REGULATION OF FRUIT DEVELOPMENT BY POLLEN IN THE OMANI DATE PALM

by

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This study and Ph.D.-thesis

is dedicated to

His Majesty Sultan Qaboos bin Said Al Said,

Sultan of Oman,

and

the People of the Sultanate Oman.

Abstract

Effects of various pollen types on the fruit growth and development in two maternal cultivars of Omani Date Palm were studied in the Northern Batinah region of the Sultanate Oman. Discrete stages in the development were identified, quantified and examined with regard to important variables including fruit set, weight, size, maturity, chemical composition, appearance and yield. Procedures were developed to compare across the different maternal cultivars and temperature environments.

The pollen types were distinct in their effects, particularly as regards weight, time to maturity, ripening, sugar content, appearance and yield of certain consumable fruit stages. These effects were influenced by the female type and differential fruit set.

True metaxenic and xenic effects were evidenced by excluding influences of fruit set. These were on fruit fresh weight, size, maturity and ripening in cv Khasab in 1996 and 1995 and in cv Khalas in 1996. Differences in cv Khalas in 1995 were due to differences in fruit set. Pollen effects could be measured in cv Khalas throughout fruit development, while they appeared in cv Khasab only in the later stages.

Khori consistently induced the highest mature fruit fresh weight (14.8 g in cv Khalas, 13.0 g in cv Khasab) compared to Bahlani (12.6 g and 12.3 g, respectively and Al Arudsabba (12.2 g and 11.1 g, respectively). However, differences in fruit set between pollen blocks in cv Khalas in 1995 caused the largest ripe fruit fresh weight (16.1 g) in the Al Arudsabba block compared to Bahlani (14.1 g) and Khori (13.4 g). The effect of high fruit set (initial set was 49 % with Khori and 34 % with Al Arudsabba) in masking and modifying pollen effects was evident because Al Arudsabba induced about 40 % less fruit fresh weight than Khori in the initial stages of development.

The response to applications of plant growth regulators was specific to the pollen type used. GA increased, by about 100 %, fruit fresh weight in Al Arudsabba pollinated Khalas fruits but reduced it to about 50 % in Khori pollinated ones. NAA caused the abscission of all unfertilized ovaries in Khori pollinated Khalas but not in those pollinated with Al Arudsabba. In the absence of syngamy physiological rather than hereditary causes were implied.

Correlations between fruit set and fruit fresh weight did not exist in the early stages suggesting that the observed pollen effects were truly metaxenic or xenic. In the later stages clear and consistent negative correlations existed for the Al Arudsabba block. Probably in the other pollen blocks some mechanism compensated this control of one variable over the other. Late correlations for the Khori block in cv Khalas suggested that high fruit fresh weight induced fruit drop. The absence of pollen effects on late correlations in cv Khasab implied a genetic cause. The strong

influence of fruit set on ripening (% ripe fruits) in Khori pollinated bunches indicated a specifically strong influence exerted by fruit set over ripening.

Time to physiological maturity was affected by pollen type only in cv Khalas where Al Arudsabba and Bahlani induced earlier maturity (7 days) than Khori. Khori pollinated fruits appeared to mature later in both female cvs except cv Khalas in 1995. Bahlani induced earlier maturity in both female cvs. Regression analysis between thermal time and fruit fresh weight provided evidence for the effects specific to Khori. As Bahlani induced the same early maturity in both female cvs.

Ripening was most uniform in Bahlani pollinated bunches, but faster in Khori pollinated ones. Correlations of thermal time and ripeness indicated that the temperature regime has a strong influence ($r=0.99$) over ripening in Bahlani pollinated bunches

Early pollen effects were probably due to physiological mechanisms, probably hormonal activity, which could be attributed to pollen type and pollination. Late effects were under the influence of male x female interactions and were thought to be genetic. Bahlani consistently induced the highest fruit fresh weight and size in the early fruit stages, but Khori in the later stages. Only in cv Khasab was Bahlani in the later stages on par with Khori in this regard. The situation was similar for fruit and seed size.

Compositional differences between pollen types were not reflected in those between the ovaries one day after pollination with different male types. This largely precluded the possibility that the early growth response was directly due to the mere addition of substances contributed by the pollen grains.

Preliminary investigations indicated that pollen types were *a priori* distinct with regard to their biochemical composition and mineral content in that Al Arudsabba and Bahlani were similar and differed from Khori. Khori's pollen grains were largest (22 μm, less than 20 μm in other types)and its pollen tube growth the most uniform (CV 56% compared to 80-110% with other types), while Bahlani had the most vigorous pollen tube growth (tube length up to 220 μm/24h). Khori contained more growth promoters, possibly GA , than Al Arudsabba.

Khori brought about relatively stable bunch yields in cv Khalas (11 kg in 1996, 15 kg in 1995) and large (about 4 cm long), heavy and sweet fruits, but delayed maturity of the fruits (7days in cv Khalas). Al Arudsabba produced a slightly higher cumulative yield (28 kg) of similar yield stability, but produced fruits of poor quality in regard to fruit size (about 3.5 cm in cv Khalas), fresh weight and a low total sugar content (less than 40% in Khalas, less than 50 % in Khasab). Bahlani had clear advantages, in that it induced sweet fruits, but produced the least stable yields of

fruits (cv Khalas: 16 kg in 1996, 7 kg in 1995) with relatively low weight and small fruits.

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Abbreviations and symbols

%	percentage
*	significantly different at a 5% level of probability
**	significantly different at a 1% level of probability
***	significantly different at a 0.1% level of probability
@	at
<	less than
=	equal to
>	more than
°	degree
°Brix	degree brix or percentage total sugar content
°C	degree Centigrade
°Cd	degree days
°F	degree Fahrenheit
µm	micrometre
A	Al Arudsabba
A,B	statistical means for treatments A and B are on par
a.i.	active ingredient
AAS	atomic adsorption spectrometer
ABA	abscisic acid
Anon.	anonymous
ANOVA	analysis of variance
ave.	average
B	Bahlani
BA	benzyl amino purine
BC	years before Christ
Br	Bissr
cm	centimetre
CV	coefficient of variation
cv, cvs	cultivar, cultivars
df	degrees of freedom
DOP	day of pollination
DZ	daminozide

E-pan	evaporation pan
exp.	expected
FAO	Food and Agriculture Organization
fert.	fertilized
F	F-ratio
FW	fresh weight
g	gram
GA_3	gibberellic acid 3
GLM	general linear model
HFCA	hydroxy fluorene carboxylic acid
HPLC	High Performance Liquid Chromatograph
HR	half Rutab
IAA	indole acetic acid
IAN	indole acetonitrile
IBA	indole butyric acid
K	Khori
km	kilometre
l	litre
LSD	least significant difference
m	metre
max.	maximum
min.	minimum
ml	millilitre
mm	millimetre
MS	mean sum of squares
MT	metric tons
N, E, W, S	north, east, west, south
NAA	naphthalene acetic acid
nm	nano metre
no., nos.	number
ns	not significantly different at 5 % level of probability
obs.	observed
P	level of probability
parth.	parthenocarpic
PGR, PGRs	plant growth regulator(s)

poll.	pollinated
ppm	part per million
r	correlation coefficient
Rt	Rutab
R.H.	relative humidity
sign., sig.	Significance
SS	sum of squares
T, temp.	temperature
TIBA	tri-iodo benzoic acid
TSS	total soluble solids
unpoll.	unpollinated
USDA	United States Department of Agriculture
UV	ultra violet
wt., Wt.	weight
X100, X n	magnification 100 times, n- times

1. Introduction

The Date Palm (*Phoenix dactylifera L.*) is a traditional fruit crop in many regions of the northern Sultanate Oman. These different regions are highly variable with regard to the prevailing environmental conditions, particularly climatic, ranging from dry and hot in mountainous areas with oasis cultivation to the flat coastal plain of the Batinah region with its hot and humid summers. The particular area of this study is near the town of Sohar in the northern Batinah, where the Date Palm is the major fruit crop.

Dates in the Sultanate Oman are produced from about 250 different female varieties which may be pollinated by any of up to 150 different male varieties (Macki, 1992). The fruits are consumed in several stages after maturity, either fresh or dried to various degrees. Several processed products are obtained from the fruits. Some of the best fruits are exported and fruits of some varieties are used to provide animal feed. The yield and quality of Dates produced in the study region are variable due to different female varieties cultivated and the use of various cultural methods including pollination by pollen of often unknown source and variety.

There is a need to work towards a standard for Date fruits and to exert control over their growth rate, their quality and period of availability. Various ways to regulate fruit growth and development include cultural methods such as thinning of fruits or bunches of fruits and by selection of suitable female and male pollen varieties. It has been claimed in publications from several date growing areas in the world (Denney, 1992; Vagvolgyi, 1987; Crane, 1980; Othman, 1974; Tydeman, 1937, Bowman, 1937; Nixon, 1928a, 1928b; Swingle, 1928) that pollen type can be used to regulate fruit set, fruit size, seed size, time to ripening as well as the quality and appearance of fruits. Local farmers in the interior regions of the Sultanate Oman have reported similar effects. Interestingly, one of the first scientific report about pollen effects in date palm in California was made by Swingle in 1928, who observed effects from the pollen of a male plant, which had grown from a seed from a palm of the female cv Fardh. The Fardh palm tree in California had originated in the Semail valley of South-eastern Arabia. Semail is in the Sultanate Oman and known for its Fardh dates.

This study aims to detect and to analyse the regulatory effect of different pollen types on fruit growth and development in important female cultivars growing under the conditions characteristic for this particular location. The study was carried out over two years and analysed the biological, physical and chemical characteristics of the fruits during their different stages of growth and development.

At present, there is no clear understanding of the pollen effect mechanisms although several modes of action have been suggested. These include the regulation of fruit growth processes through hormones contributed by, or induced by the pollen, through genetic interactions, paternal imprinting, paramutation and transposons or "jumping genes" (Denney, 1992). The hypothesis put forward for the present study is that the nature of the pollen used in the Sultanate Oman to fertilize date palm flowers will affect the processes of fruit growth and development. Early effects will depend on events occurring during pollination and substances contributed to the ovule prior to, and during fertilization, whilst later effects will be the consequence of the genetic contribution by the pollen. Interactions with maternal type are expected. The study will test this hypothesis by examining various characteristics of the pollen itself, the events of pollination, fertilization and fruit growth and their timings. It is hoped that an understanding of pollen effects will be gained that will provide criteria for reliable assessment of suitable pollen types for commercial application, thereby contributing towards the improvement of date production. Important economic criteria are reliability of pollen effects, yield and quality of fruits.

To summarize, this study aims

- to test claims of pollen effects on fruit development,
- to quantify the effects,
- to suggest mechanisms,
- to assess the commercial applicability.

2. Review of literature

The purpose of this review of the literature is to provide a summary of related work carried out by other scientists on date palms, pollen, pollination and pollen effects, fruit growth and development and other associated topics. From this will emerge development of the basic hypothesis stated above, suggestions for experimental testing of that hypothesis and indications of how limited such experiments might be. Gaps in our present knowledge will be identified and assessment made of the need to fill them. It also aims to provide a general understanding of the date palm, its commercial production and some detail on the physiology of fruit growth and development. Particular attention is given to the effects of pollen and pollination on these processes in the date palm and other species.

2.1 Botany

The date palm (*Phoenix dactylifera*) is a monocotyledonous perennial plant belonging to the family Arecaceae (Nixon,1966; Moore,1973). This family consists of 200 genera and about 2600 species. Other common, cultivated genera are the Coconut (Cocos nucifera) and the Oil palm (*Elaeis guineensis*), (Al-Saad, 1994). Although Wrigley (1995) distinguishes ten or twelve species of Phoenix, every Phoenix palm cannot be ascribed clearly to any one of them. Interspecific hybrids are numerous and fertile. Where the species meet in nature, they interbreed. All species that he examined were diploid, 2n=2x=36 and the chromosomes of the different species are remarkably similar in size and shape (Wrigley, 1995). Studies on meiosis carried out by Al-Mayah (1986) also suggested that the date palm is a diploid species.

Phoenix is distinguished from other palms by its induplicately pinnate leaves with parallel veins and the lower pinnae modified into stout spines (Moore,1973; Nixon,1966). The date palm belongs with regard to photosynthesis to the C4-plants (Franke, 1992). The number of leaves varies from 30 to 140. A frond of a vigorous variety can attain a maximum length of about six meter while most fronds are four meter long. The number of leaflets per frond varies from 120 to 240 (Dowson, 1982). Usually, the trunk has only a single growing point (Nixon ,1966). Except for brief intervals under exceptional

conditions, growth is continuous throughout the year. Palms can attain an age of more than 100 years and a height of 20-30 m (Mason, 1925).

The date palm is dioecious with flowers produced in the axils of leaves of the previous year's growth. The inflorescence is a compound spike and is enclosed before maturity in a protecting spathe (Long, 1943 and Moore, 1973). The number of buds which differentiate into inflorescences is influenced by the previous season's carbohydrate accumulation. The female flowers have three sepals, three petals, six staminodes, and three free carpels with erect ovules and sessile, hooked stigmata, which is typical for Phoenicoid palms (Plate 2-1). In pollinated flowers usually two carpels abort and only one ripens (Dowson, 1982).

Plate 2-1 *Flowers of Phoenicoid palms*

8. Phoenicoid palms. Details of *Phoenix Roebelenii* (a–t) and *P. canariensis* (u–y): **a**, portion of rachilla with staminate flowers × 2; **b**, staminate flower × 4; **c**, staminate flower in vertical section × 4; **d**, staminate calyx × 4; **e**, staminate petal, interior view with adnate stamen × 4; **f**, stamen × 4; **g**, portion of rachilla with pistillate flowers × 2; **h**, bract and scar of pistillate flower × 4; **i**, pistillate flower × 4; **j**, pistillate flower in vertical section × 4; **k**, pistillate calyx × 4; **l**, pistillate flower, calyx removed × 4; **m**, pistillate petal, interior view × 4; **n**, gynoecium entire (left) and in vertical section (right) × 4; **o**, carpels in cross-section × 4; **p**, fruit × 2; **q**, **r**, seed in two views × 2; **s**, seed in vertical section × 2; **t**, seed in cross-section × 2; **u**, staminate flower × 4; **v**, staminate flower in vertical section × 4; **w**, staminate calyx × 4; **x**, staminate petal, interior view with adnate stamen × 4; **y**, stamens in two views × 4. a–t from *Read 748, 749*, u–y from *Read 777*, all preserved in liquid.

The fruit is a single berry containing a hard stone with a distinctive furrow on one side. This furrow remains as a depression on the seed where the ovary and adjacent tissues of the seed enfolded the dorsal vascular bundles of the pericarp, and a micropyle in the other side (Reuveni, 1986). The fruit has a terminal stigma, a fleshy

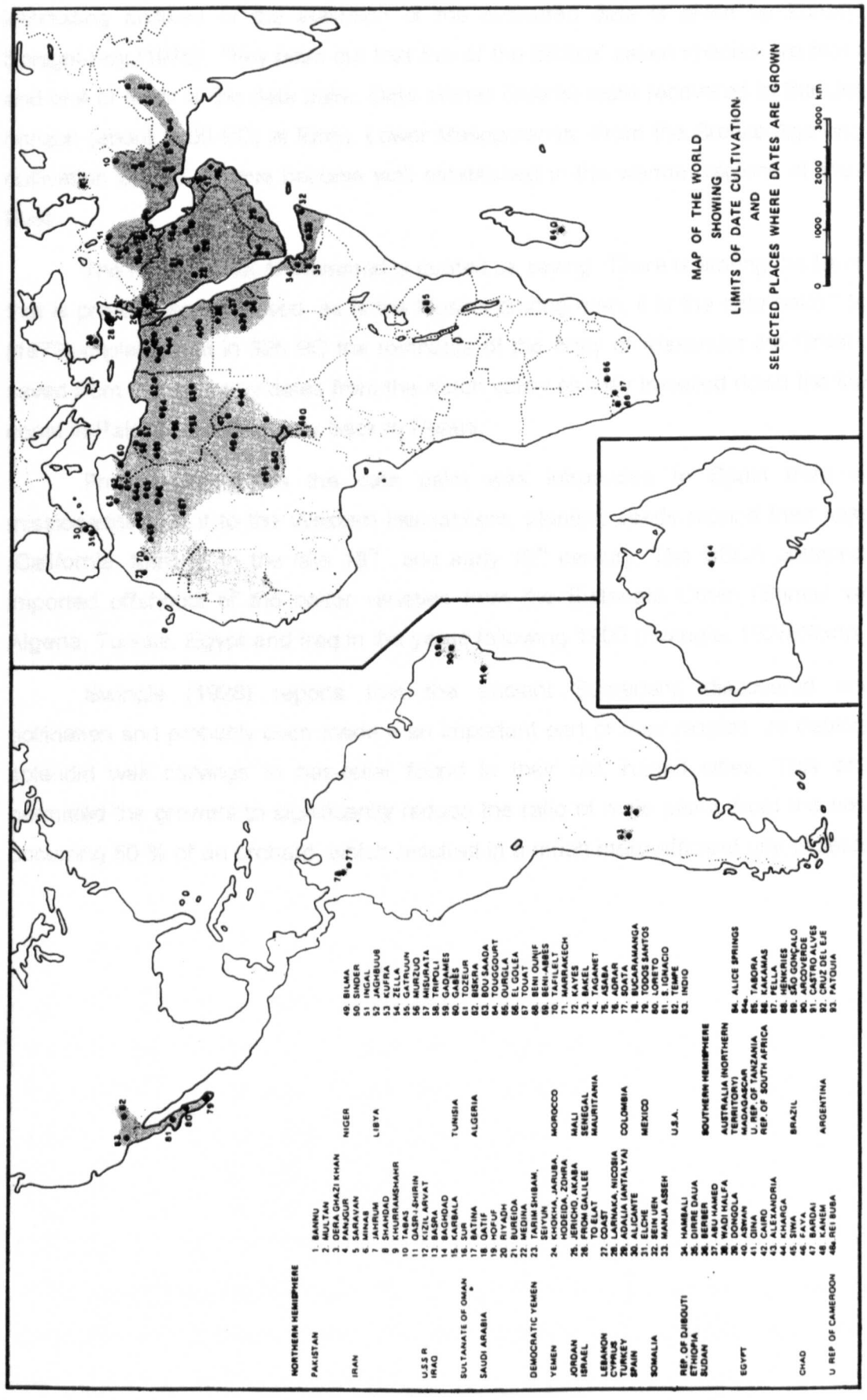
pericarp and a membranous endocarp. The seed contains a small embryo with a hard, non-starchy endosperm with cellulose deposits on the insides of its cells (Dowson ,1982). Endosperm development is first nuclear and later cellular (Reuveni, 1986). During germination the seed shows a feature unique to this family, namely that the distal portion of the single cotyledon remains inside the seed, expands tremendously in size and functions as a haustorium which absorbs and replaces the endosperm (DeMason, 1989).

2.2 Origin and History

Out of a total of 17 species of Phoenicoid palms, five are found in the Africa-Arabia-Europe region, one in the Indian Ocean islands and 12 in the Eastern tropics. The date palm is native to tropical and subtropical Asia and Africa (Moore, 1973) and probably originates from the areas surrounding the Arabian Gulf, from where it spread along the steppe belt from Northern India to Persia and across to Morocco (Franke, 1992). The limits of today's date cultivation are shown. (Plate 2-2).

The wild stock from which cultivated dates may have derived is recognized at least in general terms. The cultivated date is closely related to and compatible with a variable cluster of feral dates growing in the southern parts of the Near East. Botanists place these non-cultivated dates, with characteristic small fruits, within Phoenix dactylifera. Several other wild Phoenix species show close genetic affinities with the cultivated dates, which are distributed over North Africa, Arabia, and southern Asia. Wild forms of Phoenix border the Near East in the warm south, they are cross-pollinated, manifest a high level of variation and maintain a high level of heterozygosity. Because all wild forms reproduce from seed, repeated gene "injection" from wild to cultivated forms probably enabled horticultural varieties to become established over most of the geographic range of the wild forms in a matter of only a few millennia. Sexual reproduction when coupled with a relatively long life span favours few restrictions on recombination and considerable heterozygosity. Consequently, under domestication, the maintenance of desired genotypes became practical only by vegetative propagation, which in date is done by transplanting offshoots (Zohary and Spiegel-Roy, 1975).

Plate 2-2 *World distribution of date palms*



The date palm is one of the oldest cultivated tree crops and its fruits have long been a staple food for the people of Persia, Arabia and North Africa (Nixon, 1966). An interesting account of the evolution of the cultivated date is given by Zohary and Spiegel-Roy (1975). They point out that five of the Biblical seven species are fruit trees and one of them is the date palm. Date stones (seeds) were recovered in the Ubaidan horizon (about 4000 BC) at Eridu, Lower Mesopotamia. From the Bronze Age on, date cultivation seems to have become well established in the warmer regions of the Near East.

The holy Prophet Mohammed is quoted as saying "There is among the trees one that is pre-eminently blessed, as is the Muslim among men; it is the date palm." Moore (1973) explains that in 326 BC the remnants of the army of Alexander the Great were saved from starvation by dates from the Ketch valley as they travelled down the Makran coast in Pakistan on their way back to Persia.

From North Africa the date palm was introduced to Spain from where missionaries took it to the Western Hemisphere, planting seeds around their missions (California, Mexico) in the late 18th and early 19th century. The USDA obtained and imported offshoots of the better varieties from the Sultanate Oman (Semail valley), Algeria, Tunisia, Egypt and Iraq in the years following 1900 (Swingle, 1928;Nixon,1966).

Swingle (1928) reports that the ancient Sumerians discovered artificial pollination and probably even made it an important part of their religion, as depicted by splendid wall carvings in bas-relief found in their old, ruined cities. This practice permitted the growers to significantly reduce the ratio of male palms from the naturally occurring 50 % of an orchard, which resulted in a much more efficient use of resources.

2.3 Distribution and economic importance

2.3.1 World

Commercial culture of the date palm in the northern hemisphere extends southward to about 15 ° latitude, but ceases where the region of tropical rains begins (Mason,1925). In west Africa date production is confined to the south side of the Atlas range, although specimens of non-productive trees were found in 1925 in Algiers and other Mediterranean cities. A small but very significant commercial culture of the date palm is maintained at Elche, in south-eastern Spain, just above 38 ° latitude, the most northerly point of commercial date culture in the world. Non-fruiting trees can be seen at most points along the northern Mediterranean coast, even extending to Venice at 45 ° on the Adriatic, but fruit production reaches only a latitude of 35 ° in Mesopotamia, 34 ° in Persia and about 30 to 33 ° in Punjab. In the United States, fruit has been successfully matured only as far north as 38 ° in interior valleys.

According to Al-Mayah (1986) in 1986 there were about 90 million date palms world wide, of which about 22 million occurred in Iraq, comprising 455 cultivars. According to statistics (FAO, 1993) the World production of dates was 3,735,000 metric tons (MT) in 1992 up from 2,128,000 MT in 1971 (Table 2-1).

Table 2-1 ANNUAL PRODUCTION (METRIC TONS) OF DATES

Country	*1969-71*	*1982*	*1992*	*Rank in 1971*	*Rank in 1992*
World	2,128,000	2,630,000	3,735,000	-	-
Iran	293,000	301,000	635,000	3	1
Egypt	360,000	393,000	610,000	2	2
Iraq	410,000	400,000	580,000	1	3
Saudi Arabia	237,000	400,000	545,000	4	4
Pakistan	161,000	205,000	310,000	5	5
Algeria	145,000	207,000	210,000	6	6
Sudan	91,000	115,000	142,000	8	7
Sultanate Oman	44,000	72,000	130,000	11	8

Source: FAO,1993

World production of dates was about 1.5 million tons in 1961 and increased by about 70% to 2.5 million tons in 1977 and the same in 1986 (Kishimoto, 1990). The

percentage of dates exported world-wide decreased from around 20 % to nearly 7 % at the end of this period of time. The fruit of the date palm is grouped into soft, semidry or dry dates, the latter characterized by low water content and a high sugar content (Franke, 1992). Semidry dates are the most suitable for main export (Rehm, 1984).

2.3.2 Sultanate Oman

The date palm flourishes in all parts of the Sultanate Oman and to a lesser degree in the Salalah plain in the southern province of Dhofar. The plantations in the area of the present study , the Batinah, were at times 11 km deep along the coast and in the interior Wadi Semail the number of palms was estimated as 600,000 at the turn of the century. About 8 million date palms are growing today in the Sultanate Oman in several climatically distinct regions. They cover 35,000 ha of the total 62,000 ha of Omani land under cultivation and about 35 % of the cultivated area in the northern Batinah region (Oman Observer 1996; MOAF, Sultanate Oman, 1993). Most production is consumed in Oman, but export of dried dates touched RO 1.5 million (about 3.9 million US $) in 1994 (Oman Observer, 1996). Most palms (3.5 million) are found in the coastal Batinah region, where they are planted in roughly 1 to 2 km wide strip which runs almost 300 km parallel to the cost. In particular, the northern Batinah is a major agricultural production centre for many crops and products followed by the Dakhliyah and the Sharqiyah regions. In the latter the climate is characterized by cool winters and very hot dry summers (max. temperatures above 45 °C. at relative humidity below 40 %). According to Nixon (1966) and personal observations during my travels in the Sultanate Oman, these appear to be ideal climatic conditions for date palm cultivation.

