Response of flowering and seed production of sandalwood \textit{(Santalum album} Linn., Santalaceae) to climate changes

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\textbf{Abstract}

Response of flowering and seed production to climatic changes was observed on sandalwood ex situ genetic conservation in Yogyakarta, Indonesia, in 2005 to 2010 flowering periods. To observe flowering phenology, each of 10 individual of 7 provenances were marked and the flowering phenology parameters were observed daily during the flowering period. To measure productivity parameters (Pollination Effectiveness, PE and Reproductive Success, RS), each of 10 individuals of 7 provenances were marked, and the flowers, fertilized flowers and mature seed were then counted. PE was measured by dividing Fertilized flower to Flower. RS was measured following the formula: RS = (Fruit/Flower) x (Seed/Ovule). Fluctuation on rainfall and temperature were observed during 2005 to 2010 flowering periods. The reduction on yearly rainfall was observed during 2006 to 2007. The elevated temperature increment until 31.06°C at the early of 2007 is the most extreme one. Prolonged rainy season recorded during 2008 to 2010 in which there were no dry month occurred even in summer. Each of provenances still kept its flowering behavior similar to those expressed in their origin. Provenances of the same origin with similar genotypes performed similar flowering characters. Flowering asynchrony and plasticity observed among provenances. The value of PE and RS observed to be provenances specific, as well as seed abortion that was occurred at various developmental phases. Both flowering and seed production were strongly controlled by both genetic and climatic factors. Provenances with similar genotypes performed similar response to alteration of rainfall and temperature due to climate changes. Extreme temperature increment at early of 2007 led to shorter flowering period, higher flowering frequency, decrement of flower and fruit abundance, and higher seed abortion. In contrary, prolonged rainfall in 2010 affected to longer flowering period, later floral initiation, shorter stigma receptivity and pollen longevity, bigger size of reproductive organs and paler color of perigonium. Constantly, dry season always results to the highest production of flowers, pollinated flowers and mature fruits compared to those of rainy season.

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1. Introduction

The effect of climate changes has only been well-studied on temperate and boreal ecosystems; but there were only few attention paid for tropical region\textsuperscript{5,6,8,10,19,29}. Significant efforts has been made in the last years to investigate the effects of climate changes in the Mediterranean\textsuperscript{6,8,15,20} and Scandinavian Europe\textsuperscript{7}, Alpine, Arctic, Sub-Antarctic\textsuperscript{2,21}, arid\textsuperscript{7,10,13,19} and terrestrial region\textsuperscript{29}; but similar work in the tropics is still very limited\textsuperscript{5,6,8,10,19,29}. Research in the tropics has been made in Central and East Asia with emphasize only on such agriculture crops i.e. wheat\textsuperscript{22,31} and fruits such as, chestnuts\textsuperscript{12}, apples, pears\textsuperscript{10} and cherries\textsuperscript{5}. Little is recognized on the impacts of climate change on forest trees, particularly tropical forests\textsuperscript{5,6,8,29}. For tropical forests itself, several works have only been made in Amazonia and central Africa; while the effects of climate change in Southeast Asia are still highly uncertain\textsuperscript{6,29}.

Plant sexual reproduction is strongly affected by environmental conditions and is thus seemed to be altered by climate change. Changes in phenology have long been regarded as sensitive indicators of climatic change\textsuperscript{5,28}. Phenology varies greatly over broad geographical gradients depends to climate zone and vegetation type. Furthermore, many processes, particularly those related to the cycling of carbon (productivity and growth), water (evapo-transpiration and runoff) and nutrients (decomposition and mineralization), are directly mediated by phenology, and the seasonality of these processes is phenological-dependent\textsuperscript{29}.

The effects of climate change on plant reproductive affects the sequence of different plant reproductive stages from flowering to seed production and viability\textsuperscript{1}. These effects are expected to respond to different components of climate change, such as temperature and rainfall\textsuperscript{6}. For this reason it is important to understand how climate and phenology are related under different climatic regimes. The recording of phenological observations has a long history. However, most researches on alteration in plant phenology have only been conducted on humid-temperate climates such as Western Europe and Eastern North America\textsuperscript{19}, but only very limited studies have documented climate responses of trees in East Asia\textsuperscript{12}. Several studies in the tropics indicated correlation between phenology and climatic factors, mainly rainfall and temperature\textsuperscript{1,6}. Analysis on key of weaknesses in the current researches emphasizes a need of a better understanding of the environmental role, particularly in the tropics. One of critical gaps that are in need of further research is the environmental drivers controlling phenology in tropical region. More work is needed to understand how tropical phenological events are being influenced by climate change\textsuperscript{29}.

