1957; Charnov and Bull., 1977; Freeman., 1980; Schlessman., 1986; Korpelainen., 1998; De Jong and Klinkhamer., 2005). Resource-dependent gender plasticity is typically observed in natural plant populations, which ultimately helps to maintain gender dimorphism (Delph and Wolf., 2005). According to reports, unisexual flowers in angiosperms have evolved from ancestral hermaphrodite flowers (Renner and Ricklefs., 1995, Mitchell and Diggle., 2005). This evolution may have occurred through two potential ways, either via monoecious or gynodioecious

plants or via reverse mutation of dioecious plants that regained male function after losing female function (Barret., 2002). Genetically dimorphic breeding systems such as gynodioecy (a population with females and hermaphrodites), androdioecy (a population with males and hermaphrodites), and dioecy (a population with males and females) exist in plants, with one genetic dimorph typically functioning more as a female while the other functions more as a male (Delph and Wolf., 2005). Studies on gender dimorphism have played a crucial role in understanding the evolutionary forces that influence genetic variation. Dioecy is relatively rare in the plant kingdom, with only 6% of plants being dioecious (Renner and Ricklefs., 1995). Dioecy is believed to have evolved from either monoecy or gynodioecy, while monoecy may have evolved from dioecy, as seen in the *Momordica* genus, where it has likely occurred seven times (Charlesworth and Charlesworth., 1978; Renner and Won., 2001; Barrett., 2002; Schaefer and Renner., 2010).

It has been reported that dioecy in gymnosperms has evolved from monoecy, with the Pinopsida group being a notable example where this has occurred 10–13 times (Leslie et.al., 2013). Despite monoecy being more common in angiosperms, dioecy is actually more dominant in gymnosperms (Charnov., 1982), with the majority of Cycadales, Ginkgoales, and Gnetales species being dioecious, while conifers are predominantly monoecious (Owens et. al., 1990). However, there is uncertainty in the behavior of some species and genera, and there are reports of plasticity in which species can change from monoecious to dioecious or vice versa (Vasek., 1966). Some species also switch between male and female phases from season to season. This phenomenon is also known as diphasy. Diphasic plants suppress one or the other sex in entire season probably by arresting male or female function in flower primordia. Several studies have explored the factors that influence sex expression in gymnosperms such as age, position of strobili on the plant or shoot, growth hormones, and environmental factors in *Ginkgo biloba*, *Ephedra* Sps, *Abies* Sps, and *Pinus* Sps (Lee., 1954; Newcomer., 1954; Mehra., 1950; Wheeler et. al., 1982). However, the relationship between sex expression and the physiology of gymnosperms is not well understood.

Conifers are most studied gymnosperms and their reproductive cycle is mostly dependent upon the environmental factors, age of the plant, temperature, weather, growth hormones, branching patterns, exposure to sunlight and nutrition. Conifers are among the oldest extant seed plant lineages and their reproductive biology hold clues about seed plant evolution. The earliest fossil records dates back conifers to the carboniferous period (300 million years ago), possibly arising from chordiates, which is a genus of seed bearing gondwanan plants with cone like fertile structures. Conifers were the most dominant land plants of Mesozoic era. The massive, catastrophic evolutionary events taking place at Palaeozoic era wiped out a large number of conifers of that time. Only a few species managed to adapt and survive till this date among which most of them are large, vascular, seed bearing land plants with cone like fertile structures belonging to the division Pinophyta. They have evolved and acquired some important features in order to survive extinction like, less dependency on water, heterospory, winged pollens and others (Williams., 2009). One of the characteristic feature acquired by conifers is iteroparity i.e., recurrent production of seeds (Williams., 2009). *Cedrus deodara* is among the long lived conifers which are diplohaplontic, iteoparous, coniferous evergreen trees belonging to the family Pinnaceae. Commonly known as Himalayan cedar or deodar and native to western Himalayas in Eastern Afghanistan, Northern Pakistan, South Western Tibet, Western Nepal and India (Jammu and Kashmir, Himachal Pradesh, Uttarakhand, Sikkim and Arunachal Pradesh). *Cedrus deodara* (Himalayan cedar) is one of the most important conifer, commonly known as deodar, is indigenous to India (Dallimore and Jackson., 1996) and occurs throughout the temperate regions of Western Himalayas predominantly between 1750m to 2500m, 15°W and 80°E and 30°-40°N Chaney., 1993: Demecti., 1986: Maheshwari and Biswas., 1970). Every year *Cedrus deodara* completes its reproductive cycle e(Farjon.,

1990, either by producing a new set of reproductive organs or they do not produce any reproductive organs at all. It tends to remain in their vegetative state only. Therefore they have a good seed year once in every three to four years. Such disparity in the reproductive development of conifers has never been understood clearly hence it provides a grey area for research and *Cedrus deodara* has been chosen as a potential tree to carry out research in this area.