The Sultanate Oman aspires to produce dates of improved quality and attempts are made to extend date cultivation even to areas such as the subtropical Salalah plain which experiences a summer monsoon. Apart from improved cultural methods, this requires the selection of not only suitable female varieties but also male varieties. The males should produce pollen that can advance the time of fruit availability as well as

improve fruit quantity and quality through reducing premature fruit drop and variability, whilst ensuring adequate fruit set for stability of production.

a. Uses

This thesis is concerned with pollen effects on fruit growth and development until the stage of consumption. This stage varies depending on cultivar and consumer's choice as shown in Table 2-2:

Table 2-2 STAGES OF CONSUMPTION OF DATE FRUITS

Stage	*Name*	*Taste*	*Texture*	*Remarks*
late maturity	Bissr or last Khalal	juicy, sweet, not or little bitter	turning soft	difficult to handle and transport for long
semi ripe	Half Rutab	sweet	apical half is soft and pliable	difficult to handle and transport, ferments easily
ripe	Full Rutab	sweet	entirely soft and pliable	very difficult to handle and transport, ferments very easily
overripe	Tamr	sweet	dry like raisins	easy to handle and transport, does not ferment

Sources: Nixon, 1966; Reuveni, 1986

Besides being pleasant to eat fresh and in the Tamr stage, easily packed and transported , dates have long been also a basis for the preparation of beer, wine and Arak (Wrigley, 1995). The very best varieties yield Tamr dates which can be stored and transported to export markets. Fruits of other varieties are also used as animal feed either as entire fruits or by feeding by-products of processing such as seed or extracted pulp (Bukhaev, 1985). date palm seeds have been crushed or milled and included as an ingredient in bread making (Almana, 1994) and in food for carp (Al-Asgah, 1987). Bukhaev (1987) reports that fruits of the commercial cultivar "Zahdi" can be used for industrial purposes such as for the production of syrups, industrial spirit and vinegar. Bagged fruits are also stacked and pressed by heavy weights to express a thick syrup called 'Dibbis'.

b. *Opportunities for crop improvement*

i. Unknown sources of pollen

Different pollens can cause variations in the growth and development of fruits. From personal observations and communications with local date growers in the Sultanate Oman, it is clear that many do not own sufficient male palms to meet their requirement for pollen and so buy male spathes from the local markets. The result is that source and variety of the male palm are frequently unknown. This situation is typical for the densely farmed and populated Batinah coast, while the Dakhliyah region is different. Here, the farmer or the contracted pollinator often knows the origin of the pollen. It is necessary to plant selected male palms near to the coastal palm gardens so that pollen supply can meet demand. It is important that suitable varieties are selected and that their effects are clearly understood and used to their optimum.

ii. Non-availability of early pollen

Very early varieties like Sallani, Qash Manumah (Damoos) and Naghal produce in the Batinah region many female inflorescences as early as the end of January. At that time the local male varieties ("Fahal") have not yet produced spathes ready for pollen release. Many of the supposedly best, pollen types are very early available in the interior areas of the Sultanate, but their application to and effect on the common date palm cultivars growing in the northern Batinah has not been systematically studied to date.

iii. Consumption stages and time of ripening

Because of perishability, each one of the first three consumption stages is only available for a few weeks. During this time fruits pass from one stage to the next and

production is afflicted by pre-harvest fruit drop. Date production in the Salalah plain is limited to very early varieties which produce Bissr and Rutab-stage fruits ahead of the summer monsoon whose high humidity adversely affects fruit quality. One of the objectives of this study is to identify pollen types which can be commercially used to regulate ripening and the period of availability.

iv. Low yield and variable fruit quality

Yield is affected by fruit weight and fruit number, whereas fruit quality is determined additionally by many other criteria such as fruit colour, perishability, tannin content, sugar content, size, taste and flavour as well as appearance, which are under the influence of factors like female and male types involved, nutritional status, climatic conditions and biotic conditions. All the quality criteria include uniformity for any given fruit harvest. Pollen effects may influence the above criteria and most reports indicate effects on fruit and seed size (Swingle, 1928), on developmental timing, on ripening and colour development.

The requirement for higher yields of excellent quality Omani Dates is highlighted by the policy of the Sultanate Oman to protect its local date production by not allowing date import or by imposing 20 % customs duty in times when demand exceeds local production. This is necessary as otherwise cheap, but good quality Saudi dates would flood the market, although connoisseurs prefer Omani Dates (Oman Observer, 1996).

2.4 Fruit growth and development

Effective management of fruit growth and development may be best achieved when based on a sound understanding of the physiology of the processes involved and the accompanying physical and chemical changes in the fruits.

2.4.1 Physical changes

Changes in the physical characteristics of fruits and seeds will occur from the day of pollination until harvesting. Part of the present study will identify and quantify these changes and attempt to determine the underlying mechanisms. An understanding of the embryogenetic, morphogenetic and physiological processes involved in fruit development is important for the interpretation of data on fruit growth.

a. Normal fruit development

The following describes the typical development of a fertilized ovary into a ripe fruit, which is termed as normal fruit development. Fertilization is preceded by the pollination of a flower having a receptive stigma and viable ovary. Double fertilization of the egg cell and the secondary nucleus results in the formation of a zygote and the endosperm, The division of the endosperm cells precedes that of the zygote. The two major parts of the developed date fruits are the seed and the pericarp. In some date cultivars flower viability decreases rapidly after spathe splitting, while in others it remains longer viable (Stoler, 1971).

Fertilization of the egg cell occurred in the date cv Hayani within the first 24 hours and in cv Khadrawi about 48 hours after pollination (Reuveni, 1986; Al-Attar, 1986). Each pistillate Date flower contains three ovules and, when pollinated, only one of these normally develops to maturity, while the other two dry and slough off (Nixon, 1928b).

Reuveni (1986) provides a chronological description of fruit development in the cv Hayani (Table 2-3):

Table 2-3 CHANGES DURING FRUIT GROWTH AND DEVELOPMENT

Weeks after spathe cracking	*Changes*
0 to 3	the zygote forms within the first day after pollination (d.a.p.), ovules in aborted carpels degenerate quickly
4 to 6	the embryo sac continues to grow and the zygote cell changes its location; growth is mainly by cell division
7 to 11	from the 7 th week onwards cell division in the mesocarp has been completed with further growth being accounted for wholly by cell enlargement; carpels enlarge progressively. Towards the end of this period growth and fruit elongation is achieved mainly by cell expansion. First zygote division on 46 th and second on 53 rd day.
12 to 14	mainly pericarpal cell division; the Khimri stage with green fruit colour is reached (Mohammed, 1980); seed and embryo grow very fast.
15 to 16	seed and embryo reach their final size near the end of this period
17 to 22	fruits grow mainly in length (*)
23 to 26	little change in size; maturation starts as indicated by start of colour changing (stage Khimri to stage Khalal with Bissr at last Khalal

Source: Reuveni, 1986

(*) fruits of some other cultivars tend to enlarge rather than elongate during the final growth stage. In date palms this exceptional increase in length-to-width ratio occurs due to the activity of a basal intercalary meristem.

Reuveni's classification stops here and provides no account of the changes due to senescence changes. Long (1943) describes in case of the cv Deglet Noor the start of this period as being characterized by slow dehydration and rapid sucrose accumulation and apparently some cell walls are hydrolysed, so that they become thinner and weaker, some even completely disintegrate. Before this stage the cell walls probably lose the property of differential permeability. The next stage is Rutab with colour changing to brown in case of Deglet Noor. The final stage is Tamr, in which the overripe fruits continue to lose moisture while the sugar-to-water ratio rises.

Other examples for a long period of zygote inactivity are the Pecan, where Sparks (1986) found the zygote to remain inactive at the micropylar end of the embryosac for a minimum period of 42 days after pollination and the pistachio, where the first division occurs between four and 18 weeks after fertilization and coincides with the transition from the free nuclear syncytium to the cellular endosperm (Sedgley and Griffin, 1989).

The timing and duration of the stages described by Reuveni are particular to the cv Hayani and a broader classification is required which suits the varieties under examination. The present study will reclassify these stages to reflect changes in the growth rate of the entire fruit. This is deemed appropriate because the study will examine pollen effects on the entire fruit and seed mainly with regard to size, weight and volume. These criteria were found to pass through four distinct phases which are common for all varieties examined and are therefore a suitable base for the reclassification.

b. Fruit drop

The fruit can be viewed as a physiological entity developed through the activity and interaction of sporophytic tissues associated with, and possibly regulated by, the ovules (Browning, 1989). For the further discussion it is important to remember that fruit drop during different stages of development is the result of conditions existing prior to its occurrence and that drop itself possibly affects the subsequent development of other fruits.

In most varieties, if the unpollinated dates develop at all there is development either equally of three carpels or of only one. In the cv Khadrawi, the abortion of 2 out of 3 carpels was observed seven days after pollination (Al-Attar, 1986). Reuveni (1986) calls the unpollinated fruits "parthenocarpic triplets" and "parthenocarpic singles". The first are hollow and the second contain a quasi-degenerate seed consisting of live integuments.

Reuveni (1986) found the first wave of fruit drop, which lasted about one month, commenced between 25 to 35 days after spathe crack. At this time, one enlarged carpel in the tricarpellary ovary was already distinguishable. Shedding of fruits with three equal small carpels containing unfertilized ovules and of fruits with one enlarged carpel was

observed. In the latter type, the enlargement may have been due to parthenocarpic development or due to a fertilized ovule. About 80% of all fruits due to drop up to maturity had dropped by 70 days. The number of flowers developing into mature fruits varied between 40 to 70 %. A second wave of fruit drop started about 100 days from spathe crack and lasted again one month. Reuveni suggests that in two varieties most of the dropped fruits were parthenocarpic, while in one variety "Deglet Noor" the second drop involved fruits containing embryos. He found that with these cultivars fruit set and natural drop were fixed in each cultivar in each garden and postulated that a number of flowers contain a priori a defective ovule and, therefore, could not set fruit.

This thesis will study premature fruit drop as one of the factors possibly affecting further development of the fruit and examine fruitset, numbers and percentages of flowers, both pollinated and parthenocarpic triplets, as influenced by pollen type and female variety.

2.4.2 Chemical changes during fruit development

Of the many chemical constituents which change during fruit development, water, dry matter and endogenous plant growth regulators (PGRs) will be examined as they are functionally related to fruit growth, while tannins and sugars will be studied as indicators for maturity, ripeness and fruit quality.

Quality in terms of composition of ripe date fruits varies greatly depending on cultivar. Meligi (1983) presents his findings in the ripe stage (Bissr) of the following four soft date types, which produce fruits of yellow colour, as shown in Table 2-4. The varieties studied are soft date types.

Table 2-4 COMPOSITION OF RIPE FRUITS OF DIFFERENT CULTIVARS (% WEIGHT ON FRESH WEIGHT BASIS)

Index	*Burhi*	*Sayer*	*Halawy*	*Samani*
Total sugars	23-27	26-28	31-32	21-24
Non-reducing sugars	10-14	13-14	9-11	3-4
Reducing sugars	12-13	11-14	21	18-20
Dry Matter	35-39	45-47	46-53	36
TSS	27-34	34-36	37-38	29-31

The following review aims to provide an understanding of the roles of these constituents.

a. Fresh Weight

Fresh weight increases due to growth and accumulation until fruits reach physiological maturity and follows a sigmoid curve. Thereafter ripening starts and the fresh weight decreases due to moisture loss (Reuveni, 1986) In the young growing fruits the moisture content decreases from 75 to 80% to about 40 to 60% when softening starts. This rate then decreases rapidly. The rate of water loss of detached mature dates at temperatures between 21 and 50 °C ranged from 0.28-3.4 ml of water per 24 hours. (Van Die, 1974)

b. Dry Weight

The change and gain of dry weight in case of the varieties studied by Reuveni (1986) follows a sigmoid curve, which bears a close resemblance to the sigmoid growth curves for growth in this study. In seeded fruits the rapid increase starts at the beginning of the Khalal stage. At that time the seed entirely ceases growing, and a decrease in rate of volume and fresh weight gain is evident. A decrease in dry weight gain occurs close to full maturation.

c. Sugar

Sugar content is an important attribute of quality and its quantitative assessment is part of this study. According to Reuveni (1986) sugars are the most prevalent compounds in dates. The changes in their content and composition are as follows: at early stages of fruit development through the period of fast growth in volume and fresh weight, sugar accumulates mainly as reducing sugars. The reducing sugars have been commonly thought to be an equimolar mixture of glucose and fructose arising from the hydrolysis of sucrose. A fructose-glucose ratio of 1:1.28 was found in Deglet Noor dates. During this period, a slow but increasing rate of accumulation of total sugars takes place. When a reduced rate of gain in fresh weight and volume occurs, a decrease in rate of gain in reducing sugars and a rapid increase in accumulation of sucrose and total sugars take place reaching above 70% of dry matter at maturation time. Close to maturation a decrease in sucrose and an increase in reducing sugar occur. The rate of sucrose inversion to reducing sugar at this state differs in different cultivars and to a smaller extent in the same cultivar under different growing conditions. Sugar content in ripe (Tamr stage) fruits varied from 68 to 85% on dry weight basis which represents, very closely, values found at maturation time as the rate of sugar accumulation during and after maturation is very low.

On dry weight basis, sugar content varies within a small range in different cultivars, but more so when expressed on a fresh weight basis, as shown in Table 2-4 (Reuveni,1986). Cultivars like Hayany and Barhee represent inverted type dates, while Zaghloul and Deglet Noor are semiinverted dates (Table 2-4).

d. Tannins

Tannin content is an important attribute of fruit quality with high levels causing fruits to be bitter. The tannin content changes during fruit development and determines whether a fruit can be consumed as early as the Bissr stage or whether further ripening is necessary to lower the tannin content.

Table 2-5 shows the tannin content in the ripe stage (Bissr) of the yellow fruits of four soft types (Meligi, 1983).

Table 2-5 TANNIN CONTENT OF RIPE FRUITS OF DIFFERENT CULTIVARS

Index	*Burhi*	*Sayer*	*Halawy*	*Samani*
Tannin Content % (*)	.16-.17	.29-.41	.20-.27	.20-.23

(*) On fresh weight basis

e. *Plant Growth Regulators (PGRs)*

Changes in endogenous plant growth regulators are suspected to be one of the mechanisms involved in mediating pollen effects. Evidence reflecting on this will be sought in the present study.

It is suspected that hormones mediate pollen effects early during pollination and that they can be formed in the stylar tissue under the stimulus of pollen tube growth, or even come directly from the pollen tubes themselves (Luckwill, 1948). While there is evidence that hormone in pollen is involved only in pollen growth, studies of hormone effects on fertilization events reveal considerable complexities and hormonal specificity. Pollination generates signals preceding the wave of biochemical and cytoplasmic activity which advances before the pollen tube (Browning, 1989)

There can be little doubt that as fertilized fruits develop the seeds contribute a stimulus to fruit growth (Browning, 1989). During later stages of growth, the four main growth promoters were found in the pericarp and seed (Reuveni, 1986; Stanley, 1971) and it is interesting to review their role and activity as it might reflect on their role early on. There appears to be no close correlation between the level of any single promoter and fruit development. However, when total activity of all promoters was calculated as equivalent to indole acetic acid (IAA) and indole acetonitrile (IAN) activity, distinctly different levels were found in the three fruit types of date (fertilized, parthenocarpic single and triplet fruits) at different stage of development (Reuveni, 1986). When comparing all developmental stages, the highest levels were found in fertilized fruits, followed by parthenocarpic single and then parthenocarpic triplet fruits. High levels found in fertilized fruits originated from seed. Positive correlations between fruit set, gain in fruit size, and growth promoting activity were found throughout growth till the end of

the Khimri stage. The PGR activity was lowest in early stages, high at the stage of rapid growth, and low close to fruit maturation.

Van Die (1974) suggested that the fruit or the young or fertilized ovules simply receive assimilates and that the role of plant growth regulators and seed development is limited to creation of sink activity and regulation of the biochemical and physiological processes which lead to the histological and chemical differentiation within the fruits. This could mean that pollen effects can be caused by hormones which create different sink effects affecting fruit growth. Stages during which pollen effects appear will be examined with regard to hormone content.

2.5 Factors affecting growth, development and fruit set

The objectives of this study are to test and assess the effects of pollen on fruit growth and development. Because it is expected that pollen effects interact with many other factors, which affect fruit growth, an understanding of the nature, role and mode of action of these factors is necessary.

2.5.1 Environmental conditions

Generally, the date palm requires a practically rainless season for the perfect development of its fruit and is at its best in hot interior regions having very high temperatures and low humidity (Mason, 1925). The cardinal temperatures for the survival of the date palm are -5 °C as the minimum to and 50 °C as the maximum temperatures with 35 °C as the optimum temperature for pollen germination (Smartt, 1995). Mason (1925) observed that date palms survived extreme temperatures of -15 °C and 52 °C. Minimum temperatures of 0 °C and maximum temperatures up to 58 °C for growth have been reported by Dowson (1982). The climate in the Batinah is semiarid

subtropical and is characterized by hot summers (max. > 45 ° C) with high to very high relative humidity (>80%) and mild winters (lowest 18-20 ° C., relative humidity 40-60%) and with less than 100 mm cumulative precipitation. In comparison with the hot and dry interior valleys of the Interior of the Sultanate Oman, California and southern Arizona, date fruit development in the peculiar environment of the humid, northern Batinah region requires further study.

High relative humidity adversely affects fruit quality. Water lying on the surface of developing Deglet Noor dates caused either "checking" during the late green or Khalal stages, meaning small lineal ruptures near the fruit apex, and "tearing", which was characterized by severe, often irregular splitting of the skin. While bagging as a protection against rain increased "checking" it was successful in decreasing the occurrence of "tearing". This indicates that tearing is affected by environmental conditions, while checking seemed to be reduced in case of fruits with lesser length, diameter and weight accompanied by lesser epidermal tension near the tip (Haas and Bliss, 1935).

Soil moisture can indirectly affect fruit development by affecting leaf area. Aldrich (1942) reported that the growth of leaves measured in terms of leaf elongation could be temporarily limited both by soil moisture deficiency and by water deficits within the palm itself during periods of high transpiration, when it could be shown that soil moisture was not the limiting factor.

The effect of temperature on growth and development of fruits up to ripeness has been studied by many authors in terms of thermal time or heat summation units. Cooke (1956) calculated from data of a 20 year study in the Date Growers' Institute in Coachella, California, that from 1. December onwards 6,900 summation heat units (°F). He used the daily mean temperature and 50 °F (10 °C) was taken as zero below which the date palm ceased to grow. Swingle (1904) proposed the use of the daily maximum temperatures and a base temperature of 18 °C. Dowson (1982) used the mean daily temperature and a base temperature of 18 °C to calculate heat summation from date of pollination to harvest. The latter will be used in this study mainly to examine fruit growth across different years and months of a particular year.

2.5.2 Plant condition

Plant condition is taken here as including factors such as leaf number and area, time of inflorescence emergence, cultivar and fruit retention, the orientation of bunches and of intraplant competition for resources on fruit growth and development. The review will provide the background for the later discussion of experimental results.

a. Leaf number and area

Generally, photosynthesis in developing fruits is insufficient to support their own growth and they are dependent on photosynthates supplied by the leaves (Sedgley and Griffin, 1989). The ratio of leaf number to bunch number has a slight effect on physical quality of the fruit and a significant effect on total soluble solids (Bacha and Shaheen, 1986). Trials on the effect of leaf/bunch ratios (5:1, 7:1, 9:1) on 12 year old date palms for 3 successive years revealed that yield and average bunch weight gradually increased with increasing leaf/bunch ratios in both cultivars.

Aldrich (1942) speculated that the commercial practice of removing 20 to 25% of the leaf area does not materially affect leaf elongation. This practice results in 6 to 10 leaves left for each moderately thinned bunch. Even with half of the leaf area removed along with removing half of the fruit crop (to maintain a constant leaf/bunch ratio) only 13 % higher leaf elongation resulted. Under Omani conditions, the removal of old, dry leaves is also common practice and they are expected not to contribute photosynthetically. Nixon and Wedding (1956) studied the photosynthetic efficiency of leaves of different age and found that leaves of four years' age were only about 65% as efficient per unit leaf area as those one year old. For the present study and an understanding of the effect of such a practice of reducing leaf area on yield and mean bunch weight is important as leaves have to be removed to maintain similar source-sink ratios over the two years of the study.

b. Cultivar and fruit retention

Fruit retention or fruit set is expected to vary with variety and location (Reuveni, 1986). The number of fruits per bunch had a major effect on fruit quality in terms of marketable versus small fruit size. A fruit number of 1,200-1,300 in tall palms was estimated to be the thinning requirement to achieve 70% marketable yield (Brown,1970).

c. Orientation of bunches

Nixon and Reuther (1947) found that higher temperature as caused by the exposure of some fruits in a bunch to direct sunlight tended to advance the ripening of these fruits when compared to others in the same bunch. Paper covers caused a slight retardation in ripening probably due to decreased dehydration of the ripening fruits.

d. Intraplant competition

The experiments in this study are designed to analyze fruit growth as affected by pollen type and by the proportion of ovaries retained at different stages of development. It is expected that the stage of development and the amount of retained ovaries will determine the degree of competition that acts between them. Intraplant competition is known to affect organ development as in the case of wheat where it reduced main stem length and diameter (Hucl, 1990). In date palms it can be shown that increasing thinning severity increased total soluble solids (TSS) and the total sugar content (Hussein, 1992).

2.5.3 Endogenous Growth Regulators

It is an objective of this thesis to examine pollen effects and to suggest possible mechanisms which bring them about. The hypothesis will be tested that endogenous hormones are responsible during the early stages. A review of earlier work on this

subject is required to provide an understanding of the types, mode of action and role played by different hormones.

a. Origin and mode of action

The different types of hormones found in dates as in many other types of fruits are auxins, gibberellins, cytokinins, abscisic acid (ABA) and purines (Reuveni, 1986).

Although both siphonogamy. i.e.: fertilization by means of a pollen tube, and syngamy, i.e.: sexual reproduction involving the union of two gametes, can result in an increase of endogenous hormones, it is not clear whether the hormones were found to increase in flowers after pollination, originate in the ovules or are also generated in other tissues (Browning ,1989). Pontovich (1978) observed that the endosperm is a source of a hormonal complex governing the differentiation of the embryo. The ovary tissues participate in regulating early embryogenesis and the placenta plays a role in supplying ovules with a morphogenetic factor without which kinetin and auxin do not induce formation of endosperm in vitro.

b. Role during embryogenesis

The formation of the embryo and its supporting tissue from a fertilized ovary is termed as embryogenesis. During this process different plant growth substances regulate growth and development and interaction on a hormonal level takes place between tissues such as the embryo and the endosperm.

Vecher et al (1980) observed in vitro that embryo growth is under the influence of some compounds acting at the hormonal level. For a brief period the zygote maintains a simple organization and divides into small cells in an aqueous medium with a chemical composition suitable for the nutrition of the developing embryo. The accumulation of growth substances such as auxins, gibberellins and cytokinins is maximum during the period of the max. growth of embryo and endosperm (Stage 2 and 3 in the present study). Browning (1989) highlights the role of gibberellins and explains that the gibberellic acid (GA) synthesis inhibitor Daminozide (paclobutrazol)

disrupts embryosac development whereas exogenous GA extends embryosac longevity in pear.

c. Role in fruitset and development

Hormones are expected to influence the fruit set of fertilized fruits and the further growth of the fruit and seed and the development of tissues.

The seed is a major source of the hormones required for fruit development, for example in apple (Luckwill, 1979) and seed development and maturation, as in case of in hybrid rice, are also controlled by growth regulators (Yuan and Huang, 1993) as suggested by the coincidence of the formation of primary embryo and endosperm with the presence of cytokinins while ABA peaked during seed maturation. K application markedly reduced the number of unfilled grains due to its promoting effect on cytokinin synthesis, which resulted in less zygote degeneration.

When the parthenocarpic single fruits were compared with seed bearing fruits (Reuveni, 1986; Schroeder, 1958), it was found that there were differences in cell size but never in cell number, which leads to the conclusion that development of the pericarp with regard to cell number is autonomous, while cell size is affected by the kind of seed developed. It should be noted that pericarpal cell divisions are reportedly complete at around the time the seed reaches its full size. From this time onwards it can be reasoned that the seed controls fruit growth by affecting cell enlargement and expansion probably by hormones. However, Browning, (1989) poses a question raised while studying stimulative parthenocarpy (triggered by foreign pollen and by exogenous hormones) in apple, where hormone levels in parthenocarpic and seeded fruits change in similar ways during subsequent growth and development. Are in such parthenocarpic fruits the ovules the source of hormone controlling fruit growth or is this evidence of tissue autonomy in hormonal regulation ? Interestingly Reuveni's observations (see above) show that pericarpal development regarding cell number appears to be such an autonomous process.