Most of works bring to conclusion that climate change impacts will vary among tropical forest types, according to the degree to which the site water balance is influenced. Rising temperatures and reduced rainfall will extremely decline dry season water-limitation. Decreasing precipitation and increasing solar radiation in Amazonia may result in different phenological shifts than in central Africa where precipitation is projected to increase. Meanwhile, projections of future El Nino oscillations, which induce drought in Southeast Asia, are still highly uncertain\textsuperscript{6,29}.

Distributed naturally along China, India, Indonesia and The Philippines\textsuperscript{16,23}, an economic-important species Santalum album Linn (Santalaceae) – formerly called sandalwood – has been categorized as threatened species due to its significant degradation and/or habitat loss caused by demand on its wood and oil\textsuperscript{16}. Its heartwood, containing 1.5–5% of strong-specific fragrance of oil, is widely used for wood carving, religious and medicinal purposes. Its oil has been used as materials for cosmetics, prime sources of perfumes and aroma therapy, and was predicted to have anti-melanoma compounds\textsuperscript{25,33}. It brought sandalwood to be a most important-economic fancy wood with significantly increasing price of its heartwood to be USD 1.000–1.500 per kg\textsuperscript{25}. A ten times increasing price from 20.000 to 200.000 Rupee even observed in the last 10 years from 1997 to 2007\textsuperscript{31}. At present, this species found to be extinct in the wild in most of its native in Eastern parts of Indonesia\textsuperscript{2,28}. This research aims to determine the response of flowering and seed production to climatic changes, on sandalwood ex situ genetic conservation in Yogyakarta, Indonesia, in 2005 to 2010 flowering periods.

2. Study Site

Wanagama Forest Research Station – belongs to the Faculty of Forestry, Gadjah Mada University – is a 600 ha forest research station located in Gunungkidul, Yogyakarta (Figure 1). The soil is hard-sticky clay textured latosols with a very shallow column depth. A sediment carbonate rocks dominated by limestone and marl. It is classified into C and D of Schmidt and Fergusson climatic types characterized by 1900 mm yearly rainfall on 2 to 6 rainy months. The temperature is 27ºC in average with 80 to 90% relative humidity\textsuperscript{5}.

A sandalwood genetic trial – projected to be the ex situ genetic conservation – was established on Compartment
17 in 1993. This trial comprised 106 progenies which were selected from seven provenances and landraces representing different climatic zones in Indonesia. Buat and Netpala provenances which belong to Timor Tengah Selatan – Nusa Tenggara Timur, and Tilomar provenance that belong to Timor, represent a semi-arid to arid region. Bromo landraces that is collected from Lawu mountain, Central Java, represented a tropical highland region. While, Wanagama and Karangmojo landraces grown in Gunungkidul, Yogyakarta, and Imogiri landrace from Bantul, Yogyakarta; are several local landraces representing a tropical lowland region\textsuperscript{28} (Table 1).

![Fig 1. Study site, Wanagama ex-situ gene conservation belongs to Yogyakarta Province, Java Island, Indonesia, is indicated by ■ symbol. Origin of the provenances and landraces represents by ★ symbol.](image)