2. Materials and Methodology

The deodar tree species is commonly found in temperate regions with severe winters and mild summers, specifically at elevations ranging from 1900 to 3000 meters above sea level. Pure stands of deodar are typically located at higher altitudes, where natural populations exist. In order to conduct a study, sites representing these pure stands (natural forests) of deodar were surveyed and selected from different altitudes, but located at distant locations from each other. The selected study sites included Cheog Forest in Theog Forest Division, Himalayan Forest Research Institute (HFRI), Panthaghati, Shimla campus forest in Himachal Pradesh, and Kanasar Forest, Chakrata in Uttarakhand (as shown in Table 1). A total of 900 trees were randomly selected based on the area of the population, age, and maturity of the trees. These trees were marked in 2013 according to the appearance of male or female cones on an individual tree and their reproductive behavior was recorded from 2014 to 2016.

Table 1
Details of location of sites

Site	Location	Altitude(m)	Latitude	Longitude
Populations in Himachal Pradesh				
1	HFRI Campus Forest, Panthaghati	1898	31°04'03.63"N	077°10'21.9"E
2	Cheog Forest, Cheog	2181	31°04'11.61"N	77°18'49.42"E
Population in Uttarakhand				
3	Kanasar Forest, Chakarata	2300	30°56'33.53"N	77°50'05.46"E

Random selection was done for mature trees that were capable of producing cones, with a height of over 19ft and a diameter of 20–30 cm or more. Each site had 300 trees marked, with male cone-bearing trees identified and recorded as male trees, and assigned a code as M. Female cone-bearing trees were marked and recorded as female trees and assigned a code as F. Monoecious trees with both male and female cones were marked and recorded, and assigned a code as M\F. Trees without any reproductive organs were marked and recorded as neutral trees and assigned a code as N (as shown in Fig. 1). The production of male and female strobili within the tree crowns was manually examined through careful observations aided by binoculars.

3. Results and discussion

Observations of the reproductive strobilus of *Cedrus deodara* began in 2013, between mid-June and early July. Male cones started appearing in June and matured by August. Initially, they appeared small, measuring 2.5cm-4.6cm in length and light green in color (Fig. 1 (h), (i)). Upon maturation and during pollination, they grew larger in size and became pale yellow in color due to the presence of pollen grains (Fig. 1 (i)). Female cones started appearing at the tip of the dwarf shoots (Fig. 1 (d)) towards the end of August or early September. Initially, they were light green in color (Fig. 1 (e)), but upon maturity, they became oblong and measured 0.63cm in diameter

(Fig. 1 (f)). After ripening, the scales of the female cones opened for pollination, which occurred between mid-October and mid-November. After fertilization, the cones turned dark brown and shed their scales (Fig. 1 (g)). Table 2 provides data on the number of dioecious and monoecious trees recorded during the observation period at all three sites.

Table 2
-Number of male, female, monoecious and vegetative trees at different sites during the observation period.

	HFRI Shimla			Kanasar Forest			Cheog Forest		
	2014	2015	2016	2014	2015	2016	2014	2015	2016
M	77	98	57	48	77	48	74	80	66
F	81	53	71	10	136	19	72	160	53
M/F	62	106	152	4	42	229	103	42	163
N	80	43	20	238	45	4	51	18	18
Total	300	300	300	300	300	300	300	300	300

Table 2 displays the changes in the numbers of monoecious, dioecious, and neutral trees between 2014 and 2016, reflecting the variation in the reproductive behaviour of *Cedrus deodara* over three years. The decrease in the number of neutral trees and the increase in the number of monoecious and dioecious trees from 2014 to 2016 indicating an increase in the reproductive activity of trees at all three sites, with trees shifting from a neutral state to a fertile one. Additionally, the number of female trees increased in 2015 and decreased gradually in 2016 at each site, while the number of monoecious trees increased drastically in 2016 compared to 2015. Both these observations suggest that predominantly female trees are transforming into monoecious trees as opposed to male trees. The decrease in the number of male trees in 2016 compared to 2015 also suggests the possibility of male trees transforming into monoecious trees. The study further observed individual tree transitions in the later stages.