Gibberellins were also studied in other crops and were found in the mango cultivars Dashehari, Chausa and Langra only in the seed, where their content increased rapidly during the early stages of development, then decreased as the seeds matured. Cytokinins occurred in both seed and pericarp. Their levels increased prior to rapid cell division and cell enlargement and a second increase occurred during cell enlargement. High levels of an ABA-like inhibitor were found during the first 21 days following pollination, corresponding to the period of slow growth and heavy fruit drop. As the growth rate increased the inhibitor levels were reduced and the levels of growth promoters increased. All endogenous growth regulators were at low

levels during fruit maturation. Deficiency in cytokinins, gibberellins and auxins resulted in fruit drop but this could be overcome by applying sprays of exogenous growth regulators at fruit set. (Sant Ram, 1992; see also fruitdrop.doc, BenCheikh, 1997). However, as reported by Looney (1984), GA and benzyl amino purene (BA) applications to seeded fruits at blossom time may also inhibit development, possibly by reducing fruit set and he suggests that supra-optimal levels of GA may be responsible.

2.5.4 Pollination and pollen

A specific, extended review of pollination and pollen is presented here because this area is a major subject of the present investigation later discussed in the thesis.

a. Pollination

The natural method of pollination is by wind and according to Reuveni (1986) a fair set of fruits is achieved if enough male trees are grown next to female trees. However, in commercial practice only a very few male trees suffice to collect pollen for artificial pollination. More commonly a few strands are cut from the male inflorescence, which are then tied together and two or three of them are inverted between the strands of the female flower cluster. In the Sultanate of Oman it is common to tie each single bunch of strands, while Nixon (1966) reports that in the USA twine is tied around the pollinated cluster 2 to 3 inches from the outer end to hold the male flowers in place. From personal observations and communications with date growers in the study area, I found that depending on variety, on the number of female inflorescences per palm and on the size of both the male and the female inflorescences between 20 and 40 date palms can be pollinated from one male date palm. Swingle (1928) describes a similar ratio of 2% to 3% as suitable for artificially pollinated orchards. Today artificial pollination is standard practice in the cultivation of this plant.

In practice the female inflorescence is pollinated soon after the cracking of its protective spathe. Leding (1928) carried out several experiments on the period of receptivity of female flowers and found that the highest percentages of fertilized flowers was observed when pollination was carried out on the day of cracking or within 3 to 4 days thereof. Thereafter the percentage decreased. Other reports (Algérie,

Gouvernement Général, 1951) state that female flowers remained receptive for 12 days. According to Reuveni (1986) for a high fertilization percentage and a good fruit set to occur it is necessary to apply a larger amount of pollen particularly if its viability is low. Brown and his co-workers (1970) concluded that a lower fruit set was achieved when a lower pollen deposit was applied in the female inflorescence area. Ream and Furr (1969) and Pereau-Leroy (1957) found a higher set of fruit when pollination takes place at mid day between 10 am and 3 p.m.

As regards temperature, Furr and Ream (1969) found that in vitro date pollen germination started from 7 °C and increased with rising temperatures up to 32 °C. At 43 °C. germination was seriously impaired. Smartt (1995) reported an optimum temperature of 35 °C. This may reflect the cardinal temperatures for growth, in particular the optimum temperature. An examination of the optimum of seed germination over a range of temperatures has revealed an optimum of 35 °C, which is similar to the ones reported by other researchers. Brown et.al. (1970) measured in vivo maximum temperatures in the inflorescence area and concluded that good fruit set will occur at 22 to 26 °C or higher. Reuveni et al.(1985) determined the time taken for the pollen tube to reach the base of the style and found the fastest was 6-8 hours at 25 to 28 °C in detached pistillate flowers.

Dry winds lead to a faster drying of the style before the pollen tube can reach the ovule. (Reuveni, 1986). Rains before pollination can negatively affect fruit set (Pereau-Leroy, 1958), while rains after pollination do not under conditions of rapid drying. It is not clear whether this negative effect is due to a drop in temperatures following rain or due to physical changes occurring on the stigmatic surface. I suspect that in case of rains following pollination pollen already adheres to the stigmatic surface or that pollen tube growth has commenced, which would make physical removal of the "anchored" pollen less likely. Rains before pollination may prevent the pollen from getting into contact with the stigmatic surface, because the high surface tension of water drops on stigmata may keep the pollen afloat or stigmatic features promoting pollen grain capture or adhesion may be adversely affected.

Asif (1983) reported that the percentage of pollen germination and the rate of pollen tube growth increased in vitro with increasing concentrations (0.05 ppm to 100 ppm) of gibberellic acid, indole acetic and boric acids.

Pollination in other plants:

In Heliconia psittacorum poor fruit set was not the result of poor pollination but could be attributed to poor pollen germination on stigmata (Lee, 1994).

In Mango pollen viability and stigma receptivity ceases 3 days after anthesis (Desai, 1996). Robbertse (1996) found maximum pollen tube growth *in vivo* in Litchi at 25 and 30 °C. There have been different views regarding indicators for pollen viability. Yates (1996) found in Pecan that fruit set was a more reliable indicator of pollen viability than *in vitro* germination, while in Papaya it was found (Cohen, 1996) that pollen germination on a drop of Brewbaker medium closely reflected*in vivo* germination.

Pollination in other palm species:

Ninan (1963) observed that the copra content in coconut could be influenced by the pollen parent. In *Phoenix rupicola x P. reclinata* pollen affected the time of ripening (Nixon, 1935b).

b. Pollen

The pollen of the date palm is white and has a very distinct and pleasant odour. Asif (1987) reported that pollen size varies widely within samples taken from different palms of the male variety Fahal, the mean pollen diameter ranged from 16 to 30 μm, which is well within the limits of 17-58 μm found in the majority of anemophilous (wind pollinated) plants (Stanley, 1974). Heslop-Harrison (1971) quotes the unusually high mineral content and the comparatively low total soluble carbohydrate content (1 to 2%) of date palm pollen. He noted also the discovery of the steroid "oestrone" in date palm pollen, which is a animal sex hormone. Also Hooley (1994) reported that part of the mammalian steroid-signalling pathways may be present in plant cells and that similarities with the mechanisms for GA perception at the cellular site exist.

i. Definitions and examples of pollen effects:

Metaxenia and Xenia:

Swingle (1928) explains that the very first time he observed the differential effects of pollen from different male palms on the size of fruits was when he found that the pollen of a seedling from a male plant in Indio, California, which was originally obtained from the Semail valley in South-eastern Arabia (Sultanate Oman), produced very small fruits when compared to another pollen variety, Mosque. He defined metaxenia as the direct effect of pollen on the parts of the seed and fruit lying outside the embryo and endosperm, while xenia denotes its influence on the endosperm of the seed (Swingle, 1928). Although recently suggestions have been made to redefine the term "Metaxenia" as a form of "Xenia" (Denney, 1994), this thesis will use the term "Metaxenia" in relation to its classical definition of effects on discernible characteristics of the fruits and seeds outside embryo and endosperm as well as on yield and some yield parameters caused by pollen from different sources. Based on its classical definition, "Xenia" will be used to denote pollen effects on the seed.

Fruit set:

A fruit is defined by Sedgley (1989) as a mature carpel or carpels with or without seeds and with or without accessory structures. In this study the term fertilized fruit is used to describe the apparently fertilized fruits, while the parthenocarpic triplets and distinguishable single parthenocarpic ovaries are distinctly referred to as unfertilized fruits. Fruit drop due to numerous causes occurs throughout the development of fruits, i.e.: drop of unfertilized ovaries occurs, accompanied and followed by drop of otherwise deficient ovaries and later during development fruits drop prematurely. Fruit set is therefore not constant but changes depending on the stage of development. Sedgley points out that the term "Fruit set" is used rather loosely in angiosperm literature and normally refer either to initial or to final fruit set. The first is attained when the zygote divides to initiate embryo development, while the second refers to the number of fruits remaining in the plant to maturity. These definitions are insufficient because they would not include parthenocarpic fruits. For the purpose of this study the number of apparently pollinated and fertilized ovaries as well as unfertilized "fruits" was determined

at regular intervals during fruit development starting from a short time after pollination and was expressed as a percentage fraction of the total numbers of tricarpellary flowers initially present at inflorescence emergence. This percentage is referred to in this thesis as fruit set with the synonymous use of the terms fruits set, fruits retention and fruits retained.

Genetic effects:

The definition of Metaxenia and Xenia by the geneticist Redei (1982) gives an idea of the genetic effects which can be induced by pollen. He defines that Xenia is the expression of paternal characters in the endosperm of hybrid seed. He notes that the fruit, pericarp and seed coat are all exclusively maternal. With hybridisation, fruit characters may appear to be modified by the tissues of bisexual origin. He terms this physiological interaction, which is nonhereditary, as Metaxenia.

ii. Mechanisms

The wide spread in time over which pollen effects occur highlights the need to view different periods of fruit growth and development during which mechanism can become active.

Lag phase:

The types of and roles played by pollen hormones or not generally recognized as can be seen from the following: as reported by Heslop-Harrison (1971) indole acetic acid, gibberellins and also auxin inhibitors, were discovered in the extracts of whole pollen. Stanley (1974) noted the occurrence of six classes of plant growth regulators -auxins, gibberellins, kinins, brassins, ethylene and inhibitors- in pollen. Specific roles ascribed to them are:

1. that inhibitors can repress growth until the grain is in the correct environment., after which they are inactivated,. It has also been suggested that the maintenance of a critical level of GA is essential to pollen germination,

2. that auxins may be involved in directional growth of the pollen to the egg,
3. that gibberellins can activate amylase and thus, as the pollen move forward, cause the hydrolysis of starch to provide sugars to sustain growth. From in vitro experiments it has been suggested that lack of Gibberellic Acid 3 (GA_3) may be among the factors inducing or accompanying tube elongation.
4. That growth substances diffusing from the pollen may stimulate maturation or receptivity of the egg cell preceding fusion with the male cell and
5. that growth regulators can control tube extension in many ways, one of which is facilitating wall growth.

Stanley groups pollen growth regulators by activities into

a) those involved in tube growth and delivery of the male cell and

b) those involved in attraction or contact of the male cell to the egg cell.

Heslop-Harrison (1971), in contrast, considered it an unlikely mechanism that hormones delivered by pollen trigger a flood of more hormones throughout the flower, Although, undoubtedly, hormones are increased in flowers by pollination and fertilization., Looney (1984) also observed that pollen germination and pollen tube growth may be under the control of GA. . Heslop-Harrison (1971) notes the existence of evidence that hormones in pollen are involved only in pollen growth. However, pollination generates signals preceding the wave of cytoplasmic and biochemical activity which advances before the pollen tube. As will be reviewed in Section (iii), these signals may be generated during pollen-pistil interaction. In tobacco ovaries a sharp rise in the auxin content occurs immediately after pollination, while no increase occurs in the absence of pollination. Pollen tube growth considerably increased the extractable auxins in the style of tobacco plants, possibly due to an enzyme released by the pollen tubes that catalyzes the production of auxin. An enzyme capable of converting tryptophan to auxin was secreted by the pollen tube (Devlin, 1983). BenCheikh (1997) reported that pollination increased the GA levels in seeded citrus varieties suppressing abscission. It is possible that genes get promoted by signal, possibly hormones, already in the stages preceding morphogenesis (Devic et al., 1996), which in this study would during the zygote stage. The complexity of the dynamics of hormone fluxes have been interpreted as strategies and counter-strategies of mother and offspring tissues (Ravishankar, 1995) in regulating resource allocation through hormones.

Parthenogenesis can be induced *in vitro* by foreign pollen and *in vivo* by irradiated (dead) pollen indicating that siphonogamy provides a general physiological

stimulus for embryogenesis. This circumstantial evidence, together with the ability of exogenous hormones to trigger embryogenesis indicates that both syngamy and siphonogamy induce an increase in supply of endogenous hormones within the ovule (Browning, 1989).

It is interesting that Nixon (1955) observed that "checking" in dates, i.e.: development of minute cracks in the apical half of the fruit, is more in thinned bunches that in bunches attaining larger fruit size due to pollen source. A later study by Schroeder and Nixon (1958) suggested that fruit size is attained in thinned bunches in the later stages of development by cell enlargement, while different pollen types affect the cell number through cell division in the early stages of development.

End of lag phase to start of ripening :

During this phase the seed starts growing at an increasing rate in the date palm. In general, as fertilized fruits develop there can be little doubt that the seeds contribute a further stimulus to fruit growth (Browning, 1989). As the seed is of bisexual origin, this indicates that the effect of pollen in this stage would be indirect from the male gamete and therefore genetic.

Role of growth hormones in metaxenia in the date palm:

Although Reuveni (1986) states (see 2.4.2.d) that the growth promoter requirement is lowest in the early stages of development, in my view this does not exclude the possibility that the early differences in growth may be due growth promoters, which become active as a result of pollination, rather than the seed, which in cv Khalas is not even present except as one zygotic cell during the first 5-6 weeks after pollination.

iii. Factors affecting pollen

In this study, the male and female date palms are growing in different locations with distinct environmental conditions which change from year to year and can be expected to have an effect on pollen (and pistil !). For example, in sesame (*Linum usitatissimum*) characters of the pollen grain such as fertility and size are under the

influence of both genotype and environmental conditions and pistil characters are also influenced (Pfahler, 1996). Stanley (1974) reports that pollen diameter is influenced by night temperature and suggests that water stress increases either the amount of sterile pollen or the number of immature pollen grains. The quantity of pollen produced for example by pine trees depends directly on light exposure, i.e.: side of the tree position on tree and age of the tree. He reported that low and high temperatures can adversely affect quantity and germination response of mature pollen. *In vitro* examination of tomato pollen revealed that germination and pollen tube growth in response to heat treatment is genotype dependent (Abdul-Baki,A.A. and J.R.Stommel, 1995) and not a general predictor of fruit set under high temperature stress. Varying proportions of germinated grains - a phenomenon possibly associated with moist weather conditions- have been observed within undehisced anthers of some fruit tree types which potentially has an adverse effect on seed and fruit set (Sedgley and Griffin, 1989). Pandey (1971) observed that in *Nicotiana spp.* there appeared to be a relationship between small pollen size and self-incompatibility, which he considers both primitive characters. Townsend (1971) found that relatively high temperatures can inactivate the incompatibility mechanism acting on the style not the pollen. In *Lilium longiflorum* until 39 °C tube growth in incompatible pollen increased with temperature to a lesser extent than that of compatible tubes. In Graminae a gene action model has been proposed and data support the view that incompatibility is brought about by the induction of an inhibitor rather than the repression of an auxin of pollen tube growth.

iv. Interaction with maternal type

The examination of fruit development in this study requires an understanding and review of male-female interactions on fruit set that could possibly operate in the date palm. Differences in fruit set involving the same pollen type used in different years were observed, so that a review of the possible causes for such differences with regard to the pollen is necessary. The following reviews some of the work done on male-female interaction which may explain observation presented and discussed later on.

In palms like the Oil Palm (Long Ashton Res. Stn, 1977) no evidence of gametophytic incompatibility and in Euterpe (Bovi, 1994) no self incompatibility mechanism of any kind was found. However, in the date palm incompatibility has been observed (Al-Salih, 1987) but no further research seems to have been done on this topic.

Generally, pollen grains have to be captured by the stigma and adhere to the stigmatic surface, where they will hydrate and then development will commence with the formation of a pollen tube. There are numerous stages during which interactions take place, which can be disturbed at any stage from the moment pollen came into contact with the stigma to the interaction of the gametophytes (Vishnyakova, 1990).

In Brassica oleracea (Stead 1979) cross pollen adhered more strongly to the stigma than self pollen. Experiments with Brassica under field conditions (Zuberi and Dickinson, 1985) revealed that self pollen grains are inhibited from further growth during hydration. Complex interactions between the pollen and the stigma, and between pollen tube and stylar tissues, are involved in pollen-pistil recognition determining the extent of incompatibility reactions. Heslop-Harrison (1982) proposes a general hypothesis for incompatibility reactions during recognition according to which (1) pistil incompatibility factors are active proteins present in stigmatic secretions or the stylar tract, (2) these factors possess a complementary binding specificity to sugar arrays in the growth zone of incompatible pollen tubes, so that (3) binding in the case of incompatible partners leads to a disruption of apical growth. Kashyap and Gupta (1989) suggested that growth regulators play a significant role in pollen-pistil recognition in self incompatible systems and they thought ethylene to regulate pollen germination and further tube growth. The most accepted view is that incompatibility is the result of active recognition , i.e.: both pollen and pistil produce interacting S-allele specific recognition molecules (Van Marrewijk, 1989). In Maize, tube growth rates are influenced by the stylar genotype (Sari-Gorla, et al, 1995). While on an incompatible stigma, pollen may accumulate an inhibitor which is constantly metabolized. In Brassica it has been shown that expression of particular incompatibility genes is associated with the presence of a glycoprotein in the stigmatic papillae. The nature of these interactions and their consequences are not yet fully understood (Dickinson and Bonner, 1989).

Even after pollen tube growth commences into the stylar tissue interaction between proteins excreted by the pollen tube and other proteins in the pistil pathway occur (Willemse, 1995). It has been shown in Easter Lily that the incompatibility reaction manifests itself in the style and not on the stigma and it has been suggested that the pollen tube may be indifferent to the substances causing incompatibility as long as it has sufficient reserves to draw upon for its continued growth. In compatible pistils, the tube is able to switch during growth from autotrophic to heterotrophic growth (Rosen, 1971). With a view on the later discussion about pollen types in this study, it can be further reasoned that -assuming incompatibility exists between the studied parental types-

pollen with a higher viability and vigour is more likely to fertilize the ovary while less vigorous pollen may be inhibited by incompatibility reactions.

v. Observations in the Sultanate Oman

There are about 140 different pollen varieties used in different combinations to pollinate the nearly 250 female varieties in the Sultanate of Oman (Macki, 1992) The most commonly used pollen types of the interior areas of Oman are Ghorabi, Abu Alkhannaseer, Ghareef, Chizaini, Al Arudsabba, Duwaira, Bahlani, Khori and Faridi. Al Arudsabba is found in Rustaq, Khori in Nizwa and Bahlani in Bahla, which are all towns in the mountainous interior of the country. These three types are available early and can be supplied until late into the season. Date growers, particularly in the Dakhliyah and Sharqiyah regions distinguish the different male varieties by their effects on different female varieties in terms of Seed size, Fruit size, Colour, fruit set and earliness.

All information gathered about effects on earliness and flavour cannot be presented here, because it differs from farmer to farmer probably as a result of personal tastes or preferences as well as differences in microclimatic conditions, which vary from one oasis to another. Table 2-6 summarizes the most frequently attributed characteristic effects.

Table 2-6 CHARACTERISTIC EFFECTS ATTRIBUTED TO DIFFERENT POLLEN TYPES BY LOCALGROWERS

Pollen type	*Seed size*	*Fruit size*	*Ripe fruit colour*	*Fruit set*
Abu Alkhanassir	small	small	rose in red cvs	low
Al Arudsabba	small	big	rose in red cvs	low
Bahlani	normal	different sizes	unaffected	normal
Duwaira	no information	no information	no information	high
Ghareef	big	no information	deep red in red cvs	good, high
Ghorabi	big	big	rose in red cvs	high
Khori	normal	uniform, big	unaffected	normal
Midseri	normal	small	strong colour	high
Sabqi	small	small	unaffected	normal

This thesis will study the effects of the pollen types Al Arudsabba, Bahlani, and Khori on fruit growth and development in the female cvs Khalas and Khasab. These pollen types are selected because they are available from early on until late in the flowering season and because of their reportedly distinct effects on fruit growth and development. Al Arudsabba is earlier than Khori.

2.6 Summary of objectives

The objective of this study is to test claims of pollen effects on Omani date palm growing in the northern Batinah region of the Sultanate Oman and to determine their occurrence during different stages of fruit growth and development, to quantify them over a two year period. Various characteristics of pollen will be examined and related to the observations made on the effects caused by these pollen types. This would hopefully result in plausible suggestions for the mechanisms causing pollen effects. A further objective is to find criteria for a reliable assessment of suitable pollen types for commercial application thereby contributing towards an improvement of date production.

3. Materials and methods

3.1 History of trees

3.1.1 Paternal

The pollen types Al Arudsabba, Bahlani and Khori were selected on empirical information gathered from growers and because of their availability during the period of female inflorescence emergence in one medium late and one late variety. Khori is supposed to produce uniformly shaped fruits which are relatively large in size, while Al Arudsabba supposedly produces big fruits with small seeds and rose colour, in the case of the red fruited female varieties. Bahlani is an intermediate type regarding size, which is noted for its differing fruit sizes. From the literature review, it was concluded that characteristics such as fruit size, seed size, uniformity of fruits and developmental timing are most likely to show differences. The above pollen varieties supposedly cause different effects with regard to those characteristics.

The male palms in each variety are from vegetatively propagated male plants. Palms of the varieties Khori and Bahlani were located near Nizwa and those of the variety Al Arudsabba near Rustaq. Both locations are in the mountainous interior regions of the Sultanate.

Plate 3-1 *Male inflorescence of the date palm*

The male palms ranged in age from 12 to 15 years and yielded between 45-60 spathes per year. All trees were well cared for and standing solitary or in places shade.

3.1.2 Female cvs

Two female cultivars were studied : Khasab Omani (red fruits) and Khalas Omani (yellow fruits). Both are prime varieties which are mainly cultivated in the Interior of the Sultanate for its high quality fruit, but which are planted now also in the coastal regions of the Batinah. Khalas is medium late and Khasab is very late here. These varieties were chosen because of the wide range of developmental timing of their fruit growth and development and because of their regional commercial importance.

The trees were all about 9 years of age in 1995 and were planted as offshoots from vegetatively propagated mother plants. They have received the same cultural practices and have been exposed to similar conditions during recent years. Plates 3-2 and 3-3 show a date palm orchard and a date palm of the cv Khasab.

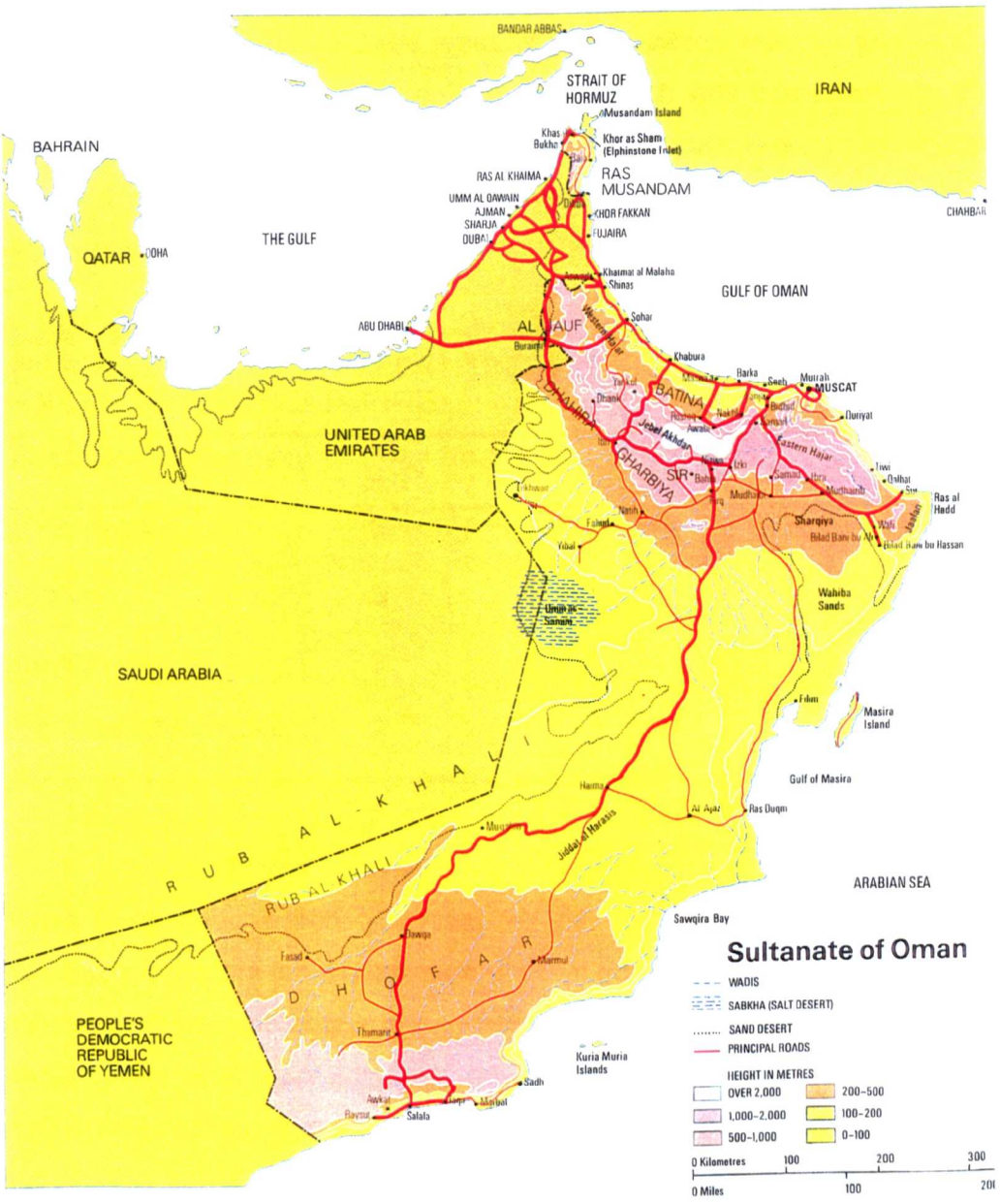
3.2 Location and meteorological factors

The experimental units (trees) are located in a farm (57°N, 24.5°E) in Sohar, which is about 200 km north-west of the capital Muscat and located 1-2 km from the Arabian Sea in a densely cultivated belt of coastal farmland (Plate 3-4). The soils are loamy and deep. Water is sweet (electric conductivity = 1,000-1,500 microSiemens/cm). The climate is characterised by hot and humid summers with maximum temperatures of 48-50 °C and relative humidity exceeding 80%. The winters are mild and cool with minimum temperatures of 10-15 °C in the nights, at 40-50 % relative humidity. (Climatic data are in Appendix 1).