**Table 1. Origin of seven provenances/landraces**

<table>
<thead>
<tr>
<th>Provenances/landraces</th>
<th>Number of mother trees</th>
<th>Origin (District; Island)</th>
<th>Geographical range</th>
<th>Altitude (m a.s.l)</th>
<th>Climatic region (Schmidt &amp; Ferguson)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buat</td>
<td>52</td>
<td>East Nusa Tenggara; Timor</td>
<td>124°12’50” E; 9°10’ S</td>
<td>750-920</td>
<td>D &amp; E; semi arid to arid</td>
</tr>
<tr>
<td>Netpala</td>
<td>26</td>
<td>East Nusa Tenggara; Timor</td>
<td>124°55’ E; 9°10’ S</td>
<td>790-1090</td>
<td>D &amp; E; semi arid to arid</td>
</tr>
<tr>
<td>Tilomar</td>
<td>3</td>
<td>Kovalima; Timor</td>
<td>125°12’50” E; 8°9’ S</td>
<td>300-340</td>
<td>D &amp; E; semi arid to arid</td>
</tr>
<tr>
<td>Wanagama</td>
<td>4</td>
<td>Gunungkidul-Yogyakarta; Central Java</td>
<td>110°50’ E; 7°50’-8° S</td>
<td>150-160</td>
<td>C &amp; D; tropics to semi arid</td>
</tr>
<tr>
<td>Karangmojo</td>
<td>7</td>
<td>Gunungkidul-Yogyakarta; Central Java</td>
<td>110°50’ E; 7°50’-8° S</td>
<td>185-190</td>
<td>C &amp; D; tropics to semi arid</td>
</tr>
<tr>
<td>Imogiri</td>
<td>5</td>
<td>Bantul-Yogyakarta; Central Java</td>
<td>110°25’ E; 7°50’-8° S</td>
<td>40-55</td>
<td>C; tropical lowland region</td>
</tr>
<tr>
<td>Bromo</td>
<td>9</td>
<td>Karanganyar; Central Java</td>
<td>112°50’-113 E; 7°50’-8° S</td>
<td>1800</td>
<td>C; tropical highland region</td>
</tr>
</tbody>
</table>

Dendrogram based on Nei’s standard genetic distance\textsuperscript{24} (Figure 2) shows closest inheritance between Buat and Netpala provenance; both provenances belong to East Nusa Tenggara, Timor Island. Tilomar provenance which belongs to Kovalima District on the same island as the two previous provenances was not closely genetically related. It presumably due to natural barriers between Kovalima and East Nusa Tenggara that is separated more than 300 km apart, resulting to disjunct population that prohibit gene flows. Surprisingly, Tilomar provenance is closely related to Wanagama that is believed as the local landrace in Gunungkidul. Both provenance and landrace are sharing the same origin, as in the past, Wanagama population was established from the genetic materials that were collected from Timor Island. This might also be the reason for the fact that Wanagama and Karangmojo landraces – both are grown at the same site in Gunungkidul region – are not closely related in genetic distance\textsuperscript{28}.

![Fig 2. Dendrogram based on Nei’s standard genetic distance\textsuperscript{24} representing a genetic distance of seven provenances of sandalwood](image)

3. Materials and Methods

Observation on flowering and seed production was conducted during six years (from 2005 to 2010) flowering periods. To observe flowering phenology, each of 10 individuals of 7 provenances were marked and the flowering phenology parameters (floral initiation, flowering phases and flowering period) were then observed daily during the flowering period\textsuperscript{4,17,20}. To measure productivity parameters (Pollination Effectiveness, PE and Reproductive Success, RS), each of 10 individuals of 7 provenances were marked and the flowers, fertilized flowers and mature seed were then counted. Pollination Effectiveness (PE) – represents the ability of reproductive organs to pollinate,
fertilize and produce a young fruit – was measured by dividing Fertilized flower to Flower. Reproductive Success (RS) – correspond to the ability of reproductive organs to form mature seeds – was measured following the formula: RS = (Fruit/Flower) x (Seed/Ovule). The air temperature was also recorded in a weekly based observation \(^9\),\(^26\).

4. Results

4.1. Fluctuation on Climatic Conditions

Fluctuation on rainfall and temperature were observed during 2005 to 2010 flowering periods (Figure 3). Wanagama was semi arid region that was – previously during 1967 to 1988 – characterized by 1900 mm yearly rainfall on 2 to 6 rainy months, with 27\(^{\circ}\)C of temperature in average\(^3\). Usually, rainy season starts on October, while dry season starts on April. The reduction on yearly rainfall was observed during 2006 to 2007 period; with merely less than 300 mm rainfall in wet season, and completely dry in summer. The temperature increased by 27.9\(^{\circ}\)C in average, and the elevated increment until 31.06\(^{\circ}\)C at the early of 2007 was the most extreme one.

Change on the pattern of rainfall was observed during 2008 to 2010 period in which there were no dry month occured even in summer. During this period, the study site received rain every month through the years, ranged from 200 to more than 400 mm per month. The prolonged rainfall during this period represented a significant anomaly from its seasonal behavior, as it occurred during normal dry season.