The Table 3 is a representation of the fluctuations in the reproductive behavior of individual *Cedrus deodara* trees at HFRI campus forest, Cheog forest and Kanasar forest over a period of three years. The table indicates that there were variations in the representation of gender by individual trees at these study sites. The gender transitions observed were from female to female (F to F), from female to monoecious (F to M/F), from female to male (F to M), from female to neutral (F to N), from male to monoecious (M to M/F), From male to female (M to F), from male to male (M to M), from male to neutral (M to N), from monoecious to male(M/F to M), from monoecious to monoecious (M/F to M/F), from monoecious to neutral(M/F to N), from neutral to female (N to F), from neutral to male(N to M) and from neutral to monoecious (N to M/F). The highlighted numbers on the table is to indicate the increasing nuber of monoecious trees in the populations of deodar at all three sites. This suggests the preference of monoecious behaviour over dioecious behaviour.

Table 3

Variation in the gender expression of individual trees at HFRI campus forest, Cheog Forest and Kanasar forest.

S.no	Reproductive behaviour of individual trees at different sites	2014 at HFRI	2015 at HFRI	2016 at HFRI	2014 at Cheog	2015 at Cheog	2016 at Cheog	2014 at Kanasar Forest	2015 at kanasar forest	2016 at kanasar forest
1	(F to F)	24	27	37	24	27	37	8	6	10
2	(F to M)	19	4	10	6	10	30	1	2	21
3	(F To M/F)	31	20	33	14	28	82	1	2	105
4	(F To N)	7	2	1	7	6	13	0	0	0
5	(M To F)	7	15	11	36	32	23	21	1	6
6	(M To M)	36	36	23	30	5	1	9	20	12
7	(M To M/F)	27	44	42	6	42	45	15	26	58
8	(M to N)	7	3	1	1	3	2	3	1	1
9	(M/F to F)	12	18	15	55	11	13	1	0	3
10	(M/F to M)	25	12	19	32	23	2	1	1	11
11	(M/F to M/F)	23	75	26	10	63	27	2	3	28
12	(M/F to N)	2	1	2	3	2	0	0	0	0
13	(N to F)	10	11	8	25	7	4	105	12	0
14	(N to M)	18	5	5	7	7	2	66	25	4
15	(N to M/F)	25	13	51	12	30	9	22	198	38
16	(N to N)	27	14	16	7	7	3	43	3	3

3.1 Variation in the gender expression of individual trees at HFRI Campus forest.

The Fig. 2 depicts the change in the sexuality of the individual trees in the population since the beginning of our observations i.e from 2014 to 2016. The above data indicates that F To M/F (female to monoecious transitions) transitions show propensity over F to M and F to N transitions. In this population, expression of female gender is dominant over expression of maleness or male gender as number of female trees increased from 2014 to 2016 and the F to M transitions showed decreasing trend. Male trees are progressively transitioning into female trees and monoecious trees, indicating an increasing prevalence of femaleness within the population. This phenomenon suggests a dominance of female characteristics in the demographic composition. The number of trees displaying transition of monoecious trees (M/F) into Male, Female, monoecious and a very few monoecious trees left in the population those went in to vegetative phase (i.e. Neutral) indicates the tendency of dioecious trees to change into monoecious trees to avoid the energetic expenditures associated with the transition to female as compared to any other gender. The data reveals a declining trend in transitions from neutral trees to

dioecious trees, and an increasing trend in transitions from neutral trees to monoecious trees. This suggests a tendency for dioecious trees to favour monoecy over dioecy in subsequent reproductive cycles. Additionally, the observed decrease in the number of neutral trees over the research period indicates an overall increase in the reproductive activity within the population.