Plate 3-2 *Date palm orchard*

Plate 3-3 *Date palm of the cv Khasab*

Plate 3-4 *Map of the Sultanate Oman showing above mentioned sites*



3.3 Experimental design

Pollination trials:

Treatments were three types of pollen, which were studied in a completely randomised block design (Table 3-2). Each bunch was considered as a replication, with mean values for one fruit being the mean of 6 fruits selected at random from that bunch. Three to nine replications were made for each treatment in two to three blocks where one tree was one block.

Table 3-1 EXPERIMENTAL DESIGN SHOWING NUMBER OF BUNCHES (REPLICATIONS) IN DIFFERENT TREES (BLOCKS) TREATED WITH DIFFERENT POLLEN TYPES (TREATMENTS).

Treatment (Pollen type)	*Tree No.1*	*Tree No.2*	*Tree No.3*
Al Arudsabba	3	3	3
Bahlani	3	3	3
Khori	3	3	3
unpollinated (not control)	2	2	2

A group of three bunches were pollinated with a particular pollen type in a tree. There were three pollen types applied per tree. Another two bunches were not pollinated to enable the assessment of the efficacy of bagging. The bunches were so chosen that the replications of one treatment in a single tree were located such that each bunch was approximately equidistant in the ring of bunches. This was considered necessary to achieve homogeneity between replicates with regard to their exposure to sunlight. The means for treatments are the averages of all replications (in all plots). The variability between trees and their interaction with pollen treatments was analysed and considered in the analysis of variance. There were two female cultivars, Khasab and Khalas, on which the experiment was carried out.

The different dates of pollination are shown in Figure 4-5 in Section 4.3.1..

Hormone treatments:

Three hormones each at two concentrations applied to bunches of trees pollinated with Al Arudsabba were studied in a completely randomized block design in 1995 (Table 3-3) and 6 hormone treatments each at one concentration applied to bunches of trees pollinated with Al Arudsabba and to another group of trees with bunches pollinated with Khori were studied in 1996 (Table 3-4). Each bunch was considered a replication with mean values for one fruit being the average of 6 fruits selected at random from that bunch. Two replications were made in two to three plots, which are the palms. The means for treatments are the averages of all replications (in all plots). The variability between (trees) and their interactions with pollen source were analysed. There were both years of the study two female cultivars (Khalas, Khasab), in 1996 one pollen type (Al Arudsabba) and in 1996 two pollen types (Al Arudsabba, Khori) on which the experiment was carried out.

Table 3-2 EXPERIMENTAL DESIGN IN 1995 SHOWING NUMBER OF BUNCHES (REPLICATIONS) IN DIFFERENT TREES (BLOCKS) TREATED WITH DIFFERENT PLANT GROWTH REGULATORS AT DIFFERENT CONCENTRATIONS (TREATMENTS). POLLEN TYPE AL ARUDSABBA.

Treatment (Hormone)	*Concentration of a.i. (ppm)*	*Tree No.1*	*Tree No.2*	*Tree No.3*
IBA	50	2	2	2
	100	2	2	2
GA_3	50	2	2	2
	100	2	2	2
Ethrel	200	2	2	2
	400	2	2	2
Water (control)		2	2	2

Table 3-3 EXPERIMENTAL DESIGN IN 1996 SHOWING NUMBER OF BUNCHES (REPLICATIONS) IN DIFFERENT TREES (BLOCKS) TREATED WITH DIFFERENT PLANT GROWTH REGULATORS 6 AND 40 D.A.P. AT DIFFERENT CONCENTRATIONS (TREATMENTS). TREE NOS. 1,2,3 WITH POLLEN AL ARUDSABBA; TREE NOS. 4,5,6 WITH POLLEN KHORI.

Treatment (Hormone)	*Concentration of a.i. (ppm)*	*Tree No.1,4*	*Tree No.2,5*	*Tree No.3,6*
NAA	100	2	2	2
GA_3	100	2	2	2
BA	100	2	2	2
HFCA	50	2	2	2
TIBA	100	2	2	2
Daminozide	3000	2	2	2
Water (control)		2	2	2

3.4 PGR applications to pollinated bunches

1995: Hormone treatments were gibberellic acid 3 (GA_3) at 50 ppm and 100 ppm, indole butyric acid (IBA) at 50 ppm and 100 ppm, Ethrel at 200 ppm a.i and 400 ppm a.i. and control being water (Table 3-3). These different levels of different hormones were used based on reports in literature (Abou-Aziz, 1983; Maximos, 1980; Devlin, 1983; Luckwill, 1979; personal communication). Similarities in fruit growth criteria between hormone treated bunches and pollen treated fruits were sought. In each of the four trees of the two female varieties twelve bunches were selected for applying hormones 24 hours and 80 days after pollination . As some pollen had to be used, Al Arudsabba was used. The first application was made to simulate hormone effects due to pollen, while the second one was to simulate hormone effects exerted through the seed. These three types of plant growth regulators were applied each in two concentrations onto bunches. The chemical solutions and the water were mixed

with a wetting agent (Citowett, BASF) to improve adhesion of the solutions to the flowers and fruits. To dissolve IBA diluted KOH was added dropwise until the reagent was dissolved and sulphuric acid was used to neutralize the solution. At least two bunches were treated with each of the six concentrations of hormones and with water as control. The bag was closed thereafter.

1996: The method followed was similar to 1995 except that applications were made at 1 and 40 d.a.p. and applications were made to female trees pollinated with Al Arudsabba (Table 3-4) and another group with Khori (Table 3-5). This second application was thought to reveal pollen effects due to the developing bisexual tissues of embryo and endosperm. Interactions between PGR treatment and pollen treatment were expected. Treatments applied were GA_3, NAA, Daminozide, benzyl amino purene (BA), tri-iodo benzoic acid (TIBA), hydroxy-fluorene carboxylic acid (HFCA) and water as control. The plant growth regulators were dissolved in water. To dissolve NAA, BA, HFCA and TIBA, diluted KOH was added dropwise until the reagent was dissolved and sulphuric acid was used to neutralize the solution. Daminozide, a GA-synthesis inhibitor and TIBA and HFCA, both PGR-transport inhibitors (Luckwill, 1979), were used to simulate synthesis and transport inhibition due to endogenous hormones.

3.5 Examination of pollen

3.5.1 Viability and germination

Viability of pollen was assessed by a pollen grain germination test according to the method described by Furr and Ream (1968).

During germination tests in this particular experiment, the flasks were placed in an incubator with temperature regulated at 21 °C. Three replicate cultures of each pollen type were incubated for 4 hours, after which they were placed in a refrigerator to stop further germination until the pollen could be examined.

Tests of germinability of pollen in 1996 indicated a mean germination percentage of 68 % for all pollen used, which had the same appearance and odour of the pollen used in 1995. Pollen with no viability was either from an immature male spathe or appeared as fermenting, dark clumps. These indicators have proved reliable criteria and compare well with germination test results.

3.5.2 Pollen tube growth

To measure pollen tube growth, the same procedure as described for the germination test was followed, but the flasks were incubated for 24 hours. Then the flasks were transferred to a refrigerator to stop pollen tube growth until examination. One or two drops of the pollen suspension in each of the three replicates and for each pollen type were placed on a microscopic slide. Using a light microscope at low power (100 x) with an ocular and stage micrometer, the length of pollen tube was measured from the point of its emergence from the pollen grain to its tip.

3.5.3 Pollination

A modified method based on Nixon (1928a) was followed.

Pollen was collected by opening the spathes and cutting the strands carrying the male flowers from the peduncle. At that time the pollen was assessed visually and by its odour. Old, possibly non-viable pollen appeared brownish rather than white, and formed clumps. Its odour would have been sour indicating fermentation, which can occur under conditions of high atmospheric humidity For each pollen type this was done in a separate room to avoid contamination. The strands were spread on a black, smooth plastic sheet, on which they were kept for 24 hours under ambient conditions, but care was taken that 18 °C was not exceeded by thermo-regulating with an air conditioner. Relative humidity was between 40 to 60 %. The strands were beaten the next day to release the pollen from those florets which had opened in the meantime. The pollen was then transferred to glass containers. The pollen was then stored in an air-conditioned room to be used within the next 8- 10 days.

Pollination was done on female spathes which had just split open. The female inflorescence was carefully pulled out of the spadix and ample pollen placed

inside the female inflorescence. Depending on cultivar and length of the inflorescence, between 3 and 5 tufts were used. Thereafter a brown double-walled paper bag was loosely pulled over the inflorescence and its neck was tightened by a string around the base of the peduncle. A layer of cotton was placed between paper and peduncle to facilitate aeration. Plate 3-5 shows an inflorescence being pollinated and in the back ground a covered inflorescence. The bag containing the female inflorescence and the pollen carrying cotton tufts was vigorously shaken to distribute the pollen. This proved to be an effective method of distributing pollen uniformly. Increased pollen application was also avoided in this manner, as this could lead to increased fruit drop (Haffar, et al, 1997). To avoid pollination by foreign pollen, the bag was kept closed for a period of 12 days, which was assumed to be the period of stigma receptivity (Governement Général Algérie, 1951).

Plate 3-5 *Pollination of a female inflorescence*

3.5.4 Pollen analysis by High Performance Liquid Chromatography

The method described by Davis (1968) was used to extract and measure gibberellin-like substances, indole acetic acid and abscisic acid.

In this particular experiment samples were injected in a Hewlett Packard 1050 High Performance Liquid Chromatograph using methanol: water = 60:40 as the mobile phase with a UV detector at 254 nm and a flow rate of 1 ml/min using a Hypersil ODS column for zeatin, zeatin riboside, abscisic acid and naphthalene acetic acid. The reference standards were diluted with methanol to concentrations of 10 ppm and then injected under the same conditions. Needle spiking was carried out to examine unclear peaks, by injecting a mixture of a standard with a sample extract. The eluting peaks were recorded.

3.5.5 Pollen extract bio-assay for PGRs.

This bioassay was carried out according to the method described by Devlin (1983). Three replicate lots of seeds of the lettuce cv 'Iceberg' were incubated and germinated under light conditions for 12 hours at 20 - 25 °C. Hypocotyl lengths were measured at 0, 2, 4, 8 and 24 hours after the addition of hormone extracts.

3.5.6 Determination of mineral content of pollen

a. Determination of Ca, Mg, Fe, Zn and Cu

Mineral content of pollen was determined by atomic adsorption spectrometry (AAS) according to the method described by Lees, 1975.

b. Determination of K and Na

The flame photometric method described by Lees (1975) was used.

3.6 Determination of peduncle size

The size of the peduncle of the female inflorescence was determined 30 days after its emergence. A vernier calliper was used to measure the lateral width and, perpendicular to it, its thickness at a point 15 cm above the axil of the corresponding leaf.

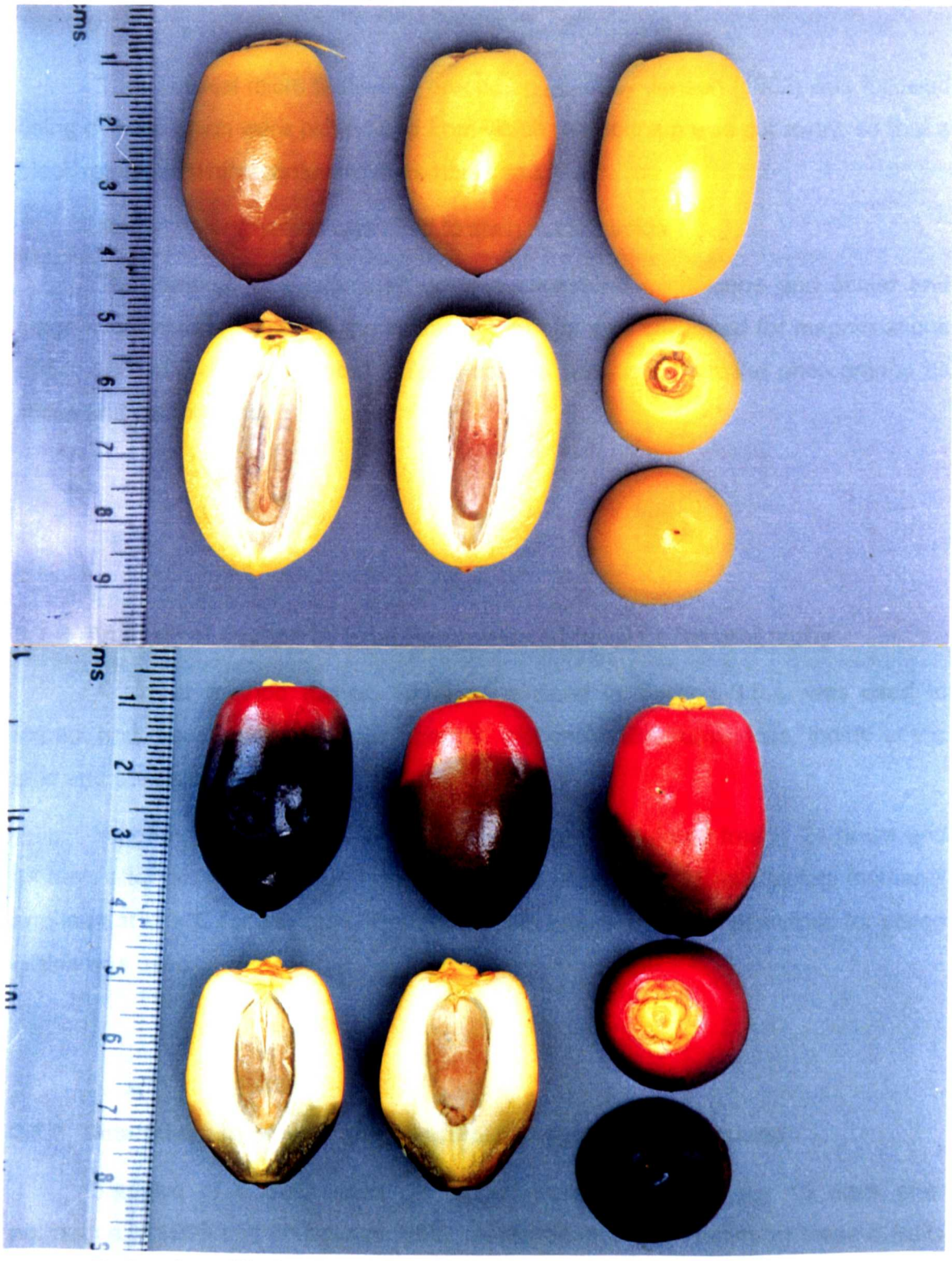
3.7 Fruit growth analysis

For measurements, future chemical analysis and reference, entire-fruit samples were collected in 1996 at 12, 30, 50, 65, 80, 95 and 110 d.a.p. and thereafter every 10 days including the day on which ripening was first observed and the day of harvesting of the marketable fruits. In 1995 the sampling interval was 30 days. The consumable stages of fruit development can be Bissr, Rutab or Tamr. Table 3-1 shows the typical stages during growth and ripening of date fruits. Plate 3-5 shows the ripe stages.

TABLE 3-1 STAGES (TYPICAL) DURING GROWTH AND RIPENING OF FRUITS IN CV KHALAS

Name	*Stage*	*Colour*
Khimri	0-110 days: rapid growth	green
Khalal	110-130 days: physiological maturity and max.size	shade of yellow
Bissr or last Khalal	130-150 days: late maturity, ripening starts	fully formed
Half Rutab	150-160 days: semi ripe	loss of Khalal colour in the apical half of the fruit
Full Rutab	160-170 days: ripe	loss of Khalal colour in the full fruit
Tamr	170-177 days: overripe	dark brown or black

Plate 3-6 *Dates in different stages of ripening.(top: cv Khalas, bottom: cv Khasab)*



Fruits of cvs Khalas (upper, yellow) and Khasab (lower, red) in different stages of ripening. The lighter colour is the colour of mature fruits and the darker colour appears when fruits enter into the half Rutab stage with about half the fruit becoming dark and soft. A full dark and soft fruit is in the full Rutab stage.

3.7.1 Histological examinations

The classical micro technique procedure given by Jensen (1962) was followed using ovaries which were picked and from which the pericarp was cut away, so that a block remained which contained the embryo sac.

Methyl green/pyronin was used to stain nucleic acids.

The material was examined using a compound microscope and ocular and stage micrometers, for which the ocular micrometer was calibrated for magnifications of 50, 100, 400 and 100 times. A Zeiss camera was used to make photographs as slides and colour prints.

3.7.2 Analysis of ovaries by High Performance Liquid Chromatography

A similar method (Davis, 1968) as outlined in Section 3.5.4. was used to extract and measure endogenous phenols, gibberellin-like substances, indole acetic acid and abscisic acid.

Instead of pollen grains, entire ovaries (5 g) were picked freshly 24 hours and 14 days after pollination, ground in a blender and mixed with 25 ml absolute methanol and kept at -20 °C for 24 hours. Thereafter the same methods as described for pollen grains was used.

3.7.3 Determination of fruit and seed fresh weight and dimensions

Samples of 6 fruits each per bunch were collected every 15 days after pollination in 1996 and 30 days in 1995. Measurements were taken on these 6 fruits and their seeds and the mean value was recorded as one observation. Fruits were cut open to measure the seeds and another 6 fruits, which were kept complete and sealed in plastic bags, were then placed in the deep freezer. About 30 g of fresh

weight material was collected from each bunch, vacuum freeze dried using an Edwards 4K Modulyo freeze drier and stored for future analysis and reference.

Fruit size was measured as fruit length from apex to base and width as the lateral diameter using a vernier calliper.

Fruit volume was determined by immersing a known number of fruits in a measuring cylinder containing water. The cylinder was shaken to release any air bubbles and the raise in water level was noted as ml-volume. The result was divided by the number of fruits to obtain the mean fruit volume.

Fruit and seed fresh weight were measured using an electronic scale and recorded to 1/1000th of 1 g.

3.7.4 Determination of sugar content

a. Rapid determination of total sugar content

In view of the large number of samples examined in the present study a Fisher hand refractometer was used at 20 °C for the rapid determination of the total sugar content.

b. Reducing sugars (glucose and fructose) and sucrose content

The method described in the Omanian Standard (1986) was followed using samples each containing about 2.5 g total sugars.

3.7.5 Maturity and ripening

a. Fruit colour

Fruit colour was determined by comparing with the coded horticultural colour chart of Graf (1985).

b. Determination of mature and ripe stages

The mature Bissr stage was indicated by the Khalal colour, whilst the half Rutab stage was indicated by the presence of about half of the fruit becoming pliable and dark. Full Rutab was indicated by almost all of the fruit becoming pliable and soft. The percentage of these stages relative to the initial number of ovaries and relative to all remaining fruits in the bunch was calculated.

3.7.6 Determination of moisture content and dry weight

The method described in the Omanian Standard (1986) was followed.

3.7.7 Determination of tannins

The method described by Burns (1971) was followed using a Unicam 8630 UV/VIS Kinetics spectrometer for readings at 500 nm. Pure catechin was used as the reference standard.

3.7.8 Determination of acidity

The method described by Lees (1975) was followed using a number of dates, which were peeled, the flesh removed from the seeds and then cut into small pieces. Acidity was calculated as malic acid %.

3.8 Environmental measurement and techniques

Measurements of maximum and minimum temperatures at 2 m and 5 cm height above ground level were recorded by a screened min/max. thermometer and a thermohygrograph. Wind speed and direction were. measured using an anemometer and wind vane. Relative humidity was also measured by a thermohygrograph. Sunshine hours were recorded by a crystal-type Sunshine Hour recorder. Evapotranspiration was calculated using the Pan Coefficient equation based on evaporation- pan readings obtained from a USDA-type E-pan (Achtnich, 1990).

3.9 Temperature with regard to growth

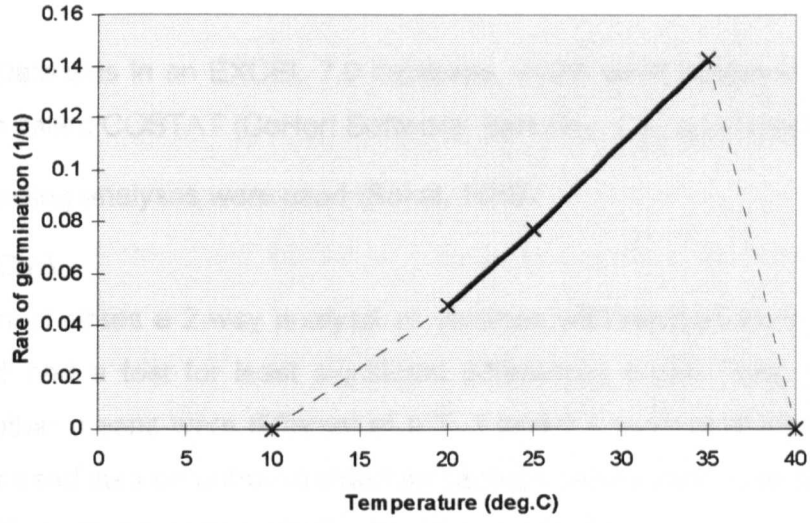
Cardinal temperatures:

Although numerous references are made to the Date Palm's tolerance to extremely high temperatures, no definite information and references are available about supra-optimal temperatures. The below experiment was designed to get an indication of this temperature by germinating Date Palm seeds at different temperatures. It is assumed that cardinal temperatures would be reflected in their germination response.

In October 1996, one year-old Date Palm seeds from a cross of the male cv Khori and the female cv Khasab were dug out from a depth of 5-15 cm in the soils immediately surrounding the irrigation basins. The seeds were subdivided into five lots of 30 seeds each, which were incubated at 10, 20, 25, 35 and 40 °C.

Five seed trays were set up using Levingtons F1 compost and each tray was well watered and allowed to drain overnight. Thirty seeds were placed evenly on the surface of the compost in six rows of 5 each. A thin layer of compost was added to just cover the seeds and finely sprayed with water before covering with black plastic. Trays were incubated at test temperatures until germination was detected. This Fison's incubator had been adapted by the University of Nottingham and its temperature control was accurate within 0.5 °C. Watering was done as necessary. The results are presented in the Figure 3-1 rather than in the results chapter as they provide only an indication of cardinal temperature. The rate of germination was calculated as the reciprocal of the number of days to 50 % germination.

Figure 3-1 *Germination rates of date palm seeds at different temperatures*



At 35 °C germination of 40 % of all incubated seeds took place after 7 days and increased to 60 % until the 9 th day. Lower and higher test temperatures resulted in delayed germination. The results indicate that the optimum test temperature for germination is 35 °C. The maximum temperature must lie between 35 ° and 40 °C, because at 40 °C almost no germination was found.

Bunch temperature:

Bunch temperature was measured during the 1996 season by using Tiny Talk data loggers for continuously recording the temperatures inside during fruit growth and development. Actual mean temperature in the north and east is about 3 % less than in the south while the min/max. average is 4% less for the north and almost the same as south for the east.

Thermal time calculation:

Thermal time or heat summation was calculated using a base temperature of 18 °C and Dowson's model (1982). The difference between the mean of daily minimum and maximum temperatures on the one hand and the base temperature on the other hand was added starting from the day of pollination.

3.10 Statistical analysis

Data was in an EXCEL 7.0 database, which were analysed using a computer program called COSTAT (CoHort Software, Berkeley, CA) and Genstat.

The following analyses were used (Sokal, 1969):

1. ANOVA

   In most cases a 2-way analysis of variance with replications was carried out (F-test) and a test for least significant differences (t-test) was used to determine whether means were different at a 5, 1 and 0.1 % level of significance. ANOVA was used also on untransformed percentage values as they were in the range 20-80 %, so that a normal distribution can be assumed.

2. Correlation

   The correlation coefficient r was estimated as a measure of linear relationship between two variables and the Standard Error of r was used as a measure of the margin of error in the estimate of r (t-test) at 5, 1 and 0.1% level of significance for the null-hypothesis (r=0).

3. Regression

   Linear regression was carried out to show the linear relationship between an independent variable, x, and a dependent variable, y. The relationship is y=a+bx. The standard error of b was calculated as a measure of the margin of error in the estimate of b. The significance of b, P(b=0), is mathematically the same as P(r=0). A t-test was carried out to determine whether b is significantly different than 0 at 5, 1 and 0.1 % levels of significance.

Sample tables of results are presented in Appendix 2.

4. Parental types

The experiments described were conducted using three male pollen types and two female types, which were applied to each other in all possible combinations. Interactions between male and female types are expected, so that an examination of male and female material is required. In the case of pollen, basic characteristics including size, chemical composition and pollen tube growth rate were measured whilst for the females, tree morphology (particularly those aspects that could be related to fruiting), flower behaviour and earliness of pollination, histological and chemical analysis of ovary tissues and fruit growth were described. Furthermore, because it is an objective of this study to analyze effects of the pollen type during pollination and later on during fruit growth and development, it is hoped that criteria pertaining to the parental material, particularly pollen type, can be determined which can be used for predicting pollen effects.