![Fig 3. Fluctuation on rainfall and temperature observed in Wanagama ex situ genetic conservation from 2005 to 2011 flowering periods. The primary y ordinate indicates the monthly rainfall (mm) represented by black dashed line. The secondary y ordinate indicates the temperature (\(^{\circ}\)C) represented by red dashed line. The horizontal x line represents the flowering periods during 2005 to 2010. The data of monthly rainfall is obtained from the meteorogical station belongs to Local Govenrment of Gunungkidul District.](image)

4.2. Flowering Characters (Floral Structure and Phenology)

Even when concurrently planted under the same environmental condition, each of provenances and landraces still keep its flowering behavior similar to those expressed in their origin. Provenances having similar genotypes that belong to the same origin perform similar characters on flowering phenology (floral initiation, flowering period and flowering frequency) (Figure 4).

Provenances belong to eastern parts of Indonesia flowered earlier compared to those of Java, with the exception to Bromo that is the latest to flower. Each of provenances flowers twice a year with a various flowering period. The groups of eastern parts of Indonesia undergo a shorter flowering period compared to those of Java, with the exception to Bromo that performs the longest flowering period. The differences on flower initiation and flowering period among provenances result to the differences on peak flowering season that lead to flowering asynchrony.

Exception for flowering frequency was occured in 2007 to 2008 flowering period; when all of provenances switched its flowering frequency from twice to be three times a year, with a shorter period, due to an extreme temperature increment in the middle of rainy season in January 2007. Mass flowers abortion occurred right after the extreme temperature increment, resulting to the in-completed flowering period. However, new shoots and flower buds emerged soon after the flowers abortion, leading to the new flowering period. Flowering frequency plasticity observed as all of provenances turning back into its normal behavior, twice flowering a year, as the climate returned into a normal condition the years after. In contrary, a prolonged rainy season in 2009 to 2010 resulted to later floral initiation and longer flowering period.
4.3. Seed Production

Flowers, fruits and seeds production observed to be provenance specific (Figure 5). During 2005 to 2010 flowering periods, the highest value of PE found on Buat and Bromo, that were in contrary always performed the lowest RS at the end of flowering period. Both provenances continuously undergo highest seed abortion. Whilst, Karangmojo landrace always performed the highest flower number and seed set, and lowest abortion rate.

Extreme temperature increment at the early of 2007 was significantly reduced the number of flowers, pollinated flowers and mature fruits in all of provenances and landraces. The increase of rainfall in 2010 affected to the high production of flowers, but there were extreme reduction found on pollinated flowers and mature fruits. Constantly, dry season always results in the highest production of flowers, pollinated flowers and mature fruits compared to those of rainy season.

Seed abortion was observed to obtain specific provenances and to identify occurrence at a given developmental
phases for each provenance (Figure 6). Imogiri and Wanagama landrace undergo abortion at post-zygotic phase (after pollination and fertilization); resulting to the high rate of young fruit abortion represented by high value of PE. Abortion on Bromo landrace occurred at the last phase of fruit development, resulting to the high abortion of mature fruit that was represented by high value of RS. Karangmojo landrace always performed the lowest abortion rate.

Extreme temperature increment at the early of 2007 was significantly increased the young and mature fruit abortion, resulting to the highest value of PE and RS. The increase of rainfall in 2010 somehow resulted to similar disturbance, as there was high abortion occurred following the declining of PE and RS, presumably due to pollination and fertilization failure.

Fig 5. Number of emerged flowers (above), young fruits (middle) and seeds (below) on seven provenances and landraces of sandalwood in Wanagama ex situ genetic conservation from 2005 to 2011 flowering periods. The primary y ordinate indicates the number of emerged flowers (above), young fruits (middle) and seeds (below), represented by seven solid lines; and the monthly rainfall (mm), represented by black dashed line. The secondary y ordinate indicates the temperature (°C) represented by red dashed line. The horizontal x line represents the flowering periods during 2005 to 2010.