3.2 Variation in the gender expression of individual trees at Cheog forest.

Figure 3 shows the fluctuations in gender expression of individual trees of a natural population at Cheog Forest. The increasing number of female trees and the increasing number of Female to Monoecious (F to M/F) transition indicates the preference of monoecious behaviour over dioecious behaviour of the trees at Cheog forest. The female to male (F to M) transitions has been observed in increasing order from 2014 to 2016. On the other hand male to female (M to F) transitions are in decreasing order from 2014 to 2016. On the perusal of Table 2, it is observed that due to good seed year in 2014, the male sexual behaviour is preferred more as compared to female sexual behaviour by the trees because female function such as seed production is more energy-intensive. Decreasing order of Monoecious to Male (M/F to F) transition again points at preference of monoecious behaviour over dioecious behaviour by the trees to reduce energy consumption required by seed production in dioecious trees. Number of neutral trees is decreasing from 2014 to 2016 indicating good fertility of deodar trees at Cheog Forest.

3.3 Variation in the gender expression of individual trees at Kanasar forest.

Figure 4 shows the variation in the reproductive behavior of trees at Kanasar Forest from 2014 to 2016 in a chart form showing the comparison between the transitions of trees. The most common type of change observed is from female to monoecious (F to M/F), with a substantial increase in the number of trees transitioning into this form from 2014 to 2016. The second most common type of change is from male to monoecious (M to M/F) and the third most common type of change is from neutral to monoecious (N to M/F), with a significant increase in the number of trees transitioning into this form from 2014 to 2016. Male to monoecious (M to M/F) is also a relatively common change, with a noticeable increase in the number of trees transitioning into this form from 2014 to 2016. These transitions indicate the dominance of monoecious behaviour over dioecious. Other transitions like F to F, F to M, F to N, M to F, M to N, M\F to M, M\F to F, M\F to N seem to be showing minimum variations in their number during the period of observation. Decrease in the number of neutral trees from minimum 38 to zero proves the high fertility of individual trees at kanasar forest.

Conclusion

This study represents the first investigation into the unpredictable reproductive behavior of individual trees belonging to the *Cedrus deodara*. Previous reports have indicated that monoecy is a common occurrence in *Cedrus deodara*. However, our findings have revealed the presence of three distinct phenotypic genders across all populations studied at the three designated sites. Thus, gender expressions within these populations have given rise to male, female, and monoecious genders, ultimately producing sub-dioecious populations. Additionally, a third type of tree characterized as neutral or vegetative was observed, which did not produce any reproductive organs during the three-year study period. Population differences exhibited a negligible effect on gender expression, although variations were observed among genders across all populations. In sub-dioecious population, male, female, monoecious and vegetative trees co-exist in the same population. This condition is also

known as trioecy (Aryala, and Ming, 2013). This phenomenon of seed masting or irregular cone production in *Cedrus deodara* can be attributed to different factors one of which is allocation of resources to any reproductive activity (reproductive effort) which can alter the course of current life-history stage and the physiology of stages of life cycle in the future of a plant. Nutrient distribution may be patchy, leading to localized areas that preferentially support either male or female functions due to the differential energetic costs associated with each. Female functions, particularly seed production, are generally more energetically demanding. These unpredictable reproductive activities of an individual tree or the species in a population can also be affected by current environmental constraints (biotic as well as physical factors) that limit the availability of resources for survival (maintenance and repair), growth, and reproduction (Pianka., 1978).

Insightful observations made at HFRI campus forest, Cheog Forest and Kanasar Forest, for the reproductive behaviour of *Cedrus deodara*, and the data recorded for three years concluded that the year 2015 and 2016 were reproductively active years for the species therefore, they are considered as good seed year at all three sites. This proved that *Cedrus deodara* has good seed year once in every 2 to 3 years. The change in the number of trees indicates the change in the reproductive behaviour of *Cedrus deodara* in three years. It was also observed that the number of female trees increases in 2015 and gradually decreases in 2016 at each site. Also, the number of monoecious trees drastically increased in 2016 as compared to 2015. Both the phenomenon indicates that mostly female trees transform into monoecious trees as compared to male trees. This again points towards the aggregation of resources at the time of reproduction by female trees which help them to produce both male and female trees. Whereas less male trees seemed to be transforming into monoecious trees as the aggregation of resources in male trees is lesser than female trees. This is the same reason why monoecious trees seemed to be transitioning into male trees (Table 3) as compared to female trees, as female cone production requires more resources allocation hence physiological sex determination was favoured. The data suggests that the male trees has more tendency to change into monoecious than female trees. After a good seed year the trees are left with less availability of nutrients and energy hence production of male cones is more preferred over female cones by monoecious trees and they tend to transition into male tree. This makes it very difficult to predict the sex of the tree in the next fruiting season. These changes are not constant and do not appear every year.