4.1 Examination of paternal material

The three pollen types in this study have been examined *in vitro* with regard to their size, physiological activity and chemical composition.

4.1.1 Size of pollen grains

The pollen grains of the date palm are spherical, so that the diameter provides a suitable indicator of size. None of the pollen grains examined showed any signs of germination before the test, so that they were considered to be in a stage of dormancy.

Table 4-1 MEAN, MINIMUM, MAXIMUM DIAMETERS (μm) AND COEFFICIENT OF VARIATION (%) OF DIFFERENT POLLEN TYPES

Pollen type	*Mean*		*Min*	*Max*	*Coeff.of Var.*
Al Arudsabba	19.83	b	16.8	22.4	9.47
Bahlani	19.55	b	14.0	22.4	10.71
Khori	21.47	a	16.8	28.0	13.41
GRAND MEAN	20.28				10.78

LSD @ P<0.01 = 1.6 μm

Table 4-1 shows that the pollen grains of the male type Khori were significantly larger (10% at P<0.01) than the grains of Al Arudsabba and Bahlani. It is noteworthy, that in species of *Nicotiana* with a smaller pollen grain size, self-incompatibility is more common than in species with a larger size (Pandey, 1971). The coefficient of variation for Khori was higher than for the other two types.

Khori's larger pollen grain size may indicate a lower level of incompatibility and a higher ploidy level (Stanley, 1974), whilst its higher variability may reflect a higher degree of heterozygosity.

4.1.2 Viability and germination of pollen grains

Pollen viability and germination at different temperature regimes was not affected by pollen type. The mean germination percentage at room temperature was 68 %. Furr and Ream (1968) observed *in vitro* that 70 % of all pollen grains germinated at a temperature of 26.7 ° C within the first 100 minutes after pollination in Date Palms. This temperature is approximately the same as the one prevailing during pollination in the present study.

4.1.3 Growth of pollen tubes

Pollen tube growth rates *in vitro* are possibly indicative of the vigour of a pollen type, i.e.: its ability to penetrate into stylar tissue and consequently the time required to reach the ovule and the female gamete.

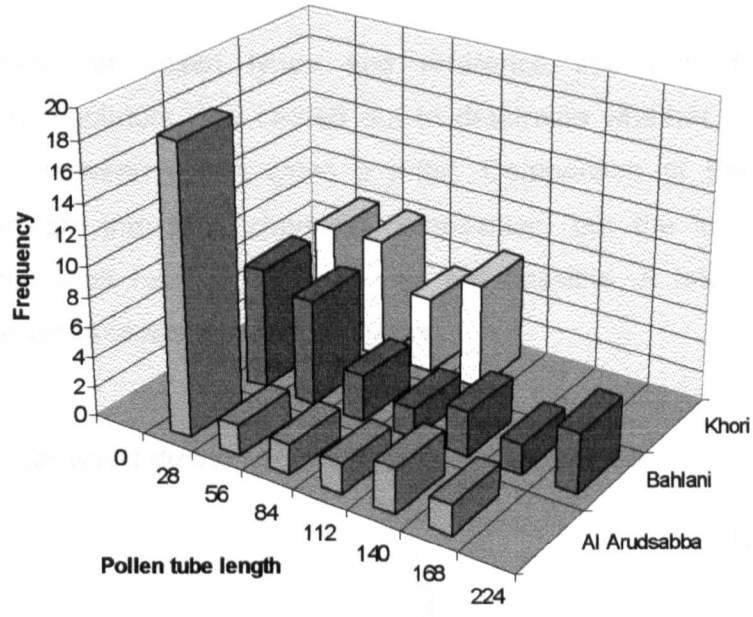
During its growth the pollen tube reportedly interacts with the style (Willemse and Vletter, 1995; Zuberi and Dickinson, 1985). Vigorous pollen types may overcome incompatibility mechanisms better than less vigorous ones (Rosen, 1971). Incompatibility in the Date Palm has been only observed in one specific intervarietal cross but the possibility of more far reaching incompatibilities exists (Al-Salih, 1987; Reuveni, 1986). Therefor, *in vitro* observations on pollen grains, which germinate in a medium lacking the binding proteins, recognition molecules and the environment specific to a particular female pistil and which govern incompatibility reactions in other plants, would permit at this stage only interpretations regarding the characteristics of the paternal type rather than regarding its interaction with the female type.

Table 4-2: MEAN OF POLLEN TUBE LENGTH (μm) AND COEFFICIENT OF VARIATION (%) AFTER 24 HOURS AT 21°C

Pollen type	*Mean*		*Coeff.of Var.*
Al Arudsabba	48	b	111
Bahlani	85	a	78
Khori	61	ab	56
GRAND MEAN	64		85

LSD @ P<0.05 = 28 μm

Figure 4-1 *Frequency distribution of pollen tube length after 24 hours at 21 °C*



Bahlani was significantly faster in pollen tube growth than Al Arudsabba (Table 4-2) and attained almost double the mean length in 24 hours. Khori was the most uniform of the three pollen types while Al Arudsabba was the most heterogeneous (Figure 4-1). Only 30% of Al Arudsabba pollen grains had tubes longer than 56 μm after 24 hours, compared to 43% and 48 % in Khori and Bahlani, respectively. Bahlani was the most vigorous of the three types, while Khori was the most uniform.

Assuming that *in vitro* observations would be reflected in pollen tube growth *in vivo,* it could be reasoned that faster pollen tube penetration would occur in a larger number of flowers pollinated with Bahlani, and possibly Khori, than with Al Arudsabba. However, it may be recalled from chapter 2 (Rosen, 1971), that possible incompatibility reactions in the style may be responsible for differences among pollen types regarding fertilization and consequently for pollen effects on fruit set. In the absence of such reactions, pollen-pistil interactions, many events mediated thereby and fertilization may occur early in the first two types and later in Al Arudsabba.

4.1.4 Chemical analysis of pollen

HPLC analysis of pollen types and reference standards for common endogenous growth regulators was carried out to determine whether compositional differences existed between pollen types *a priori*. Comparison of the absorption curves gave an insight into their chemical composition, but the identification of particular PGRs and their relative contents was not possible. A later chapter will examine the female types (ovaries) after pollination.

Figure 4-2 *Peaks observed during HPLC analysis of pollen types*

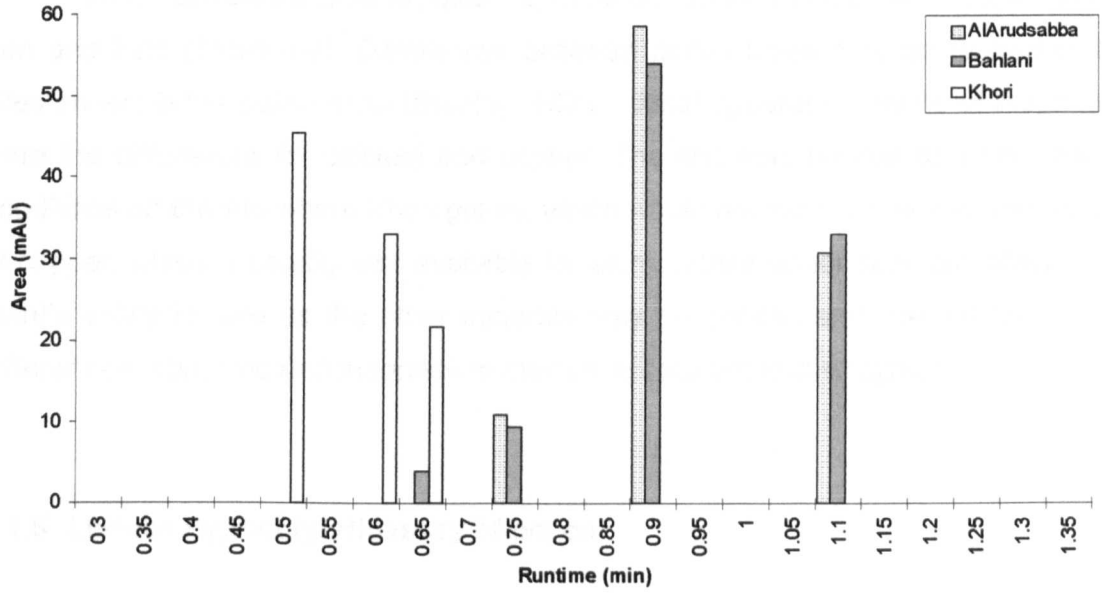


Figure 4-2 shows the retention time for major peaks and their proportional area of the integrated curve. The curve's area has been calculated from after the time of solvent peak appearance to the end of the HPLC run. It is evident that Al Arudsabba and Bahlani were similar in qualitative and quantitative composition, while Khori was distinctly different in both aspects.

Atomic absorption spectrometry revealed the following differences between pollen types with regard to some minerals:

Table 4-3: MINERAL CONTENT (% DRY WEIGHT) OF GRAINS OF DIFFERENT POLLEN TYPES

Pollen type	*K*	*Mg*	*Ca*	*Na*	*Fe (x10)*	*Zn (x 10)*	*Cu (x 10^3)*
Al Arudsabba	0.94	0.17	0.57	0.11	0.20	0.13	0.553
Bahlani	0.95	0.23	0.88	0.27	0.12	0.13	0.072
Khori	1.01	0.21	0.94	0.25	0.14	0.12	0.884

When compared to Al Arudsabba, Khori contained more of all minerals except Iron and Zinc (Table 4-3). Differences between pollen types may be related to the sites on which the palms grow (Stanley, 1971). Most apparent in terms of magnitude were the differences for calcium and copper. The first may be due to more alkaline conditions on the site where Khori grows, which would however not explain the excess of copper, which is usually less available for plant uptake under such conditions. The plant's ability to take up the other minerals may be genetic and responsible for the differences. Iron, zinc and magnesium may be associated with enzymes.

4.1.5 Lettuce Hypocotyl Bioassay of pollen

In addition to the chemical analysis a bioassay for the growth rate of the Lettuce hypocotyl was carried out which may indicate the presence of hormones, particularly gibberellins (Devlin, 1983; Hooley, 1994). Work with various plant species indicated that pollen is rich in endogenous GA (Looney, 1986). In this experiment hormones were extracted from pollen of the different types and the acidic fraction was applied to wetted disc of paper on which germinated lettuce seedlings were placed (Chapter 3: materials and methods). The gain in hypocotyl length after 8 hours is presented in Table 4-4.

Table 4-4: GAIN (%) DURING 8 HOURS IN THE LENGTH OF HYPOCOTYLS OF LETTUCE GROWING ON THE ACIDIC FRACTION OF POLLEN EXTRACTS

Pollen type	*Mean*	
Al Arudsabba	35.8	b
Bahlani	49.2	ab
Khori	57.3	a
Control	48.3	ab
GRAND MEAN	47.4	

LSD @ P<0.05 = 15 %

The growth rate on a medium from pollen type Khori was 63 % higher (P<0.05) than that of Al Arudsabba, while Bahlani and a control medium without pollen type was intermediate (ns). The results are indicative for a higher content of growth promoters, possibly GA, in Khori than in Al Arudsabba. The lettuce-hypocotyl test is sensitive to GAs (Hooley, 1994; Devlin 1983; Stanley, 1974).

Summary:

The experimental results provided clear evidence for differences between Khori and the other two pollen types with regard to physiological and compositional characteristics. The difference was most apparent between Khori and Al Arudsabba in all aspects. Bahlani was intermediate in all aspects except pollen tube growth. Khori had the largest pollen when compared to the other two types which were similar in size, while it had the most uniform rate of pollen tube growth. Assuming that *in vitro* observations are indicative of events occurring during pollination, pollen tubes of Bahlani would reach the ovule earliest, followed by Khori then Al Arudsabba. The chemical composition of pollen of the type Khori as revealed by HPLC was distinctly different from the other two types which were similar to each other. Chemical analysis and a bio-assay of the pollen types showed that Khori had a comparatively higher content of minerals and possibly also of gibberellins or other growth promoters. GA in pollen has been reported to control pollen germination and pollen tube growth (Looney, 1986).

4.2 Examination of female cultivars

The two female types Khasab and Khalas Omani in this study were examined with regard to characteristics which are thought to have an influence on fruit growth and development.

4.2.1 Leaf area and number

In the date palm, the inflorescences and bunches are sinks while the leaves are the major source for photosynthates (Sedgley, 1989) and it is known (Bacha, 1986) that leaf-to-bunch ratio is related to yield and mean bunch weight. The measurements in the present study were on leaf area and number, which was related to bunches. This should provide a general basis for comparing fruits between years, which grow on palms with comparative leaf-to-bunch ratios. Similarity is a necessary prerequisite for the direct comparison and interpretation of observations on fruit growth and development later in this study.

It is necessary to recall that the procedure followed in this study was designed to ensure as much as possible retention of only the photosynthetically active leaves. The fronds (leaves) are borne in a crown on top of the trunk, where they arise from buds produced in a year and they have a life of three to seven years (Dowson, 1982). Old and dead leaves are not shed, but are removed under cultivation (Nixon, 1966). Nixon and Wedding (1956) studied the photosynthetic efficiency of leaves of different age and found that leaves of four years' age were only about 65% as efficient per unit leaf area as those one year old. In the experimental trees, as in all commercial date palms, only the photosynthetically active leaves were retained. During the present study leaves were removed as soon as the leaflets had dried and the rachis had started turning brown. The age of the removed leaves was between 4 and 5 years. Observations on active leaves were taken at the beginning of the season.

Table 4-5: MEAN LEAF AREA (m^2), LEAF NUMBER AND RELATIONSHIP WITH THE MEAN NUMBER OF BUNCHES RETAINED IN A TREE IN DIFFERENT CULTIVARS AND YEARS.

CV: Khasab

Year of study	*Area per leaf*	*No.of leaves*	*Leaf area per palm*	*Number of bunches*	*Leaf Area per bunch*	*No. of leaves per bunch*
1995	2.61	71.5	185.6	11.7	15.9	6.1
1996	2.45	78.5	192.1	11.7	16.4	6.7

CV: Khalas

Year of study	*Area per leaf*	*No.of leaves*	*Leaf area per palm*	*Number of bunches*	*Leaf Area per bunch*	*No. of leaves per bunch*
1995	3.03	64	194.2	10.5	18.5	6.1
1996	3.03	72	218.1	11.3	19.3	6.4

Leaf area and leaf number per bunch are important criteria of the source and were expected to influence fruit size and number in the following year. A comparison of leaf area per bunch (Table4-5) revealed that there was hardly any change over the two study years in cvs Khasab and Khalas. Khalas had a higher leaf area per bunch than Khasab.

While leaf area per bunch and leaf number per bunch are criteria attributed to the source (leaves) of photosynthates, they do not say much about the sink, i.e.: the bunch. It must be emphasized that the number of bunches/tree *per se* is no measure of sink effects, because the number and weight of fruits have to be taken into account. However, the number of bunches is indicative of the potential crop load which a palm tree is able to bear. This was here an important economic consideration.

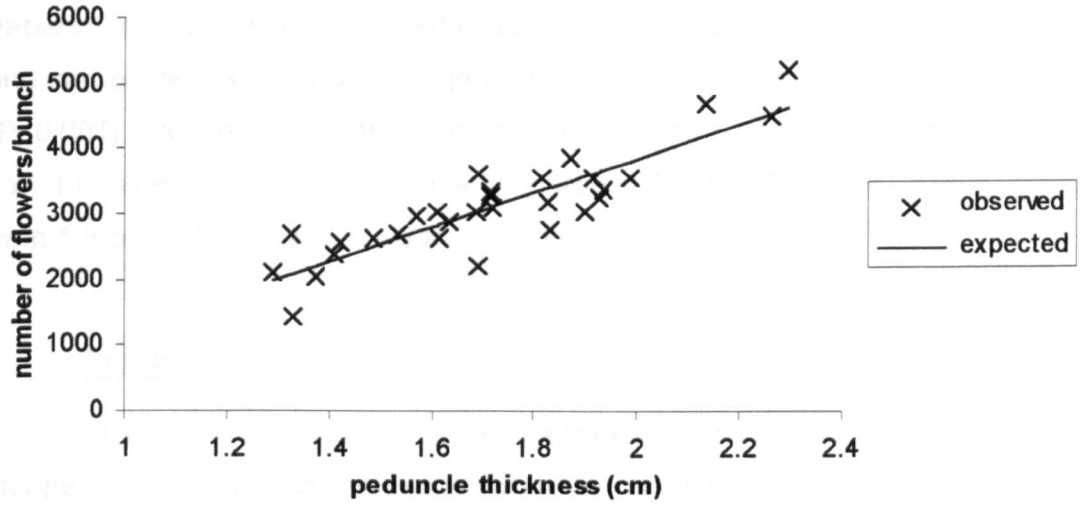
4.2.2 Number of flowers and peduncle size

An examination and understanding of the number of flowers and of the peduncle's size of the spathe was considered necessary to determine whether the

number of fruits per bunch or the percentage ovaries retained out of the initial number of ovaries should be used for fruit set examination. During differentiation of buds into generative buds the inflorescence's organs including peduncle, the branches thereof and the floral primordia develop. It is reasonable to assume that in a fertilized inflorescence, flower number determines the strength of the sink effect and the potential fruit load of the bunch, while the peduncle's size limits the hydraulic rate of flow of photosynthates from the source to the sink especially during periods of high requirement. Reuveni (1986) associated specific capacities of the vascular system with the peduncle diameter. Both criteria (flower/fruit number and peduncle size) are, in turn, expected to influence fruit growth. Results obtained on two cultivars are presented in Figure 4-3 and Figure 4-4.

CV: Khasab

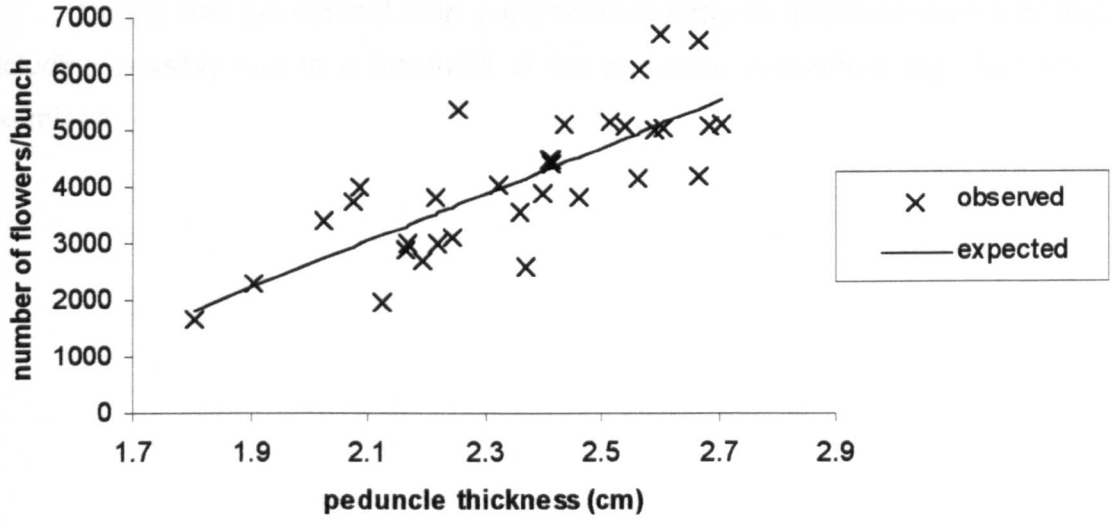
Figure 4-3 *Peduncle thickness and number of flowers in cv Khasab*



In this cultivar a very significant ($P<0.001$) correlation between the thickness of the peduncle (x) and the number of flowers (y) was found and can be represented by the linear equation $y= -1,371 + 2,607\ x$, where $r^2=0.774$. While the product of (width) x (thickness) is also correlated ($P<0.001$), peduncular width is not as strongly and clearly correlated. The mean flower number is 3,105 per bunch ranging from 2,053 to 5,200, while thickness ranges from 1.3 cm to 2.3 cm with a mean of 1.7 cm.

CV: Khalas

Figure 4-4 *Peduncle thickness and number of flower in cv Khalas*



Also in this cultivar a very significant ($P<0.001$), but even stronger correlation between the thickness of the peduncle (x) and the number of flowers (y) was found and can be represented by the linear equation $y= -5,617 + 4,126\ x$, where $r^2=0.604$ ($P<0.001$). Peduncular width is not as strongly and clearly correlated. The mean flower number is 4,105 per bunch ranging from 1,659 to 6,696, while thickness ranges from 1.8 cm to 2.7 cm with a mean of 2.4 cm.

Summary:

The relationship between peduncle thickness and number of flowers was much steeper in Khasab than in Khalas, while the number of flowers per inflorescence increased less than in Khalas.

It is worth mentioning that the present study does not employ thinning of fruits within bunches to attain a given number or percentage of flowers per bunch to achieve statistical uniformity. What is more important is to reduce intraplant competition and biennial bearing effects by limiting the number of bunches. The peduncle's cross sectional area is indicative of the number of fruits carried by a bunch. It is reasonable to assume that it is a limiting factor for the flow of sap particularly in period of rapid growth and high temperatures, both of which increase

the demand for sap. The peduncle is the natural "bottle neck" between source and sink. Given the above described strong correlation it is reasonable to assume that better uniformity exists between unthinned bunches because this provides physiological, rather than numerical uniformity.

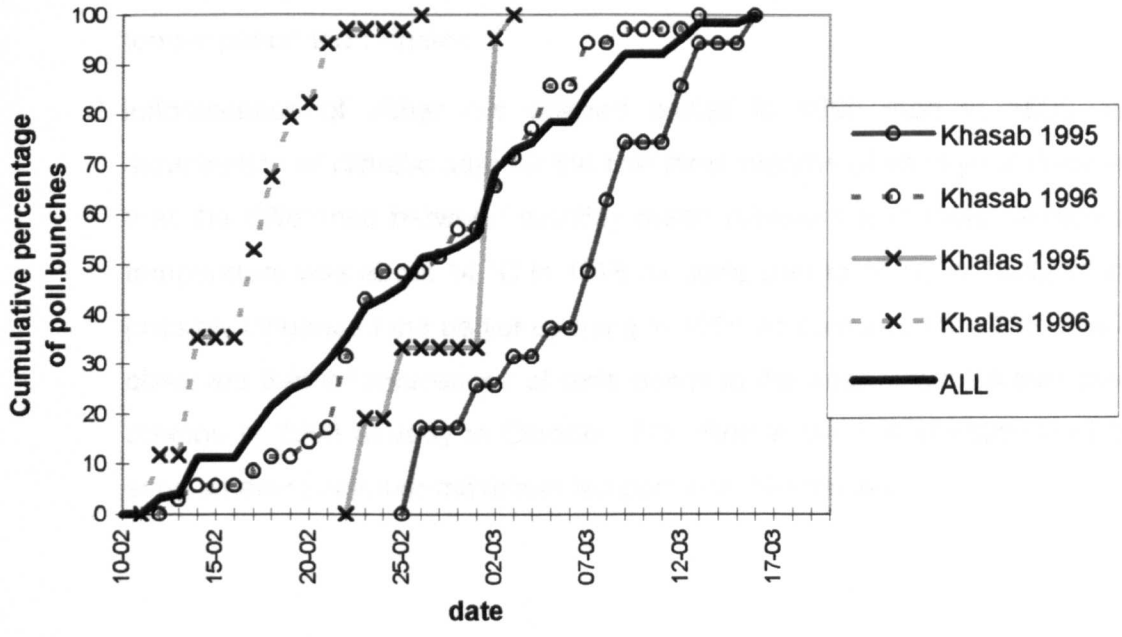
During later growth fruit drop is expected to occur in response to several factor including possibly due to a threshold of the peduncle to conduct sap. This will be examined.

4.3 General growth and development

4.3.1 Date of pollination

The date of pollination is the date of the opening ("cracking") of the inflorescence and is in this study "day zero" for all observations and for the calculation of thermal time. An understanding of its occurrence during and over the years and in different varieties is necessary to relate meteorological conditions to different stages of growth and development.

Figure 4-5 *Cumulative percentage of bunches pollinated at the day of opening of the inflorescence during January to March in different cultivars and years*



CV: Khasab

In 1995 it took about 3 weeks from end February to mid March for all inflorescences to open. 50% had opened and been pollinated by 7.March.

In 1996 it took 4 weeks and 50% was reached already on 27.February.

CV: Khalas

In 1995 it took about 10 days from 22.February to 2.March for all inflorescences to be pollinated with the majority placed near the end of this period.

In 1996 it took 13 days from 11. To 24.February with 50% having been pollinated on 17.February.

Figure 4-5 shows that inflorescence emerge earlier in cv Khalas than in cv Khasab and in either cvs earlier in 1996 than in 1995.

Summary:

1. The opening of inflorescences in Khasab occurs later and extended over a longer period than Khalas.
2. Inflorescence of either cvs opened earlier in 1996 than in 1995. An examination of climatic data for the first three months of each year revealed that the difference between monthly mean minimum and mean maximum temperature was about 14 °C in 1995 as compared to 10 °C in 1996, which possibly influenced the earlier opening in 1996 as compared to 1995. I have observed that inflorescences of date palms in the subtropical Salalah plain opened in 1996 already in October. The climate there is characterized by even smaller minimum-maximum temperature differences.