Figure 6. The value of PE (above), RS (middle) and seed abortion (below) estimated on seven provenances and landraces of sandalwood in Wanagama ex situ genetic conservation from 2005 to 2011 flowering periods. The primary y ordinate indicates the value of PE (above), RS (middle) and seed abortion (below), represented by seven solid lines; and the temperature (°C), represented by red dashed line. The secondary y ordinate indicates the monthly rainfall (mm), represented by black dashed line. The horizontal x line represents the flowering periods during 2005 to 2010.
5. Discussion

The observation on phenology during 2005 to 2010 flowering periods which undergo fluctuation on annual climatic conditions suggested that the flowering behavior may correspond to the alteration of temperature and rainfall. Similar findings also recorded for *Pinus nigra*¹, legumes¹⁵ and shrubs⁶ in Meditteranean Europe, as well as Oxalis groups⁷,¹³,¹⁴, grasses¹⁹, apples and pears¹⁰ in South Africa. Some researchers pointed out the importance of temperature¹,⁶,¹⁰,¹⁴,¹⁵, rainfall¹,¹³,¹⁶, soil water status¹³, photoperiod¹,⁵,²⁷ and genotype¹,¹⁴,²⁷ as the main factors affecting flowering phenology. Yet for the tropical regions, flowering depends mainly on rainfall affecting soil water status and relative humidity¹,¹³.

Flowering time plasticity, as observed in this research, has frequently been documented as a common adaptive feature of plants, particularly in arid and semi-arid environments¹⁹. Generally, plants turning back into its normal flowering behavior as the climate returned into a normal condition.

This section discussed the environmental and genetic aspects that might control such reproductive performances. The aspects of flowering and seed production of sandalwood that were affected by changes in environmental condition were also examined.

5.1. Environmental Factors (Temperature and Rainfall)

This research records fluctuation on rainfall and temperature during 2005 to 2010 flowering periods that was resulting to the alteration of the flowering behavior of sandalwood. The temperature has increased by 0.90°C over decades, and the elevated increment until 31.06°C at the early of 2007 was the most extreme one. The reduction on yearly rainfall was observed during 2006 to 2007 period; with only less than 300 mm rainfall in wet season, and completely dry in summer. In contrary, increment of rainfall was observed during 2008 to 2010 period in which there were no dry month occurred even in summer. During this period, the study site received rain every month through the years, ranged from 200 to more than 400 mm per month.

Global surface temperature has increased by an estimated 0.74°C over the past century, a change that is widely believed to result primarily from the effects of anthropogenic emissions of carbon dioxide and other greenhouse gases⁵. Increasing temperatures and changing patterns of precipitation have had considerable effects on the timing of plant phenology⁷,¹⁰,¹⁹. Other factors such as water and solar radiation may modify its effects. But in tropical region, flowering is more affected by rainfall through its role in controlling soil water status and relative humidity¹,¹³.

In the tropics, climate change may have a considerable impact on flowering and seed production, especially through the change of the amount and distribution of rainfall⁶,²². Tropical dry, wet and rain forests are differentiated by the amount and seasonal variability of temperature, precipitation and site water balance⁵,⁸,¹²,¹⁴,¹⁵,²⁰,²¹,²²,²⁹,³¹; thus variation in phenology tend to be driven by the duration of the dry season. However, solar radiation has also been recorded as a major cue for phenology, in both seasonal and a-seasonal tropical forests²⁹.

Soil moisture determines the flowering time and germination of plants¹,¹⁰,¹⁹. Given that soil moisture is mainly controlled by precipitation aspects, temporal patterns of flowering in the tropical, arid and semi-arid region are strongly determined by rainfall seasonality, and the flowering time of some indigenous species is influenced by both seasonal temperature and the onset of winter rains¹,¹⁰. As recorded in sandalwood in this research, the abundant flowering in Shorea was also correlated to the preceding dry period resulting to the fluctuation on temperature and precipitation rate⁴,¹¹.