The transitions of gender made by individual trees were very evident at all three sites. Perusal of Tables 2 & 3 shows that most of female trees have undergone transitions in their gender into monoecious trees producing both male and female cones. According to different workers, nutrient availability and ratio of growth hormones that is auxin and gibberellins, in plants greatly influences the pattern of reproductive and vegetative growth in conifers. (Irish and Nelson., 1989, Kumar and Jaiswal., 1984, Phular., 2020). Auxin is a limiting factor in cone production in long day plants (Schaffalitzky de Muckadell., 1959, Duff and Nolan., 1958 and Phular., 2020). Auxin and gibberellins ratio in plants greatly influences the pattern of reproduction, low concentration of auxins, along with high concentrations of gibberellic acid is responsible for inducing cone production in conifers (Pharis., 1980, Phular., 2020). Aggregation of resources and effect of hormone concentration coupled with affect of environmental factors by trees to produce female cones in 2014, affected the cone production in 2015 and 2016 and led the trees to produce male cones and become monoecious or become completely dioecious (Chailakhyan., 1979, Pharis., 1980 and Phular., 2020). Transition into monoecious trees is more economical for female trees and male trees as compared to transitioning into the opposite gender and become dioecious. Monoecious trees were found to be transitioning into female trees as compared to male trees. Auxin concentration was found to be low in highly reproductive branches of the trees (Phular., 2020). Hence effect of low concentration of auxin and high concentration of gibberellins and its effect on reproductive mechanism is the reason behind the unpredictable

expression of gender by individual trees (Phular., 2020). These Physiological and biochemical factors work together and influence the sexual representation of plants. However the exact reason behind this mechanism is yet to be understood. As monoecious behaviour of trees was found to be dominant in all the sample populations (Table 2), number of neutral trees growing into monoecious trees was the highest.

This study has given us an idea that the change in the reproductive behaviour of *Cedrus deodara* is an attribute adopted by conifers to survive the drastic changes occurring in the environment. It has kept a foundation for further research on the factors responsible for the change in the reproductive behaviour of deodar. Although the study has revealed that, the monoecious behaviour was more dominant than the dioecious behaviour, and the individual tree changes its sexual representation depending upon the rate of seed production the previous year. The wide variations observed in the gender expression by individual trees of all selected populations make *Cedrus deodara* a potential model plant to understand the evolutionary and genetic factors responsible in instability of sexual behaviour in conifers. Long term research on the factors responsible for reproductive behaviour of conifers such as physiological, biochemical and environmental factors is required to be done for understanding the mechanisms behind sex morphing in gymnosperms especially conifers.

Declarations

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Conflict of interest:-

There is no conflict of interest.

Declaration of Funding: - It is to inform you that this paper is based on my Ph.D thesis work. My research topic was "**Studies on the factors responsible for unpredictable reproductive behaviour of *Cedrus deodara* (Roxb.) G. Don.**" Hence my whole Ph.D work was self-financed and not funded by any agency. My institute does not provide any financial aid to its research scholars until they are recruited as project assistant under any project run by the institute itself. This paper is the representation of first objective of my Ph.D work.

Data availability statement:- Data used to generate the paper is part of my Ph.D thesis and already a lot of information is provided in the article itself. Hence I cannot make the data public or accessible to everyone.