4.3.2 Histological examination of fertilized ovaries of the cv Khalas

The objective of this study was to examine pollen effects and to suggest mechanisms causing early effects, possibly due to the contribution of growth regulators by the pollen, and late effect due to genetic contribution. It is necessary to histologically examine the ovary during its development, so as to determine at which time the diploid embryo and triploid endosperm start developing. Apart from the synergids these are the two bisexual tissues which result from the fusion of maternal and paternal genetic material. All other tissues of the ovary are maternal. Plates 4-1 to 4-6 show micrographs taken in the cv Khalas, Plate 4-7 major seed tissues.

Plate 4-1 Zygote, 30 days after pollination; (x400)

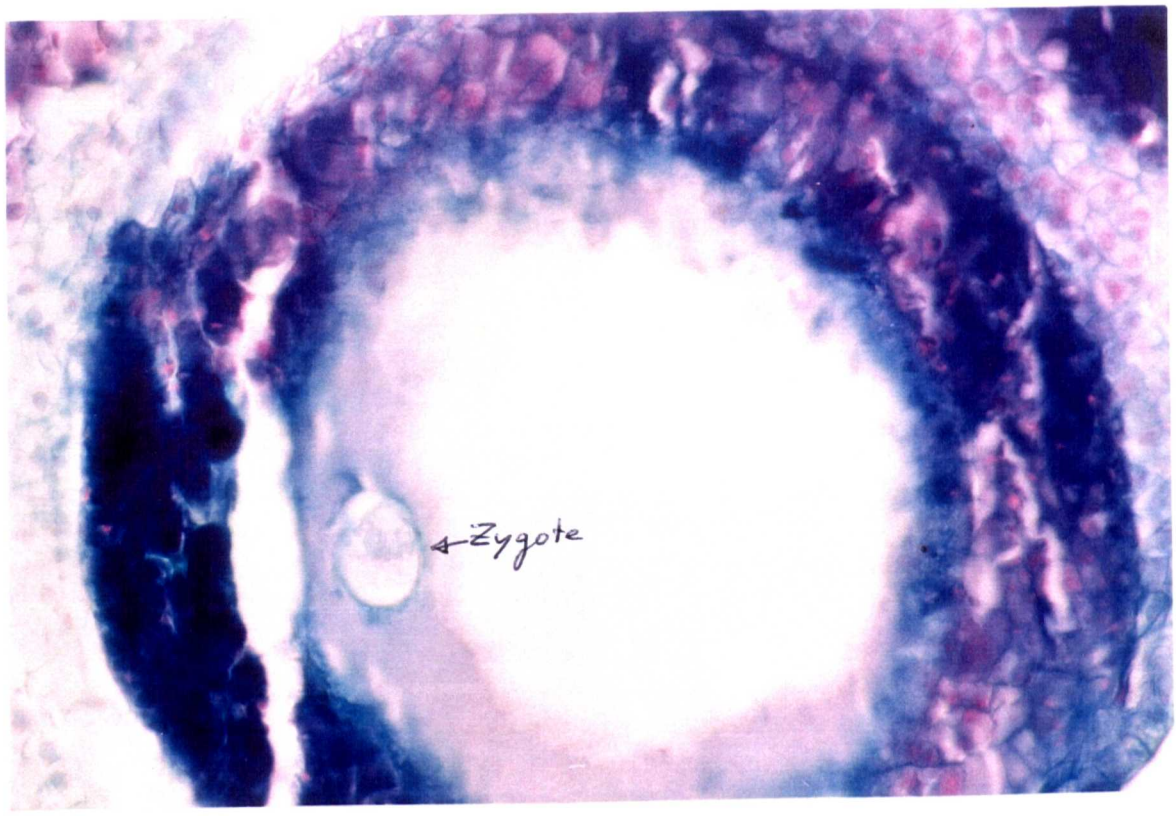


Plate 4-2 Four-celled proembryo at 35 d.a.p.. The micropyle is visible by the dark stained adjacent isthmus; (x400)

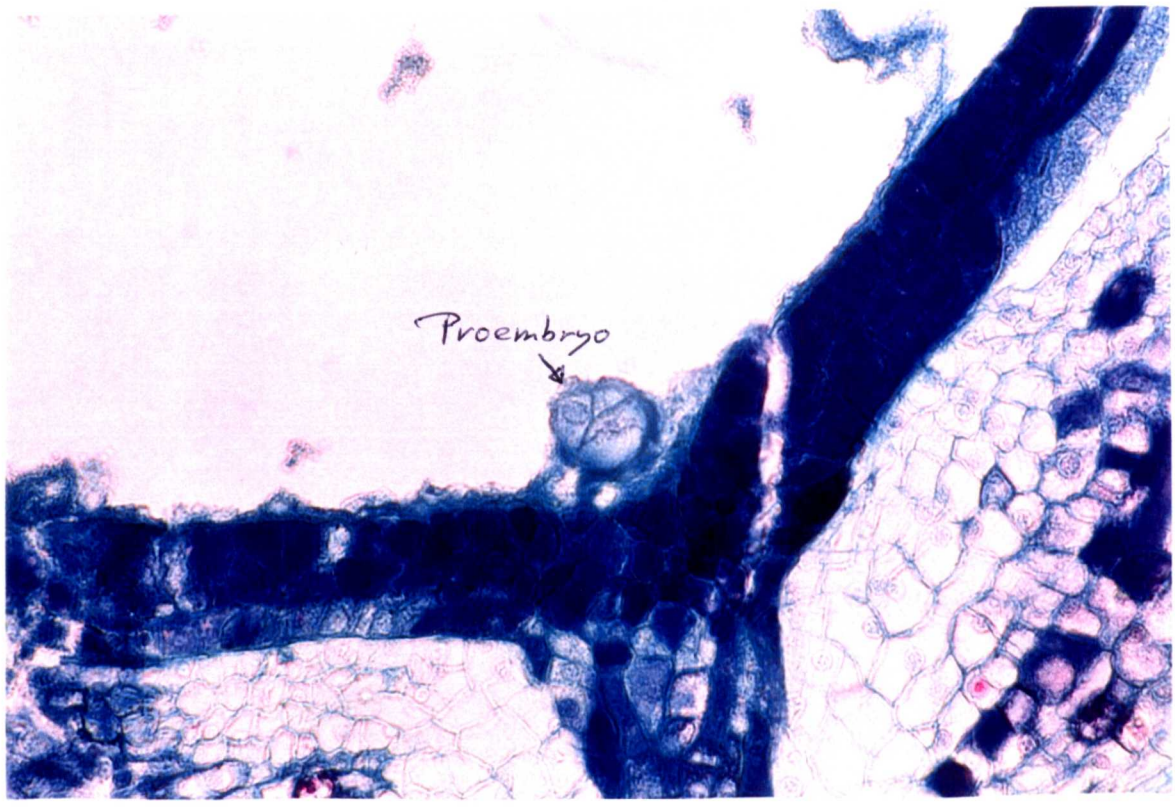


Plate 4-3 Proembryo and possibly a suspensor in a region with active cell division (green stained area) at 40 d.a.p.; (x400)

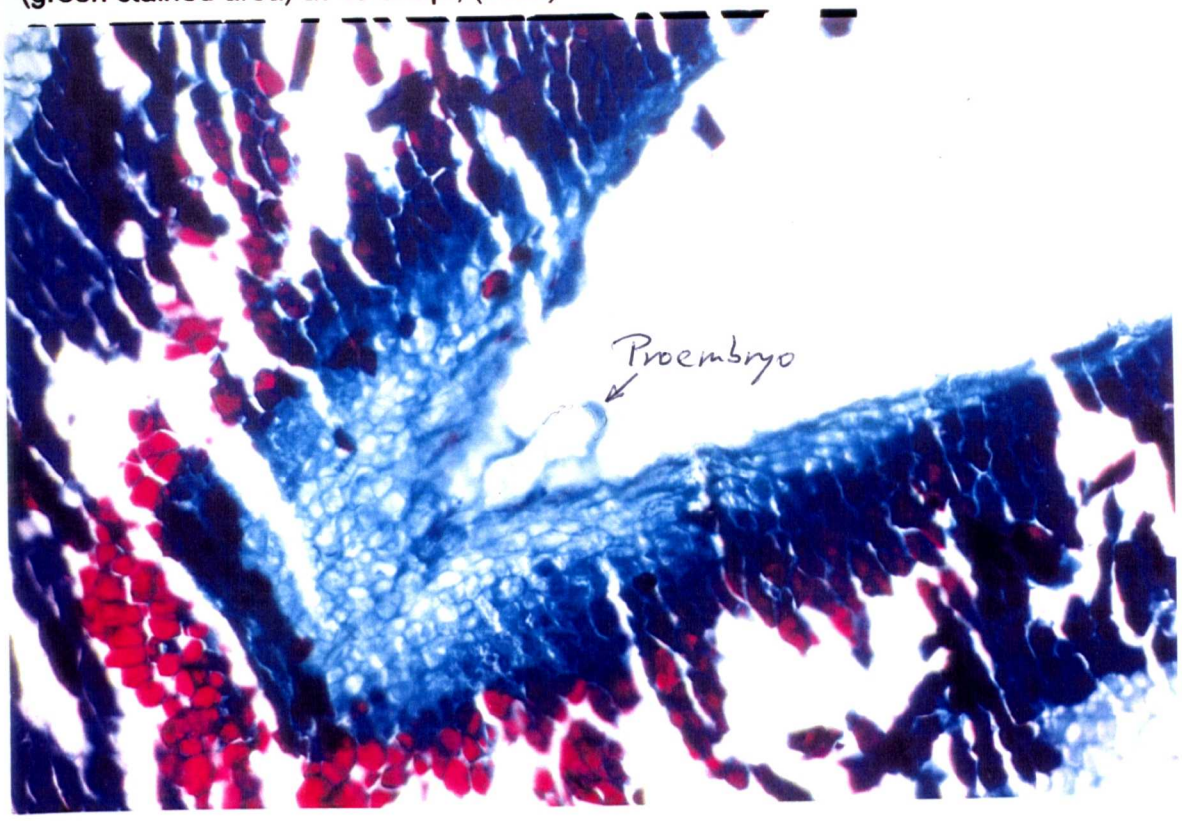


Plate 4-4 Nuclear endosperm cells in a syncytium at 50 d.a.p.; (x400)

Plate 4-5 Cellular endosperm lining the embryo sac at 55 d.a.p.; (x400)

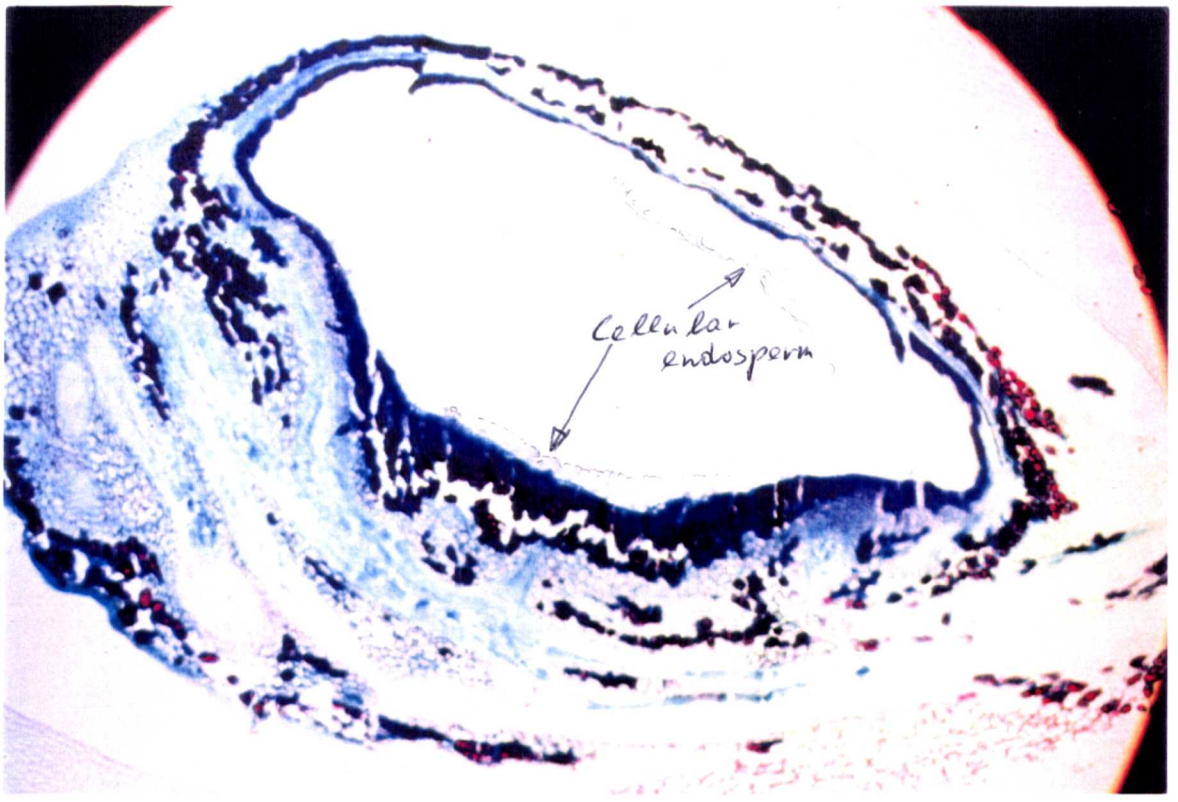


Plate 4-6 Invagination possibly an embryo at 60 d.a.p.; (x25)

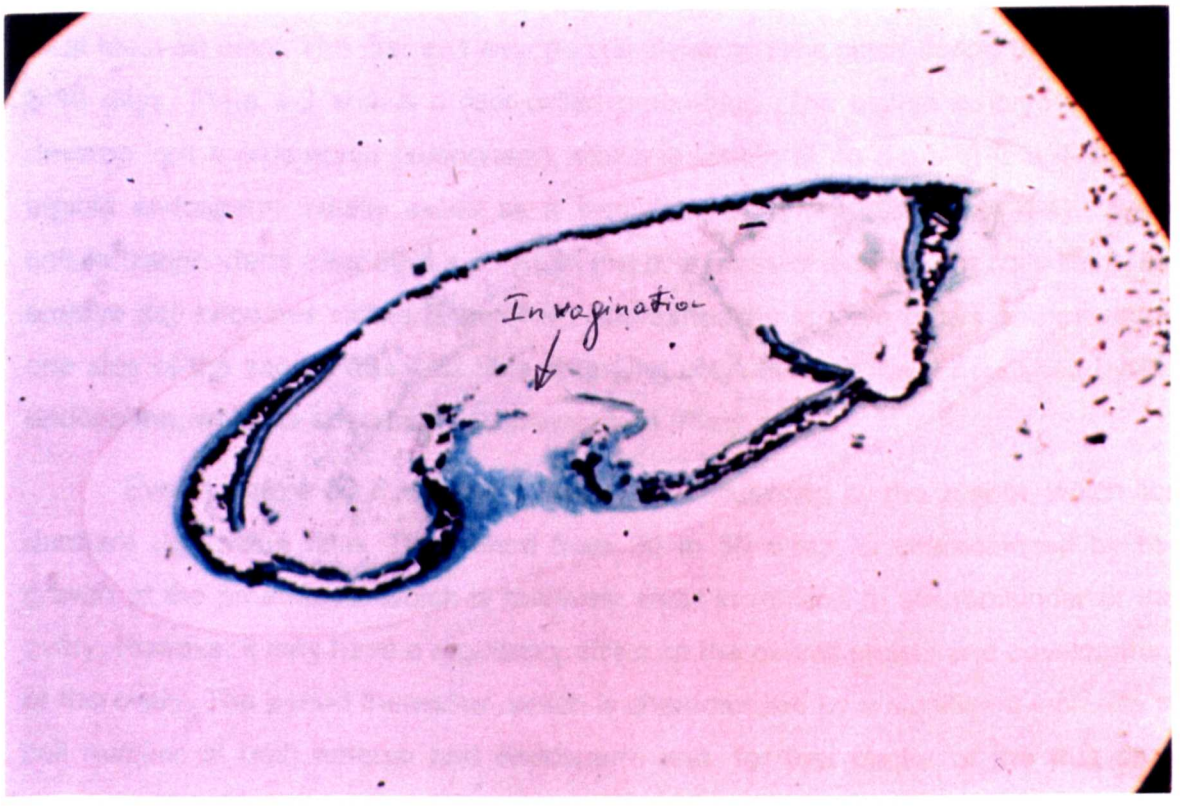
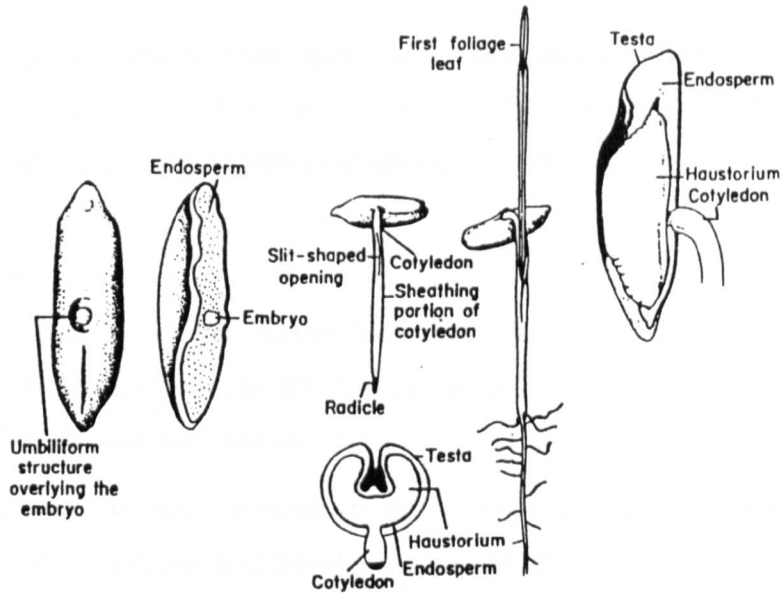


Plate 4-7 Seedling and cross section through the seed with haustorium absorbing the endosperm.



The above plates set a time sequence for events during embryogenesis which are relevant to this study. The diploid zygote (Plate 4-1) remains dormant for a period of at least 30 days. The first and second cell divisions take place during the following 5-10 days. Plate 4-2 shows a four-celled proembryo. The diploid embryo starts to develop into a proembryo (suspensor), which is visible at 40 d.a.p. (Plate 4-3). The triploid endosperm initially exists as a syncytium of few nuclei (Plate 4-4) , while cellularization starts after 50 d.a.p.. At 55 d.a.p. a mass of endosperm cells lining the embryo sac becomes visible (Plate 4-5). Thereafter the embryo grows and moves to one side of the seed (Plate 4-6). The emerging cotyledon is initially nourished by the endosperm, which is absorbed by a haustorium (Plate 4-7).

Events before 30 d.a.p. are probably not influenced by the zygote, which lies dormant up to that time. The period from 30 to 50 d.a.p. is characterized by the growth of the proembryo, which is relatively small in relation to the remainder of the ovary. However it may have a regulatory effect on the overall growth and development of the ovary. The period thereafter, which is characterized by a significant increase in cell number of both embryo and endosperm and, for that matter of the fruit as a whole, is most likely influenced by the genetic contribution of the pollen.

4.3.3 Fruit and seed weight for each cultivar

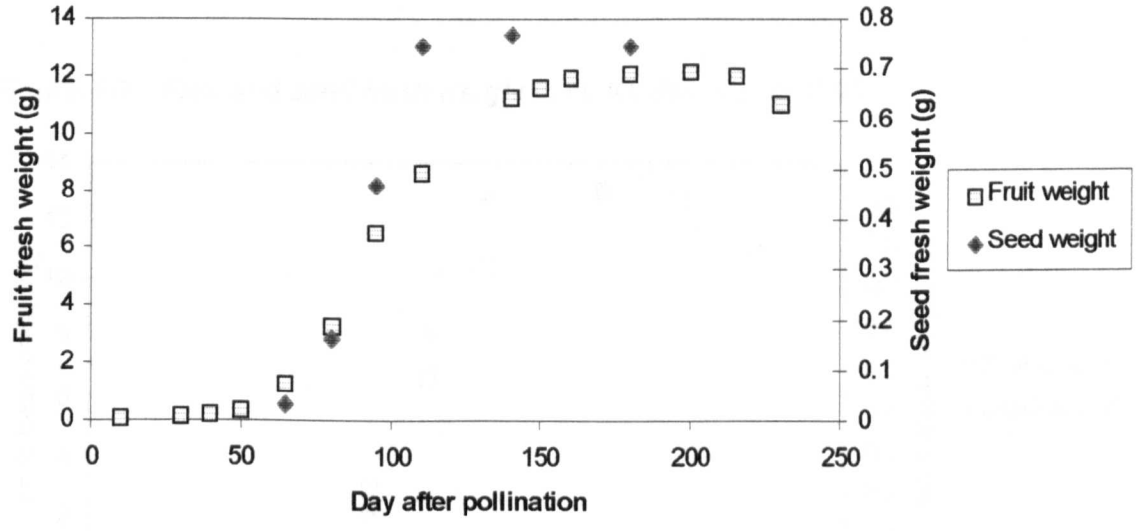
The growth rate of fruits and their seeds varies depending on the stage of development and cultivar. For the further discussion and the identification of phases common to all cvs it is necessary to examine the growth curve for fruits and seeds.

CV: Khasab:

Khasab is a very late cultivar producing red fruits, which are consumed in all stages from Rutab to Tamr, in some areas also as Bissr. The fruit can reach a fresh weight of 13 g as was the case in 1995.

Figure 4-6 shows the fresh weight of the seed and whole fruit in cv Khasab during 230 days of growth and development in 1996.

Figure 4-6 *Fruit and seed fresh weight in cv Khasab during 1996*



Khasab fruits grew very little for 50 days but then there was markedly accelerated growth until about 90 d.a.p.. Colour changes from green to red appeared between 120-140 d.a.p.. Although a few fruits reached maturity and Bissr stage already at 140 d.a.p., the majority required 160-180 days to reach full maturity as indicated by the cardinal red mature colour. Thereafter most fruits passed through the stages Bissr (180-200 d.a.p.), half-Rutab (200-230 d.a.p.) and Rutab (215-245 d.a.p.). From 200 d.a.p. onwards the majority of fruits lost moisture and the reduction in fresh weight continued until the 250 th d.a.p..

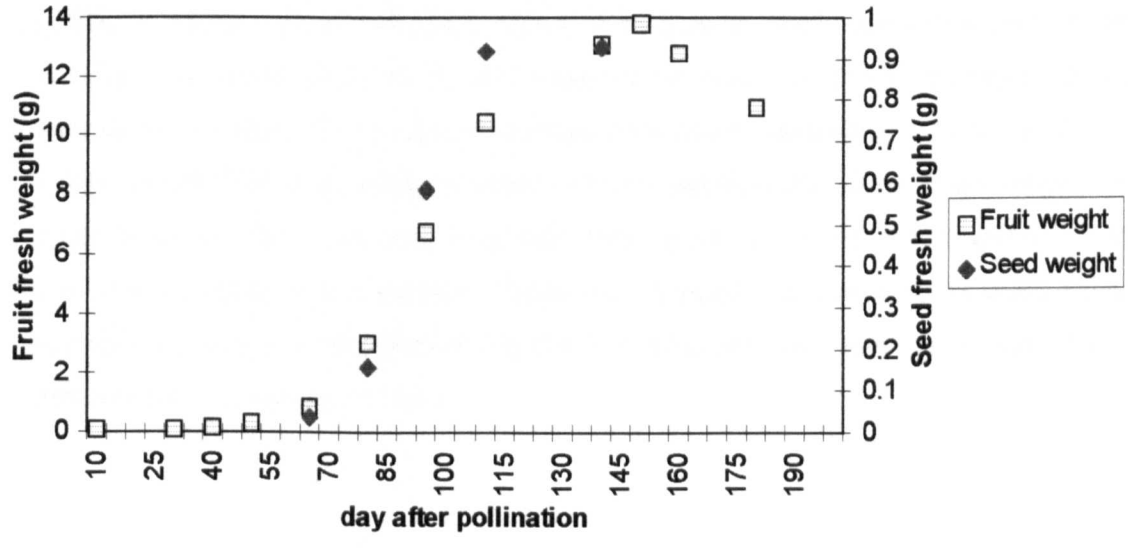
The seed behaved like the fruit during the first 50 days and grew at the fastest rate between 65 and 95 d.a.p.. At 110 d.a.p. its colour started changing from a cream white to golden yellow and reached 98% of its maximum weight which remains thereafter about the same. The mature brown and gold colour had developed by 140 d.a.p.. The growth curve for 1995 was similar except for the reduction in fresh fruit weight commencing from 180 d.a.p..

CV: Khalas

Khalas is a medium late cultivar producing yellow fruits, which are consumed in all stages from Bissr to Tamr. The fruit can reach a fresh weight in excess of 15g as was the case in 1995.

Figure 4-7 shows the fresh weight of the seed and whole fruit in cv Khalas during 180 days of growth and development in 1996.