Several Aspects of Flowering and Seed Production of Sandalwood that Were Affected by Climate Changes

Flowering Initiation, Flowering Period, Sexual Organs Maturity and Floral Colors

This research shows that each of provenances planted in genetic trial still kept its flowering behavior, similar to those expressed in their origin. Provenances belong to eastern parts of Indonesia flowered earlier compared to those in Java, with the exception to Bromo that was the latest to flower. The groups of eastern parts of Indonesia undergo a shorter flowering period compared to those in Java, with the exception to Bromo that was performing the longest flowering period. This phenomenon indicated strong influence of climatic factors in their origin. Buat, Netpala and Tilomar provenances belong to Timor island represented a semi-arid to arid region; a climatic condition that was similar to those experienced in Wanagama ex *situ* conservation. Bromo landrace that was collected from Lawu mountain - Central Java, a tropical highland region, may undergo tough environmental adaptation while replanted...
into semi arid condition. Wanagama, Karangmojo and Imogiri landraces were grown in tropical lowland region of Yogyakarta, Java island, that was almost similar to semi arid condition. Therefore, they did not have to experience such heavy adaptation process. According to history of establishment of Wanagama landrace, the seedlings were all collected from Timor island. This could be the explanation for the behavior similarity of Wanagama landrace and provenance which belong to Timor, Tilomar.

In 2007 to 2008 flowering period, all of provenances switched its flowering frequency from twice to three times a year, with a shorter period, due to an extreme temperature increment in the middle of rainy season in January 2007. Mass flowers abortion occurred right after the extreme temperature increment, resulting to the in-completed flowering period. However, new shoots and flower buds emerged soon after the flowers abortion, leading to the new flowering period. Flowering frequency plasticity observed as all of provenances turning back into its normal behavior, twice flowering a year, following the better environmental condition the years after.

In contrary, a prolonged rainy season in 2009 to 2010 resulted to later floral initiation and longer flowering period. The onset of flowering was one to two months delayed due to the increase of yearly rainfall. The extremely prolonged rainy season also resulted to the extended flowering period to be two to three months longer. Yearly observation recorded the consistent period of stigma receptivity: Tilomar and Imogiri were the shortest to maintain its stigma receptivity, while Wanagama was the longest one. The prolonged rainy season resulting to a shorter stigma receptivity period to be one day shorter. Many researches found that the extremely increment of rainfall might have consequential effects on the drop of temperature that was in turn resulting to the shorter stigma longevity. In this research, Tilomar and Imogiri with less than 5 days stigma receptivity performed the shortest period, while Wanagama with 8 days stigma receptivity was the longest.

Similar to those which happened in female reproductive organs, the male ones was also undergo one day shorter period of longevity due to the prolonged rainy season. This shortening period of pollen longevity was suggested to be the effects of rainfall and air humidity increment. Buat and Netpala provenance were observed to be the shortest with 2 days pollen longevity, while Karangmojo with 6 days pollen longevity was the lowest. The differences on flower initiation and flowering period among provenances was resulting to the differences on peak flowering period. The onset of flowering was one to two months delayed due to the increase of yearly rainfall. The extremely prolonged rainy season resulting to a shorten period, while Wanagama with 8 days stigma receptivity was the longest.

Similar to those which happened in female reproductive organs, the male ones was also undergo one day shorter period of longevity due to the prolonged rainy season. This shortening period of pollen longevity was suggested to be the effects of rainfall and air humidity increment. Buat and Netpala provenance were observed to be the shortest with 2 days pollen longevity, while Karangmojo with 6 days pollen longevity was the lowest. The differences on flower initiation and flowering period among provenances was resulting to the differences on peak flowering season, that was leading to the flowering asynchrony.

Previous study observed that changes in environmental condition was also affecting the size of reproductive organs. Landraces of Java island were having filament and stylus that was similar in length. In provenances belong to eastern Indonesia, filament were 1.5 times longer than stylus, resulting to a heteranthery structure. Prolonged rainfall resulting to the longer size of filament and stylus, that was assumed to be the effect of the increase of soil water status activating cell regeneration, expansion and elongation.

Previous study recorded that the increase in duration and amount of rainfall was also resulting to the paler color of perigonium for all of provenances and landraces, particularly at the fully and late anthesis. Its ranging from the palest color of Buat and Netpala provenances perigonium that turning into reddish white, peachy orange in Tilomar and Imogiri, pale maroon in Wanagama and Karangmojo, and yellowish brown in Bromo. The alteration in perigonium that was turning into paler color probably due to the increase of ambient water status resulting to the weak expression of pigment. A long history of researches have found the correlation between edaphic factors, such as nutrients and water status, with the changes of floral colors. Anemone coronaria, Eschscholzia californica, and Viola calminaria grown in cooler environment in California were performing paler flowers compared to those grown in warmer condition in Chile. Nutrients plays important role in pigments production, translocation and accumulation. Water status was affecting more to the regulation of the expression of color spectrum. A wide range distribution of Encelia farinosa from a high mountain in southern Sonora to the lowest valley in the northern parts, were affected more by rainfall and soil water status. The gradation of flowers color from bright yellow to brownish purple were documented along the elevational gradient. Other researches highlight phisical factors such as altitude, that consequentially lead to the differences on light intensity, shading and temperature, for the sense of floral color alteration.