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Figures

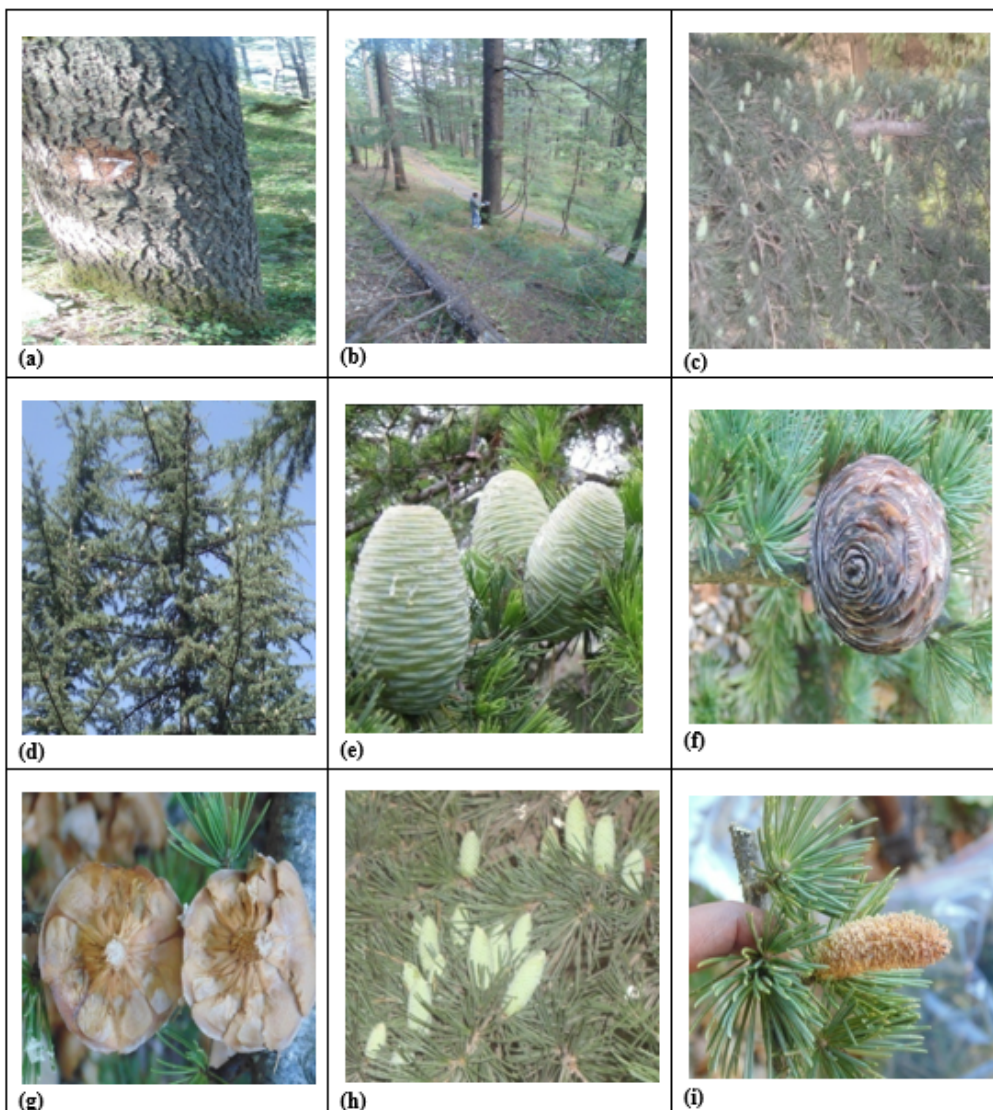


Figure 1

a) Marking of trees b) Pure stand of trees c) Male cones growing at lateral ends of the lower branches d) Female cones growing at lateral ends of upper branches e) Young female cones h) and f) Mature female cones g) Female cones after fertilization shed their scales. h) Young male cones. i) Mature male cones after pollination.