Figure 4-7 *Fruit and seed fresh weight in cv Khalas during 1996*



Similar to Khasab the first 50 d.a.p. were characterized by very little growth of both entire fruit and seed. Thereafter the growth rate increased until about 90 to 95 d.a.p.. The seed reached its maximum fresh weight around 110 d.a.p.. In the fruit this occurred at 150 d.a.p. corresponding to about 14 g fresh weight. The seed's fresh weight remained constant, while the fruit started losing moisture and fresh weight. The

colour of the fruit started changing from green to yellow between 110 and 120 d.a.p. and Bissr stage fruits were produced from 120 to 170 d.a.p. onwards, with the maximum being produced around 140-150 d.a.p.. Half Rutab and Rutab fruits appeared after 150 d.a.p. and they were the maximum fraction of the bunch's crop load at 170 d.a.p. The seed started changing colour at 110 d.a.p. and all seeds had attained the golden and brown mature colour at 140 d.a.p..

Summary:

1. In both cvs fruit fresh weight followed a sigmoid curve. In 1996 fruits of cv Khasab reached a maximum fresh weight of about 12 g at 200 d.a.p., whilst those of cv Khalas reached about 14 g at 150 d.a.p. Thereafter, fruit fresh weight decreased.
2. Seeds of both cvs reach their maximum fresh weight between 110 and 140 d.a.p., but no or little weight loss occurred thereafter.
3. Fresh fruit weight at 140 d.a.p. in cv Khalas was significantly higher (*) in 1995 (15.6 g) when compared to 1996 (13.5 g), while this value was similar in both years for cv Khasab . The difference in cv Khalas was not observed before 110 d.a.p. and may have been due to lower minimum relative humidity (43.6% in 1995, 32.0% in 1996) 130 to 140 d.a.p. On 4. And 5.June 1996, hot winds brought the maximum temperature to 45 °C and evaporation readings of 10 mm/day (USDA E pan) were recorded. These circumstances increased transpiration from the plant at a time at which an increasing number of fruits reached the softer Bissr stage. This could have caused a reduction in growth rate resulting in lower fresh weights at the end of the period. A comparison (Table 4-6) reveals that dry weights were similar during the years, thereby confirming that the difference in fresh weight was due to differences in moisture content.

Table 4-6 COMPARISON OF DRY WEIGHT OF ENTIRE FRUIT IN CV KHALAS BETWEEN TWO YEARS

Year	Mean (g)	
1995	3.71	a
1996	4.06	a

In comparison, in cv Khasab no such differences were observed, possibly because at that time (4. And 5.June) the fruits of cv Khasab were still in the hard Khimri stage. The 140 th d.a.p. (later referred to as stage 3) in cv Khalas corresponds in 1995 to the 130 th d.a.p. (later referred to as stage 2.5) and in 1996 to the 133 rd d.a.p. (mean) in Khasab.

4.3.4 Definition of stages

Fruit and seed growth are characterized for both female cultivars by typical sigmoid growth curves, which have stages or phases corresponding to periods distinguished by particular growth rates, colour changes, stages of maturity and ripeness. For the examination and discussion of pollen effects it is therefore necessary to compare variables of fruit growth and development at physiologically corresponding stages.

The examination of the main and particularly the interaction effects of sampling date (dap), pollen type and female cultivar on fruit fresh weight for the year 1996 as presented in Tables 4-7 to 4-10 supports this approach.

Table 4-7 ANOVA OF THE EFFECTS OF DATE OF SAMPLING (dap), POLLEN TYPE (poll) AND FEMALE CULTIVAR (cv) ON OVERALL FRUIT FRESH WEIGHT IN 1996

Source	*df*	*Type I SS*	*MS*	*F*	*P*
Main Effects					
dap	3	4272.478857	1424.1596	1500.7113	.0000 ***
poll	2	23.18890068	11.59445	12.217677	.0000 ***
cv	1	14.67528403	14.675284	15.464112	.0001 ***
Interaction					
dap x poll	6	19.42998004	3.23833	3.4123972	.0038 **
dap x cv	3	30.07399381	10.024665	10.563512	.0000 ***
poll x cv	2	3.744945181	1.8724726	1.973122	.1435 ns
dap x poll x cv	6	6.612680986	1.1021135	1.1613545	.3316 ns
Error	120	113.878771	0.9489898<-		
Total	143	4484.083413			

Table 4-8 EFFECT OF DATE OF SAMPLING ON OVERALL FRUIT FRESH WEIGHT (g) IN 1996

dap	*Fruit fresh weight (g)*	*n*	
40	0.17	36	c
80	3.09	36	b
140	12.20	36	a
160	12.45	36	a

LSD @P<0.001 = 0.77 g

Table 4-9 EFFECT OF POLLEN TYPE ON OVERALL FRUIT FRESH WEIGHT IN 1996

Pollen type	*Fruit fresh weight (g)*	*n*	
Al Arudsabba	6.56	48	b
Bahlani	6.85	48	ab
Khori	7.52	48	a

LSD@ P< 0.001 = 0.7 g

Table 4-10 EFFECT OF FEMALE CULTIVAR ON OVERALL FRUIT FRESH WEIGHT IN 1996

Female cv	*Fruit fresh weight (g)*	*n*	
Khasab	6.66	72	b
Khalas	7.30	72	a

LSD @ P< 0.001 = 0.55 g

All main effects are highly significant (P<0.001). Fruit weight (Table 4-8) increases with a later sampling date and levels of toward maturity. Pollen type Khori caused about 15 % higher overall mean fruit fresh weight than Al Arudsabba (Table 4-9), while the effect of pollen type Bahlani is intermediate. Fruits of the cv Khalas were about 9 % heavier than those of the cv Khasab (Table 4-10)..

The highly significant interaction between date of sampling and pollen type (P<0.01) is because response patterns of initial pollen effects differ from later ones.

Most importantly, the highly significant (P<0.001) interaction effect of date of sampling and female cultivar is due to the different growth curves of the two female cultivars in that observations at equal real times are on fruits in different stages of growth and development. It is therefore necessary to identify equivalent physiological stages to provide a basis for comparisons between varieties at times which are physiologically equivalent with regard to fruit growth and development.

The below defines common stages on an indexed basis. The criteria measured are the fresh weight and length of fruit and seed. Fresh weight rather than dry weight and size were chosen because they reflected the various endogenous and environmental conditions, which influenced fruit growth.

Stage 1: from day of pollination to end of lag stage

This stage started at the day of pollination and was characterized by very little growth of the ovary as a whole. Any pollen effects mediated by substances contributed to the ovule would be expected during this stage. The end of this period coincided with the time of endosperm cellularization and the commencement of seed growth and rapid fruit growth. Most unfertilized ovaries (triplets) dropped during this stage. The following periods were observed in Khasab and Khalas (Table 4-11).

Table 4-11 DURATION OF STAGE 1 (LAG PHASE) IN CVS KHASAB AND KHALAS

Cultivar	*Duration of Stage 1*
Khasab	0 to 50 d.a.p.
Khalas	0 to 50 d.a.p.

Stage 2: end of the lag stage to the inversion of the sigmoid growth curve

The rapid growth of both seed and entire fruit commenced and continued at an increasing rate up to a point from which the overall growth of fruits continued but at a diminishing rate. In the sigmoid curve for fresh fruit weight this was apparent as an inversion of its slope (Figures 4-6, 4-7, 4-8). Cellularization of the triploid endosperm took place during this stage and the embryo differentiated. Because most bisexual tissues (embryo and endosperm) formed during this stage, any pollen effects due to a genetic contribution by the pollen would be expected to appear during this stage. Some unfertilized triplets and seeded fruits dropped during this stage (Table 4-12).

Table 4-12 DURATION OF STAGE 2 (FIRST RAPID GROWTH PHASE) IN CVS KHASAB AND KHALAS

Cultivar	*Duration of Stage 2*
Khasab	51 to 90 d.a.p.
Khalas	51 to 90 d.a.p.

Stage 3: from the inversion of the sigmoid curve to the beginning of ripening

This stage was characterized by fruit growth at a decreasing rate and seed growth reaching an inversion point. Any genetically mediated pollen effects would be distinguishable during this and possibly the following period. The change in fruits from green to either red or yellow occurred during this stage and the seed attained its maximum fresh weight. Thereafter seed weight remained constant or even decreased slightly. Both fruit and seed attained their mature colours. The fruit reached its maximum fresh weight at the end of the stage. Some unfertilized triplets and seeded fruits dropped during this stage. The duration of this period (Table 4-13) depended on the cultivar.

Table 4-13 DURATION OF STAGE 3 (2^{ND} RAPID GROWTH PHASE) IN CVS KHASAB AND KHALAS

Cultivar	*Duration of Stage 3*
Khasab	91 to 200 d.a.p.
Khalas	91 to 150 d.a.p.

Stage 4: from the beginning of ripening to last harvest of the product

This stage was characterized by a decrease in fresh fruit weight and a seed weight which remained constant or even declined slightly. The loss of fresh weight was due to the loss of moisture during ripening and senescence. The fruit progressively ripened passing through the Half Rutab and Rutab stages. If it was retained in the bunch, it eventually shriveled reaching the Tamr stage. Many mature fruits can drop during this stage. The duration of this period depended on the time to the last possible harvest which depended on fruit drop and cultivar. Observations in the following ranges (Table 4-14) will be examined and discussed:

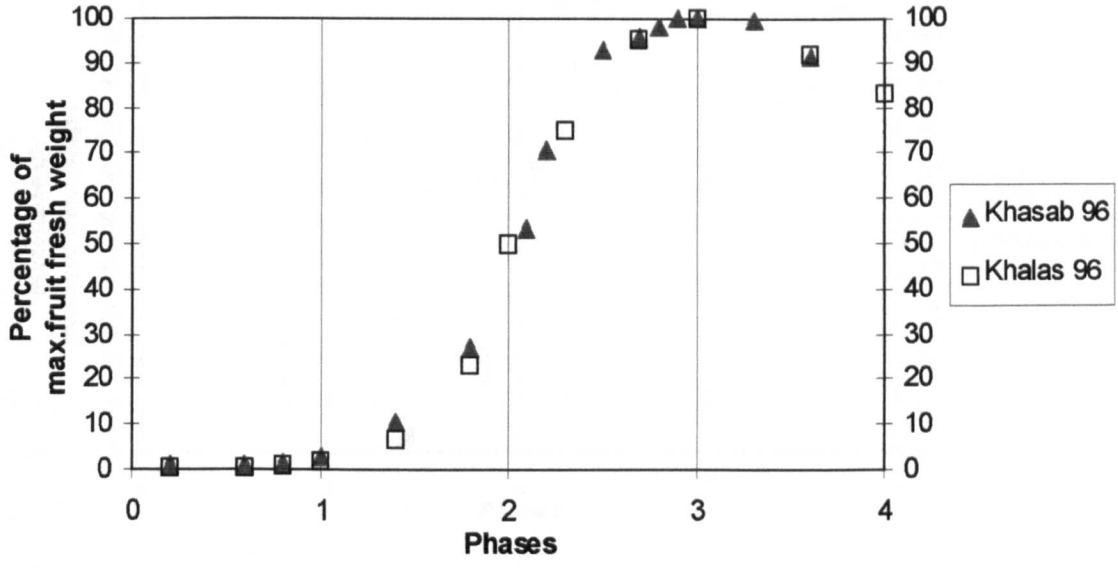
Table 4-14 DURATION OF STAGE 4 (RIPENING) IN CVS KHASAB AND KHALAS

Cultivar	*Duration of Stage 4*
Khasab	181 to 245 d.a.p.
Khalas	151 to 170 d.a.p.

4.3.5 Indexed fruit and seed weight

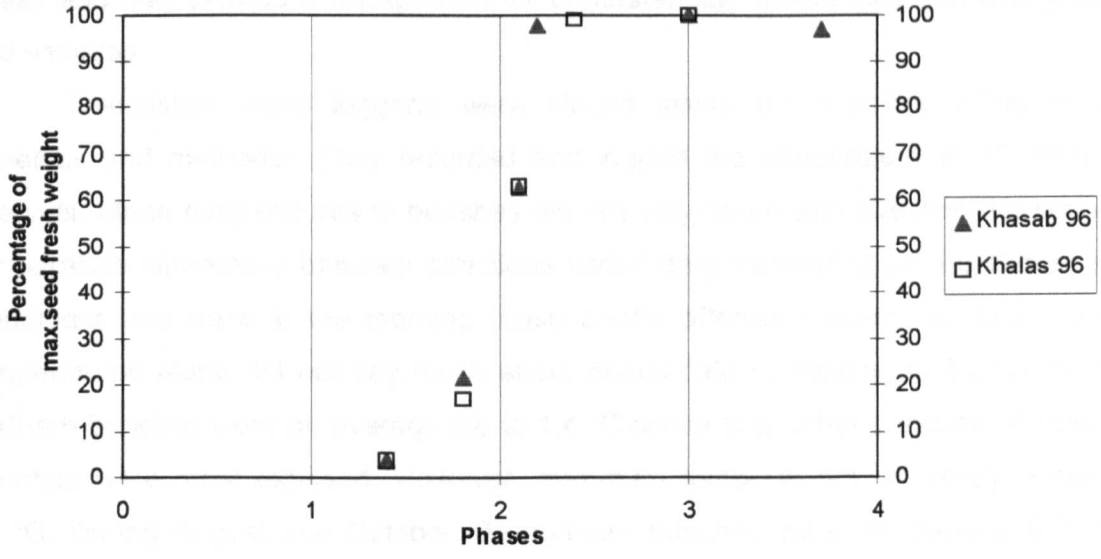
As could be seen in the growth curves for each cv, similar stages were reached in each variety at different days after pollination. To compare observations in different varieties, fruit and seed growth needed to be examined on the basis of the defined stages (x-axis) using fruit and seed weight as a fraction of their maximum weight (y-axis). This allowed discussion of fruit and seed weight at physiologically equivalent points during growth and development.

Figure 4-8: *Changes in indexed fruit weight during different phases in two cvs*



The good fit of the phase-weight index curves for fruits reveals the validity of defining phases for the postulated periods. The graph is important for the further discussion as it identifies the observations that can be compared between varieties on the basis of physiological equivalence. In both cvs about 2 % of the maximum fruit fresh weight was attained at the end of stage 1 and about 50 % at the end of stage 2. Also at the end of stage 3 the maximum fresh weight was reached for both cvs decreasing thereafter at almost identical increments. Using the model of fitting fresh weight as a percentage of maximum fruit weight against phases resulted in one standard sigmoid curve, which fitted the growth behaviour of both cvs although they were distinctly different with regard to their chronological developmental timing.

Figure 4-9 *Changes in indexed seed weight during different phases in two cvs*



The curves for seed weight reveal that the lag phase for seed growth (fresh weight) lasted until the first third of stage 2. Seed weight gain was fast in comparison with fruit growth and the growth rate inverted just after commencement of stage 2. It may be speculated that the rapid seed growth after stage 2 required an increasing amount of photosynthates, which decreases availability for the growth of the pericarp thereby inverting the growth rate for the entire fruit. The growth rate reached maximum just before the middle of stage 2 remaining almost constant thereafter.

Summary:

- Sections 4.3.5. and 4.3.6. show that fruit and seed growth on the two female can be subdivided into four developmental stages.
- A unified standard sigmoid curve for fruit growth was found for both cvs using these stages instead of real time as x-axis and fruit or seed fresh weight as percentage of their respective maximum fresh weight as y-axis.

4.3.6 Orientation of bunches

Effects of bunch orientation on growth and development of the fruits through differences in incident sunlight receipt and the associated changes in temperature were expected. Investigations of this possibility was merited as periods during fruit

growth and development that were particularly sensitive to high temperatures or water stress and may provide a background for understanding differences between years and varieties.

Thermistors (data loggers) were placed inside the bunches (Chapter 3: materials and methods). They recorded and logged the temperature at 30 minute intervals. Mean temperatures in bunches did not vary much with direction. However, temperature differences between directions varied daily depending on the degree of cloudiness and haze in the morning (east) and/or afternoon (west), so that mean temperatures alone did not say much about actual field conditions. In March 1996, northern bunches were on average 0.6 to 1.4 °C cooler than other bunches. Western bunches were most exposed. However, maximum temperatures did rarely exceed 35 °C. During August and October '96 northern bunches were on average 0.7 °C cooler than other bunches when all 24 hours were taken into account. When the day time temperatures alone were analyzed, the difference was about 1.5 °C. Only eastern bunches experienced maximum temperatures in excess of 40 °C, mostly around 9 AM. Western bunches were often exposed to maximum temperatures above 35 °C around 2:30 PM, but below 40 °C in comparison to northern bunches which were exposed to maximum temperatures below 35 °C at the same time of the day. Furthermore, it should be borne in mind that physiological stress is likely to be more pronounced in the afternoon than in the morning.

a. Effect on fruit weight

CV: Khasab:

Table 4-15 FRUIT FRESH WEIGHT IN BUNCHES IN DIFFERENT DIRECTIONS AT 30 D.A.P. IN CV KHASAB IN 1996

Direction	*Fruit fresh weight (g)*	
North	0.15	a
South	0.15	a
East	0.15	a
West	0.13	b

LSD @ P< 0.05 = 0.02 g

Table 4-15 shows that in 1996, bunches emerging on the western side of a cv Khasab tree produce significantly (P<0.05) lighter ovaries 30 d.a.p. (stage 0.6), when

compared to other directions, and there is an indication that they were also the lightest at 50 d.a.p. (stage 1.2). An examination of the dry weight revealed no differences at 30 d.a.p., so that the effect was on the moisture content of fruits. The western bunches were exposed to the sun in the afternoon unlike the eastern bunches which were exposed to the morning sun. It can be speculated that western bunches would be more affected by high temperatures because the tree would experience during the afternoon a higher water pressure saturation deficit as it would have already lost moisture during the first half of the day. Eastern and even southern bunches were exposed to the sun early in the day when the tree had still a relatively low water saturation deficit. Because, no such observations were made at any other time during fruit development and also not in 1995, it is likely that the observed effect was entirely due to climatic conditions at the time.

CV: Khalas:

Table 4-16 FRUIT FRESH WEIGHT IN BUNCHES IN DIFFERENT DIRECTIONS AT 65 D.A.P. IN CV KHALAS IN 1996

Direction	*Mean*	*Groups of not significantly different means*
South	1.0	a
East	0.9	ab
West	0.8	b
North	0.7	b

LSD @ $P<0.05$ = 0.2 g

In cv Khalas a bunch direction effect was observed (Table 4-16) in 1996 at 65 d.a.p. (Stage 1.4) when the northern and western ovaries were the lightest with regard to fresh weight while there were no differences among treatments as regards dry weight. The differences are therefor due to moisture content. In comparison Khasab fruit were that time at 58 d.a.p. (Stage 1.3). The low weight of fruits in western bunches can be explained as was done in cv Khasab. The low weight of northern ovaries may have been caused by the lack of surrounding vegetation, which exposed cv Khalas trees more to the desiccating effect of the prevailing winds from the North East than trees of cv Khasab.

In 1995 no such effects were observed in any of the two cultivars. The above highlights the sensitivity of stages 0.6 to 1.4 to environmental stress which can alter the moisture content of developing fruits, while it has no effect thereafter.

b. Effect on colour development

The changing colours in cv Khasab between the stages Khimri (green), late Khalal (dark maroon), half Rutab (black and maroon) and Rutab (entirely black) have been examined with regard to the orientation of bunches on palms. No effects of orientation on colour development have been observed. In cv Khalas the same observations have been made.

These results indicate that colour development was not affected by incident sunlight or changes in temperature caused by it. Since colour development was indicative of maturity this interpretation can be extended to the time required to attain maturity. Findings presented in the previous section that fruit weight at maturity is not affected by direction support this interpretation.

c. Effect on time to ripening

While colour development can be accurately observed, ripeness of fruits in a bunch extended over a sequence of developmental changes starting from the softening of the fruit to the stage when the apical tip of the fruit started darkening and rapidly lost turgor. The effect of bunch direction on ripeness was examined, but no effect on ripening was apparent.

The above results indicate that there was no effect of incident sunlight and associated differences in temperature on ripening in the above two cultivars.

Summary:

1. The results presented in this section indicate that the orientation of the bunch affected fruit fresh weight in the early stages of growth, which may have been brought about by the described diurnal changes in water stress in the bearing palm tree and by the direct effect of prevailing winds. However, maximum fruit fresh weight was unaffected. The pattern of diurnal water stress merits further research.
2. Physiological processes of colour development and ripening were unaffected.

5. Fruit set

A separate preliminary examination of fruit set was considered necessary, because in any study on pollen effects, a key question must be whether effects on fruit development were indirect and merely a consequence of differential fruit set or whether they acted independently of fruit set and were directly attributable to pollen.

After pollination, ovaries either abort or "set" as fertilized or unfertilized (parthenocarpic) fruits. The number of ovaries and fruits per bunch then decreases continuously due to abscission and consequently both the sink effect exerted by the bunch and the dynamics of fruit growth and development within the bunch would be expected to change. Study of any effects of pollen on fruiting must first take account of these changes in fruit development. Two female cvs with three pollen types were involved. The effect of pollen treatments on fruit set in the different cvs will be examined in the next chapter (3.3.1.) which separately discusses pollen effects. As male and female genotype interactions were expected each cultivar is discussed individually.

In view of the results on peduncle size and fruit set and as the number of fruits varied widely between bunches even on the same palm, the percentage of retained ovaries out of the initial number of flowers instead of an absolute number was used as the criterion for fruit set.

5.1. Timing of fruit abscission and possible PGR involvement

The timing and extent of fruit drop are expected to be characteristic of the female genotype and will possibly be affected by the pollen type as well. It was possible that these effects would be modified by applied plant growth regulators. Exogenous hormones applied at different stages may cause effects, which are similar to those of particular pollen treatments and may simulate the effect of endogenous plant growth regulators.

CV Khasab:

Fruit set and abscission:

Two data sets are presented in Figure 5-1 to describe fruit set, firstly of pollinated ovaries apparent as single fruits and secondly of unpollinated and unfertilized ovaries which are parthenocarpic triplets. Abscission of most parthenocarpic fruits is expected. If pollen type influences fruit set by way of plant growth regulators then that may be reflected in the pattern of abscission and consequently the total number of ovaries retained.

Figure 5-1 *Fertilized and unfertilized fruits retained after pollination as percentage of the number of flowers in cv Khasab in 1996.*

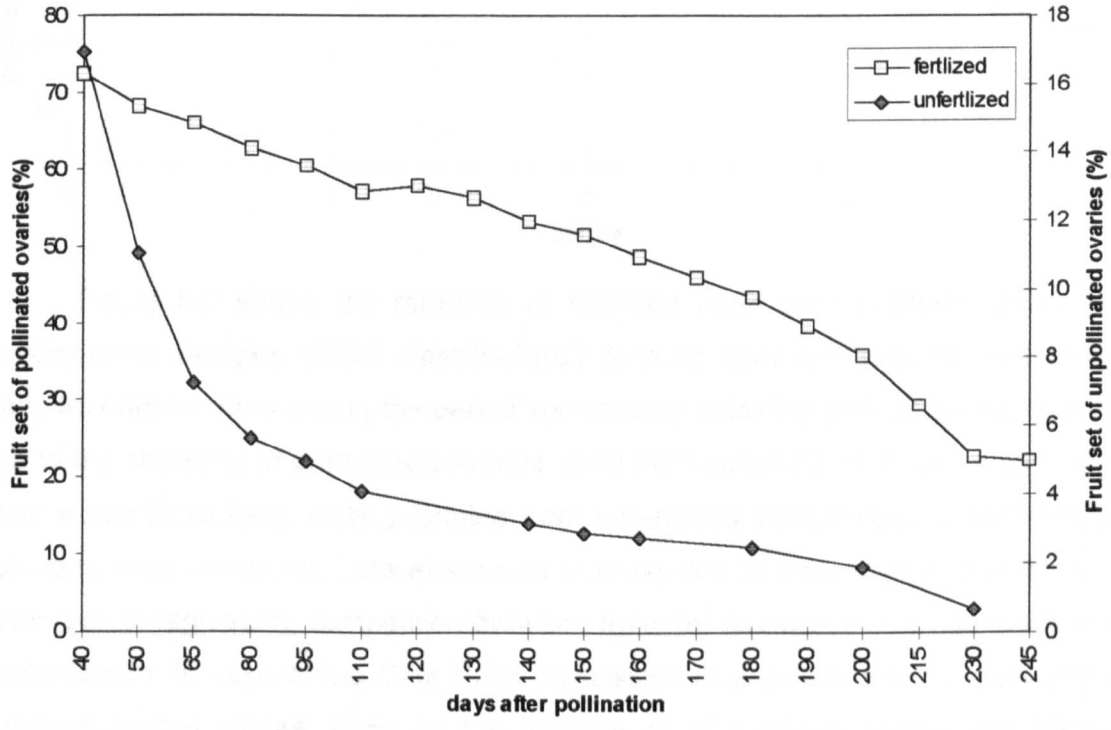


Figure 5-1 shows that fruits of both types drop continuously from the time of pollination until ripeness. Most fruit drop during the first 40 days after pollination and a relatively large proportion of unfertilized fruits (parthenocarpic triplets and singles) is retained at that time. This proportion decreases then continuously.