**Seed Production**

This research records that extreme temperature increment at the early of 2007 was significantly reduced the fruit production in all of provenances and landraces due to the mass flowers and fruits abortion. The increase and prolonged of rainfall in 2010 affected to the high production of flowers, but there was extreme reduction found on seed production, presumably due to the pollination and fertilization failure. In constantly, dry season always resulting to the highest production of mature seeds compared to those of rainy season.
Flowering is considered as the critical stage, because environmental controls during the reproductive phase have a major impact on final yield. Reproductive performance can be influenced by changing temperature and rainfall through direct effects on both plant phenology and reproductive structures production. Indirect effects include the disruption of plant-animal interactions and changes in the size of plants and populations. Alterations to the phenology of flowering and reproductive output associated with climate change seem to be mostly due to the strong influence of temperature and rainfall changes. Specifically, the numbers of flowers, fruits and seeds set, as well as seed viability, can be strongly correlated with water availability. This relationship between climate and reproductive performance is particularly relevant in semi-arid ecosystems, where water is already the most important factor limiting plant development.

However, reproductive performance of some arid and semi-arid species is affected more by drought and warming environmental condition due to climate change, emphasizing the importance of changes in both rainfall and temperature, and the sequential relationship between reproductive stages. Phenological patterns also contribute to species differential responses to climatic change, due to the relationship of these patterns with resource availability, environmental conditions and plant–pollinator interactions. The projected climate change for the arid and semi-arid region might prove disadvantageous for flowering and seed set of forest trees, brought the consequences on the quantity and genetic diversity of the seed production.

The sexual reproductive phase seems to be sensitive to temperature fluctuations in every practical stage depending on the intensity and extension of temperature stress and on genetic material under study. However, understanding on temperature stress physiology during reproductive process still incomplete and more research is needed. Researches on the effects of temperature stress during the flowering phase on seed set show that (i) both low and high temperature stresses during the flowering phase might be the reason for the failure of seed set; (ii) the reproductive organs are specially sensitive to temperature stress; and (iii) genetic variation that likely reflect adaptation to temperature stress does exist at both the inter-specific and intra-specific levels.

Sandalwood was pollinated by insects belong to hymenopterans, lepidopterans and dipterans. Changes in the timing of flowering or fruiting could result in failure to produce offspring or have them adequately dispersed. Similar cases were also observed in bee-pollinated spring wildflowers of deciduous forests set fewer seeds during warm springs as the activity of bees were declined. One of the effects of a warmer and drier climate may also be the lack of flowering synchronization, as pollen shedding might be finished before stigma reached receptivity resulting to the fertilization failure. Plants and animals in a given area have often responded at different rates to temperature change, which is likely to change patterns of interaction between plants and their pollinators.

5.2 Genetics

Flowering patterns occur as a result from the interactions between genetic and environmental factors. Time of flowering is mainly influenced by genotype, temperature and photoperiod. While the genetic basis for flowering variation in commercial plants is often well understood, merely limited studies have been conducted to investigate these patterns in endangered plants of sandalwood. Works on the genetics of this endangered sandalwood were resumed from Southern India, Western Australia, South Eastern parts of Indonesia and New Caledonia, resulting to similar findings of genetic depletion and concluding that habitat loss and degradation were the main factor causing the extinction of sandalwood all over the world.

This research notified genetic control on the sandalwood response to the alteration of rainfall and temperature due to climatic changes. Provenances having similar genotypes belong to the same origin, performed similar response to the alteration of rainfall and temperature. Provenances with same genotypes were observed to perform similar characters on floral structure, flowering ontogeny and sexual organs maturity as well as its flowering phenology. Genotypes control was also observed on sexual organs maturity and longevity as well as floral structures and arrangements, in which each provenance performed specific characters. However, all of provenances observed to be both protandrous-dichogamous in sexual systems and heterostyly in spatial structure.