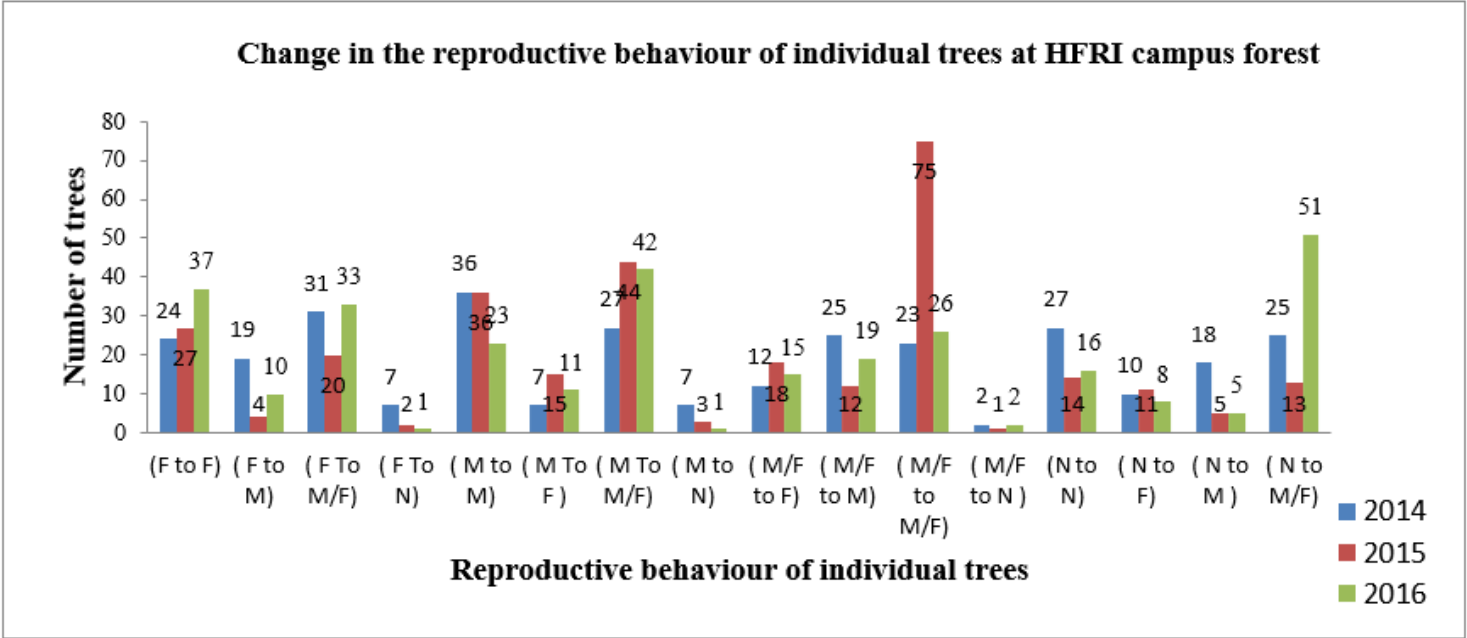


Figure 2

Change in the reproductive behaviour of individual trees at HFRI Campus Forest in 2014, 2015 and 2016.

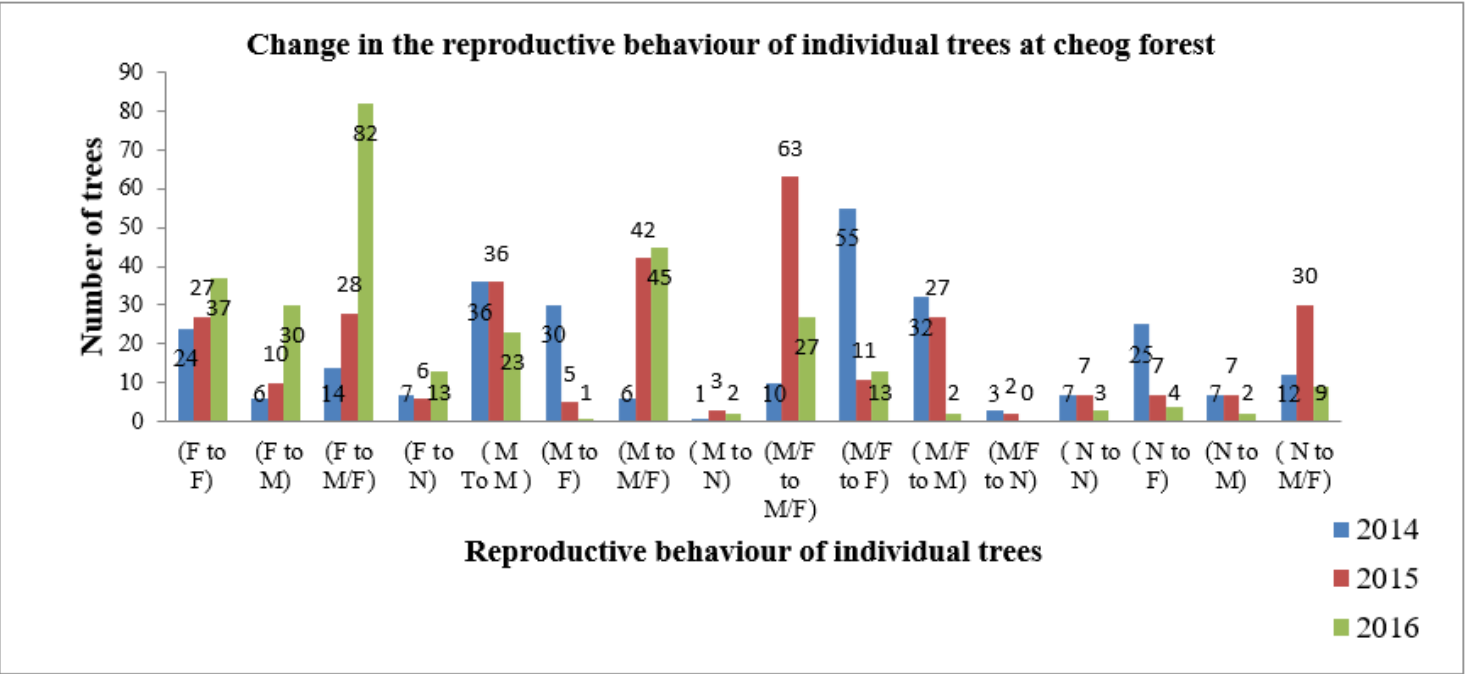


Figure 3

Change in the reproductive behaviour of individual trees at Cheog forest from 2014 to 2016

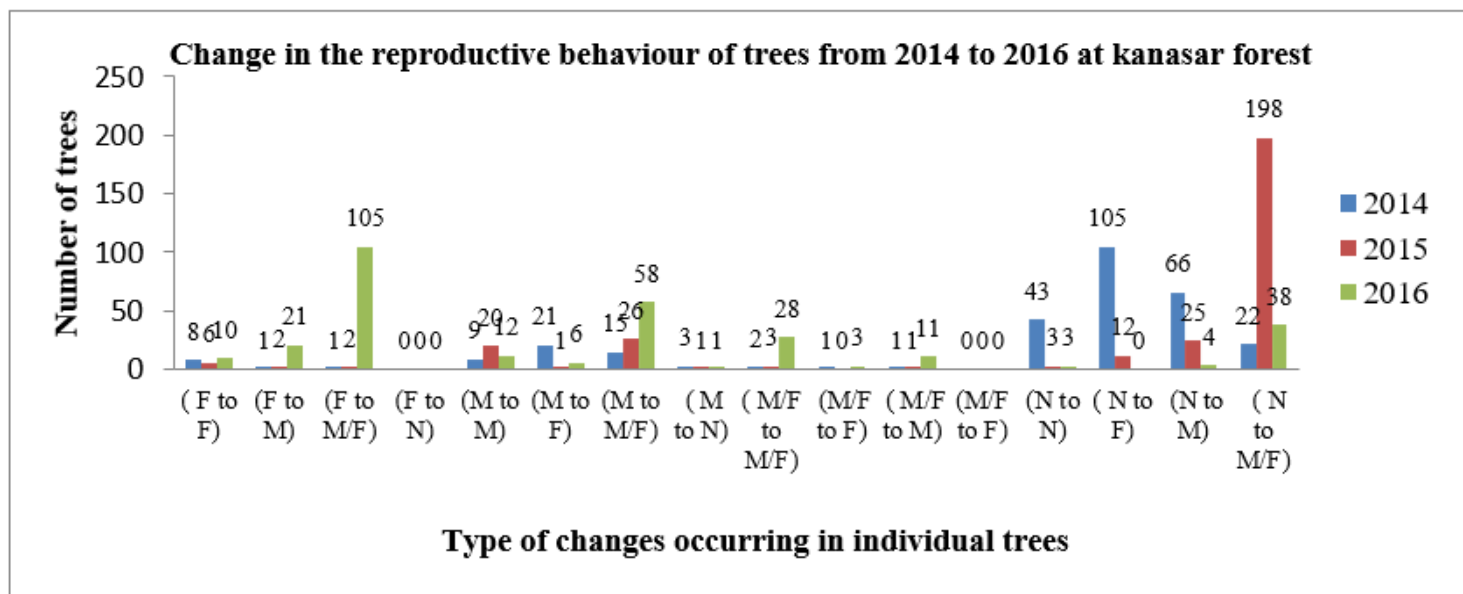


Figure 4

Change in the reproductive behaviour of individual trees of *Cedrus deodara* at Kansar forest.