Flowers, fruits and seeds production was also observed to obtain specific provenance. During 2005 to 2010 flowering periods, the highest value of PE always found on Buat and Bromo, that were in contrary always perform the lowest RS at the end of flowering period. Both provenances continuously undergo highest seed abortion. Whilst, Karangmojo landrace always performed the highest flower number and seed set, and lowest abortion rate. Seed abortion was observed to obtain specific provenance and identify occurrence at a given developmental phases for each provenance. Imogiri and Wanagama landraces undergo abortion at post-zygotic phase (after pollination and
fertilization); resulting to the high rate of young fruit abortion represented by high value of PE. Abortion on Bromo landrace occurred in the last phase of fruit development, resulting to high abortion of mature fruit that was represented by high value of RS. Karangmojo landrace always performed the lowest abortion rate.

Works comparing the flowering responses out of the different genotypes growing in the same environment have also been made on Ficus microcarpa, Kolkwitzia amabilis, Pinus nigra and various agricultural temperate crops. Results suggested similar findings to those have been done in sandalwood that the genotypes performed different flowering responses even under the same environment. In temperate crops, the effect of temperature stress is covered by the complex male–female interaction of the individual reproductive behavior of each sexual organ. Interestingly, results showed that genetic variation does exist in reproductive behavior under temperature fluctuations. In Kolkwitzia amabilis, the different wild genotype flowered earlier and was distinctly different from other accessions based on flowering and the clustering constructed from RAPD markers bands. Post-census genotyping at microsatellite loci distinguished 16 genetic groups of Ficus microcarpa that were presented higher variation on flowering and fruit production. Change in climatic conditions observed to be an emerging factor that was crucial regarding the timing of flowering and seed production in Pinus nigra. In silver birch, early flowering trees tended to have a higher variation in germination rate than later flowering trees. Inter-tree variations in fecundity were high, and seeds and pollen were mostly produced by only a few types of genotype.

6. Conclusions

Fluctuation on rainfall and temperature were observed during 2005 to 2010 flowering periods. The reduction on early rainfall was observed during 2006 to 2007 period; with only less than 300 mm rainfall in wet season, and completely dry in summer. The temperature has increased by 0.9°C, and the elevated increment until 31.06°C at the early of 2007 is the most extreme one. Prolonged rainy season recorded during 2008 to 2010 period in which there was no dry month occurred even in summer.

Each of provenances still kept its flowering behavior similar to those expressed in their origin. Provenances having similar genotypes that belong to the same origin performed similar flowering characters (floral display, sexual organs maturation and flowering phenology) as well. All of provenances was both protandrous-dichogamous in sexual systems and heterostyly in spatial structure. Flowering asynchrony observed among provenances. All of provenances switched its flowering frequency from twice to be three times a year, with a shorter period, following an extreme temperature increment in the middle of rainy season in January 2007. Mass flowers abortion occurred right after the extreme temperature increment, resulting to the in-completed flowering period. In contrary, a prolonged rainy season in 2009 to 2010 resulted to later floral initiation and longer flowering period. Flowering frequency plasticity observed at all of provenances following the environmental condition.

The value of Pollination Effectiveness and Reproductive Success observed to be provenances specific; as well as the seed abortion that was occurred at various developmental phases. Extreme temperature increment at the early of 2007 was significantly reduced the number of flowers, pollinated flowers and mature fruits, and increase seed abortion. The increase of rainfall in 2010 affected to the high production of flowers, however there were extreme reduction found on pollinated flowers and mature fruits. The increase of rainfall in 2010 was somehow resulting to the similar disturbance, as there was high abortion occurred following heavy flowering, presumably due to the pollination and fertilization failure. In constantly, dry season always results to the highest production of flowers, pollinated flowers and mature fruits compared to those of rainy season.

Both flowering and seed productions were strongly controlled by genetic and climatic factors. Provenances with same genotypes were observed to perform similar response to the alteration of rainfall and temperature due to the climate changes. Extreme temperature increment leads to shorter flowering period, higher flowering frequency and decrement of flower and fruit abundance. In contrary, prolonged rainfall affected to longer flowering period, later floral initiation, shorter stigma receptivity and pollen longevity, bigger size of reproductive organs, and paler color of perigonium.
References