Parthenocarpic fruits are distinguishable 40 d.a.p. when they constitute about 17 % of all retained ovaries (Figure 5-1). This proportion drops to 7% by 65 d.a.p. and thereafter declines steadily to about 2 % at the Bissr stage. It is reasonable to assume

that some competition exists between the fruits in the bunch during the early stages of growth and development up to 65 d.a.p., but not thereafter owing to their small numbers.

Figure 5-2 *Indexed fruit set (fertilized ovaries) during different stages of development in cv Khasab in 1996.*

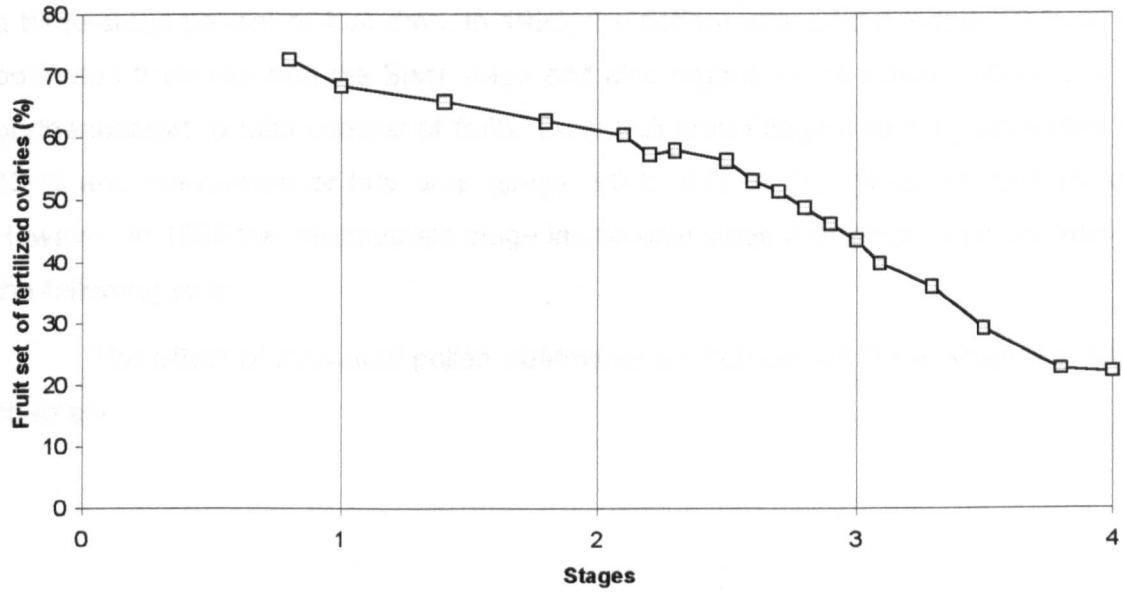


Figure 5-2 shows the retention of fertilized fruits during different stages of development. Sedgley (1989) classified fruit drop as early and late, or pre-harvest. Early fruit drop occurs during the period immediately following pollination and may be due to the shedding of unfertilized ovaries. Only from about 70 d.a.p. onwards normal fruits would have been distinguishable from unfertilized parthenocarpic single fruits, but none were observed. Late abscission may be due to senescence, the effect of plant growth regulators, competition between fruits for resources or a combination of these factors. In case of the Date Palm, abscission of parthenocarpic triplets and of fertilized ovaries occurs. Early on the majority of all abscised ovaries are triplets, which are unfertilized ovaries. During the stage 1 to 2.5 (50 to 140 d.a.p.) most abscised ovaries are parthenocarpic triplets and only a few are single fertilized fruits.

The late pre-harvest abscission is characterized by the drop of fertilized fruits. 43% of all flowers reach stage 3.0 (Bissr) in 1996, which is the stage of the harvestable and consumable product. This may be the result of competition for substrates or due to the effect of hormones being produced around the time of maturity to early senescence.

It becomes apparent that fruit drop occurs at a similar rate during all stages with the exception of stage 1.0 to 2.5, during which only 8 % of all fruits due to drop fall. The latter period is the rapid growth phase for the entire fruit and seed in terms of fresh weight.

The relative effects of female genotype and environmental factors on the pattern of abscission was studied in 1995 as well. Experiments in both years revealed a three-stage pattern of fruit drop. In 1995, the pattern was similar in that 50 % of all pollinated fruits reached the Bissr stage and also regarding the similar proportions of parthenocarpic to total number of fruits. Early fruit drop (stage 0 to 1.1) amounted to 43 % and pre-harvest or late drop (stage 3.0 to 4.0) to 28.5 % of all fruits to fall. However, in 1995 the intermediate stage lasted until stage 3.0, which is longer than in the following year.

The effect of individual pollen treatments on fruit set will be examined in later chapters.

Effect of applied PGRs:

In 1995 hormones were applied at the first day after pollination and at 80 d.a.p.. No hormone effects were observed during fruit growth and development, probably because the stages of application were inappropriate.

The examination of fruit development in 1995 and the histological examinations in 1996 revealed that pollen effects appeared already in Stage 1, so that the application at 80 d.a.p. was probably too late to simulate hormonal mechanisms coincident with the start of bisexual tissue development around 30-40 d.a.p.. Similarly, hindsight showed that the choice of the day of pollination in 1995 for the first application probably influenced pollen germination and tube growth so that simulation of hormonal pollen effects were *a priori* interfered with. The 6th day after pollination, which was chosen for the first PGR application in 1996, was more suited because pollination and fertilization would have been complete by that time (Reuveni, 1986). The 1996 results take therefore preference over those of 1995.

An understanding of the possible effects of endogenous plant growth substance on growth is expected by examining the effect of exogenous ones. Plant

growth regulators were applied to each bunch of cv Khasab twice during fruit development, i.e.: 6 d.a.p. and 40 d.a.p. in 1996. The first application was at the beginning of stage 1 when the zygote (Section 4.3.2.) was still undivided. This would cause similar effects as the endogenous hormones, imported, formed or activated as a result of pollination and fertilization. The second application at 40 d.a.p. may simulate the effect of hormones produced as a result of the formation of the bisexual embryonic and endosperm tissues, which started developing rapidly at the time (Reuveni, 1986).

NAA, GA_3, BA, HFCA, TIBA and Daminozide were dissolved with a wetting agent (Citowett®) in different concentrations in water and sprayed onto bunches pollinated with Al Arudsabba and others pollinated with Khori (Chapter 3: materials and methods). The control treatment consisted of water and wetting agent and would show the effect of pollen type (here: only Al Arudsabba) without the additional plant growth regulator.

Figure 5-3 *Unfertilized (dark) and fertilized (light) ovaries as percentage of the initial number of flowers during different stages of growth and development of bunches in cv Khasab treated with different plant growth regulators in 1996.*

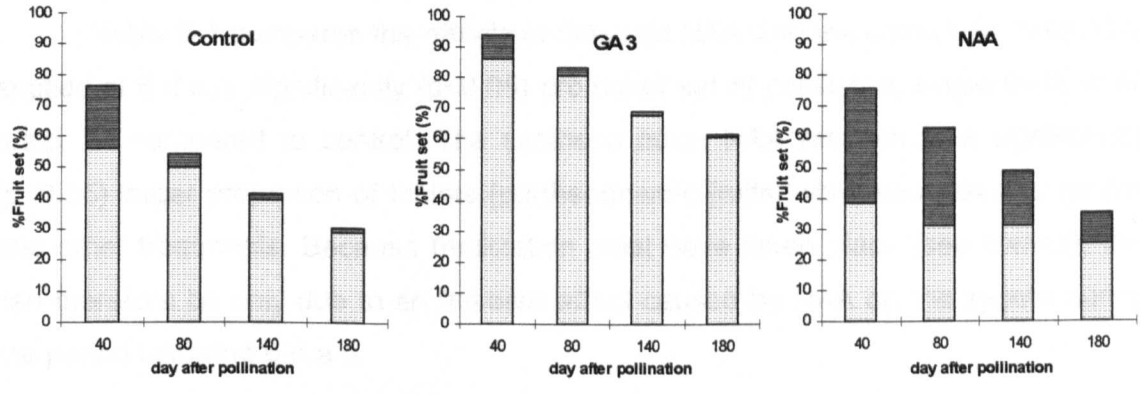


Figure 5-3 shows that bunches treated in 1996 with gibberellic acid (GA_3) had significantly ($p<0.05$) higher retention of fertilized ovaries at 40 d.a.p. than control, which would have to be an effect of the application at 6 d.a.p., while thereafter no significant differences where observed. No significant effects on the unfertilized and total absolute number of ovaries retained were observed.

Bunches treated with NAA when compared with control bunches had similar retention of fertilized ovaries at 40 d.a.p, but a significantly lower retention ($p<0.05$) in

comparison with bunches treated with gibberellic acid. Thereafter no effects of NAA on the percentage of fertilized ovaries were observed. However, NAA resulted in the highest percentage ($P<0.05$ from 40 to 65 d.a.p. and $p<0.001$ thereafter) of retained unfertilized ovaries as compared to control bunches and bunches treated with GA at any time during growth and development. The effects observed at 40 d.a.p. can be attributed to the treatment at 6 d.a.p., while all following effects may be either due to the treatment at 40 d.a.p. or the one at 6 d.a.p. or on interaction of these two applications.

Table 5-1 EFFECTS OF EXOGENOUS HORMONES APPLIED 6 D.A.P. (GA_3 AT 100 PPM, NAA AT 100 PPM) ON FRUIT SET 40 D.A.P. IN CV KHASAB IN 1996. THE POLLEN TYPE WAS AL ARUDSABBA.

Growth regulator	*Mean fruit set (%) of fert. single fruits*		*Mean fruit set (%) of parth. triplets*	
GA_3	86.0	a	7.8	c
Control	56.2	b	20.1	b
NAA	38.1	c	37.5	a

Fertilized fruits: LSD @ $P<0.05$ = 16.8 %; Unfertilized fruit: LSD @ $P<0.05$ = 12.1 %

Table 5-1 compares the effects of GA_3 and NAA with the control. In 1996, GA_3 applied at 6 d.a.p. significantly ($p<0.05$) promoted set of pollinated, single fruits at 40 d.a.p. as compared to control. The synthetic auxin NAA resulted in a significantly ($p<0.05$) larger proportion of triplets (parthenocarpic fruits) when compared to control and other treatments. Because fertilization must have taken place (see control), this can therefore be only due to an adverse effect caused by NAA on the zygote during the period following 6 d.a.p.

It can be concluded from the above that apart from pollination and fertilization as determining events resulting in fruit set, the subsequent survival of the zygote until the start of embryogenesis around 30.d.a.p. was equally important. GA_3 had possibly a conducive effect when present from 6 d.a.p. onwards, while it had no effect if applied just following pollination (1 d.a.p.) or at 40 and 80 d.a.p..

In the following the timing of fruit set and the possible involvement of plant growth regulators will be looked at for cv Khalas.

Summary:

1. Fruit abscission occurred in three clear phases, i.e.: early, intermediate and pre-harvest.
2. The duration of stages was influenced by environmental conditions (year).
3. GA_3 application during the early stages of zygote development (6 d.a.p.) promoted early fruit set (40 d.a.p.). No such effects appeared for earlier or later applications.
4. Naphthalene acetic acid application during the early stages of the zygote (6 d.a.p.) had an adverse effect on early fruit set (40 d.a.p.) by increasing the proportion of unfertilized ovaries as compared to control, while no such effects appeared for earlier or later applications.

CV: KHALAS

Fruit set and abscission:

This was examined in the same way as cv. Khasab. The key differences to cv Khasab were the higher proportion of unfertilized ovaries and the faster rate of abscission of fertilized ovaries in the initial stage.

Two sets of data will be examined, i.e.: pollinated and fertilized ovaries and unfertilized ovaries retained. Figure 5-4 shows them plotted against the day after pollination.

Figure 5-4 *Fertilized and unfertilized ovaries retained after pollination as percentage of the number of flowers during growth and development in cv Khalas in 1996.*

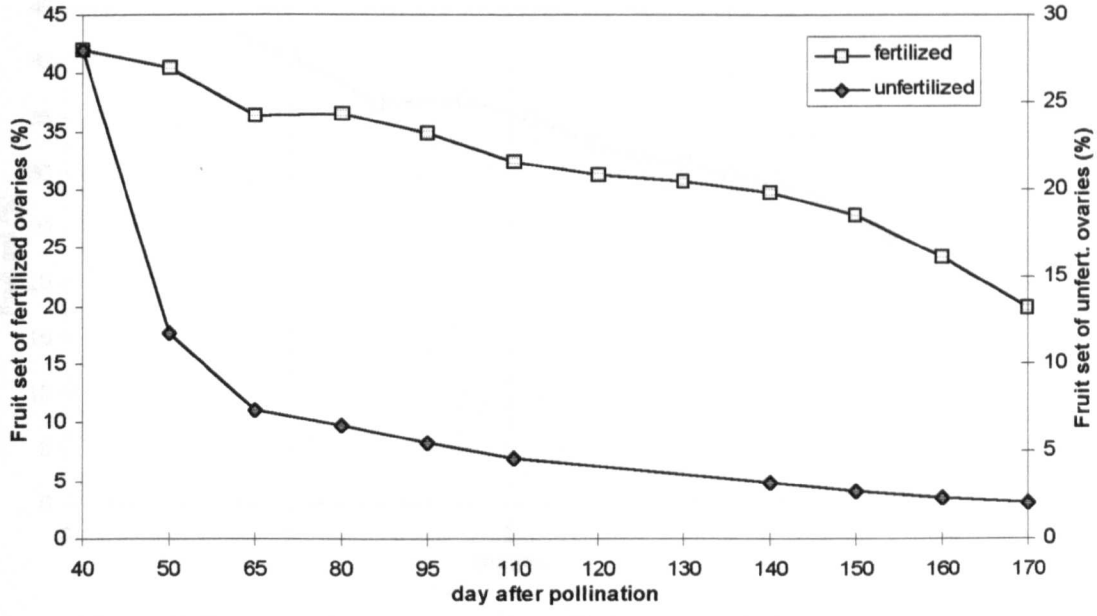


Figure 5-4 shows that fruits of both types dropped continuously from pollination to the time of ripeness. About 40 % of all ovaries due to drop, had done so in the first 40 d.a.p.. By that time the total number of ovaries retained amounted to 70 % of the initial number of flowers and the proportion of fertilized to unfertilized ovaries was about 40: 30. From this time onwards until 150 d.a.p., at which 28 % pollinated fruits were present in the Bissr stage, 14 % of all pollinated flowers dropped. Between 50 and 110 d.a.p. unfertilized fruits decreased from 18% to 8 %. About 30 % of all ovaries reached the consumable Bissr-stage.

The following examines the percentage of pollinated fruits plotted against an x-axis with the stages of development. With this scale the principal stages of fruit drop became apparent as they relate to the later chapters in this study.

Figure 5-5 *Fertilized ovaries retained during different stages as percentage of the number of flowers during growth and development in cv Khalas in 1996.*

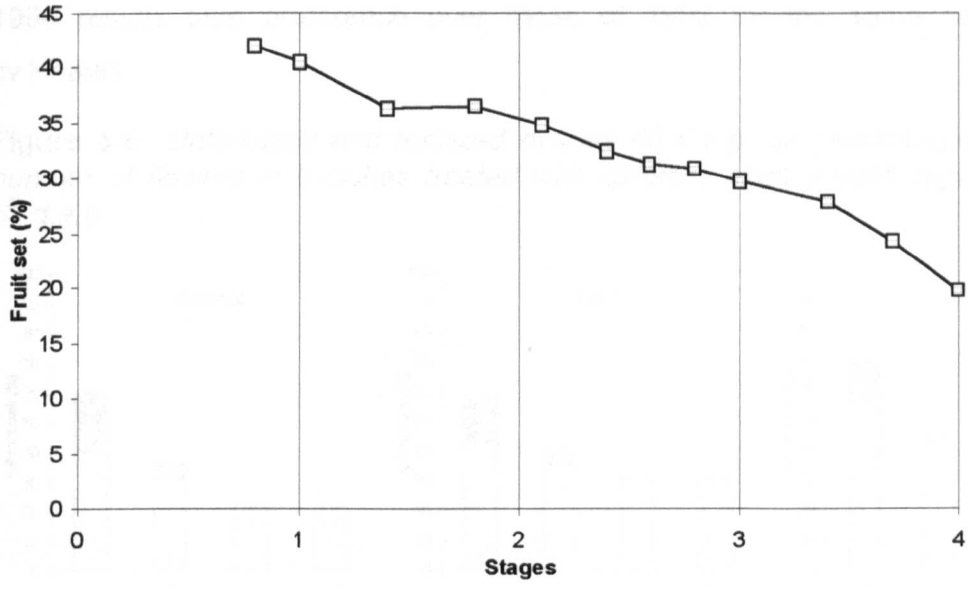


Figure 5-5 shows that in case of cv Khalas early fruit drop occurred during the period immediately following pollination and may have been due to the shedding of unfertilized ovaries. Later abscission was much less remarkable than in cv Khasab.

In comparison to cv Khasab the above described pattern (Figure 5-5) was distinguished by a much faster initial drop for both fertilized fruits and parthenocarpic triplets, but with a relatively higher proportion of parthenocarpic triplets. This was followed by a much longer intermediate phase of little abscission, while the final stage was similar with regard to period but distinguished by a slower rate of drop.

From about mid Stage 2 (70 d.a.p.) onwards fertilized fruits can usually be distinguished from unfertilized parthenocarpic single fruits (Reuveni, 1986), but none were found. Between stages 1 and 3 only about 10% fertilized ovaries dropped and another 10 % between stages 3 and 4. Fertilized ovaries amounting to a third of all flowers reached stage 3.0 (Bissr) in 1996, which is the stage of the harvestable and consumable product. In this cv the patterns of fruit drop in both years of the study were similar.

Effect of applied PGRs:

Plant growth regulator treatments were the same as in case of cv Khasab. The 1996 results take preference over those of 1995 for the same reasons as in cv Khalas.

Figure 5-6 *Unfertilized and fertilized ovaries 40 d.a.p. as percentage of the initial number of flowers in bunches treated with different plant growth regulators at the 6th d.a.p..*

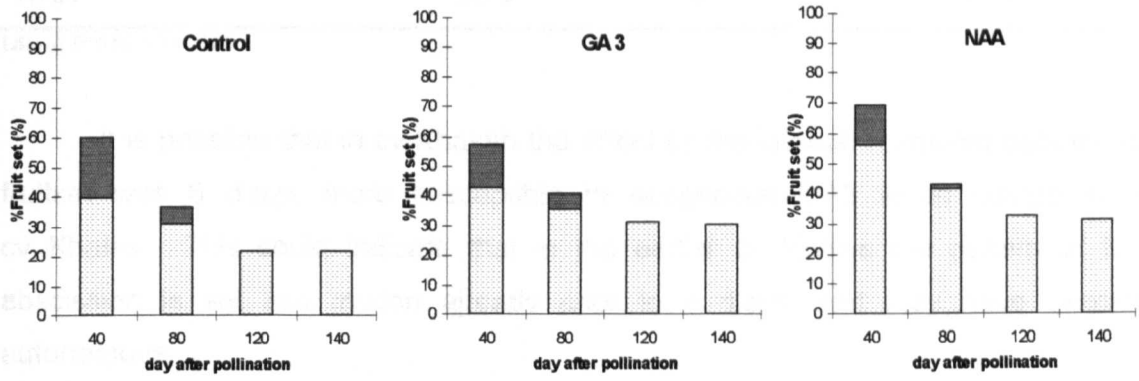


Figure 5-6 shows that bunches treated with NAA when compared with control bunches had a significantly higher ($P<0.05$) retention of fertilized ovaries at 40 d.a.p in comparison with control bunches and those treated with gibberellic acid. Thereafter no effects of NAA of the percentage of fertilized ovaries were observed. The NAA-effects observed at 40 d.a.p. can be attributed to the treatment at 6 d.a.p.. No differences in any of the examined variables were observed afterwards.

Bunches treated with gibberellic acid (GA_3) did not differ in the retention of fertilized ovaries compared to control. No effects on the unfertilized and total amount of ovaries were observed.

A comparison of the two female cvs revealed that NAA induced a higher retention of fertilized ovaries than GA_3 in cv Khalas whilst it induced a lower retention in cv Khasab. GA_3 induced a higher retention in cv Khasab than control, but not in cv Khalas.

Table 5-2 shows the effects of treatments with GA_3 and NAA together with the control on fruit set at 40 d.a.p..

Table 5-2 EFFECT OF HORMONES APPLIED 6 D.A.P. (GA_3 AT 100 PPM, NAA AT 100 PPM) ON FRUIT SET 40 D.A.P. FOR CV KHALAS IN 1996. THE POLLEN TYPE WAS AL ARUDSABBA.

Growth regulator	*Mean fruit set (%) of single fruits*		*Mean fruit set (%) of parth. triplets*
GA3	42.6	b	14.7
Control	39.7	b	21.4
NAA	56.3	a	12.9

LSD @ P<0.05 = 13.7 %

It is possible that in cv Khasab the effect of the internal hormonal balance on fruitset was 6 d.a.p. more susceptible to exogenous GA3 when compared to cv Khalas. This could indicate that in the earlier cv Khalas the pattern of fruit abscission is set into motion already prior to 6 d.a.p. and may have become autonomous.

Hormone treatments at the day of pollination and 80 d.a.p. had no effect on fruit set in 1995.

Summary:

1. Fruit abscission occurred in three phases, i.e.: early, intermediate and pre-harvest.
2. GA_3 application during any stage had no effect on fruit set.
3. NAA application during the early stages of the zygote (6 d.a.p.) had a conducive effect on early fruit set (40 d.a.p.) by increasing the proportion of fertilized ovaries, while no such effects appeared for earlier or later applications.

COMPARISON OF FRUIT ABSCISSION TIMING AND POSSIBLE PGR INVOLVEMENT IN THE TWO CVS:

Summarizing the results presented in this chapter it is apparent that fruit drop occurs in three different phases: an initial stage of heavy drop, followed by an intermediate stage of little drop and then a pre-harvest stage during which fruit drop increases again.

1. Early fruit drop occurred in both cvs within the first 50 days after pollination. This coincides with the embryo in its early stages of development. This may indicate the presence of postzygotic incompatibility mechanisms. Sedgley (1989) observed that early abscission in Avocado occurred when the embryo is at the globular stage and was caused by a genetic selection against fruits containing seeds with homozygous loci.

2. The low rate of drop during the intermediate period coincided with rapid seed and fruit growth. This may have caused the fruits to be retained. Once the full seed weight and 90 % of the maximum fruit weight was attained, most of the remaining parthenocarpic and some of the pollinated ovaries dropped. Such relationships have also been reported in apple (Lakso, 1989), where fruit abscission occurs after a critical reduction in fruit growth rate. The relationship between growth rates and abscission rates will be explored in some detail in later sections (3.2.3.).

3. Exogenous plant growth regulators had an effect on fruit set when applied 6 d.a.p. and the effect became apparent at 40 d.a.p.. Earlier and later applications had no effect.

4. The effect of hormones was cv-specific. While GA_3 promoted set of normal fruits in the cv Khasab, this was not the case in cv Khalas. In case of cv Khasab, gibberellic acid appears to promote fruit set possibly by promoting the viability of the fertilized ovule (zygote), so that GA_3-treated bunches contain eventually more fertilized (seeded) fruits than control. Generally, in unfertilized stone fruits gibberellins are known to induce parthenocarpy, but they play also a major role in the natural development of seeded fruits. Gibberellins promote cell enlargement and nucleic acid synthesis (Devlin, 1983). Reuveni (1986) explains that during the 7^{th} to 11^{th} week after pollination in cv Hayani (corresponds in cv Khasab to the

transition from stage 1 to 2) cell enlargement takes place, which is a process known to be promoted by gibberellic acid.

In line with Browning's description of hormonal peaks (1989), this would indicate that in cv Khasab GA supports fruit set particularly during stage 1 and the transition to stage 2. Once fruits have set and embryo development commences, less abscission will take place resulting in the period of low fruit drop during stage 2 to 3.5. In 1995 the same concentrations were applied 1 d.a.p., but no effects were found at 50 d.a.p.. Exogenous gibberellic acid appears to be no longer effective if applied late in stage 1 or during stage 2 (applied at 40 d.a.p. in 1996 and at 80 d.a.p. in 1995).

NAA had a promoting effect in cv Khalas not found in cv Khasab. In contrast to cv Khalas, NAA increased the number of unfertilized ovaries in cv Khasab.

In cv Khalas NAA had a promoting effect on fertilized fruit set, while GA had no effect what so ever. The above discrepancy points at the possibility that exogenous hormones acted on internal hormonal balances, which were *a priori* distinctly different between the two cvs.

The abscission occurring from stage 3 onwards is possibly the result of endogenously produced plant growth regulators such as ethylene. However, the latest applications (stage 1.8 or 80 d.a.p. in 1995) were not found to have an effect on any parameter of fruit set after that time in both cv Khasab and Khalas.

5.2. Early fruit set and time of spathe opening

The time of spathe opening may have an effect on fruit set in that both duration of spathe opening and the date of that period may have an influence. Such effects could be mediated through competition between bunches or by possible male and female incompatibility mechanisms resulting from weakening incompatibility control in older flowers as has been observed in other plants (Sedgley, 1989) with regard to self-incompatibility control. Hypothetically , shorter periods of opening may lead to lower fruit set as a result of the competition for resources from inflorescences

opening almost in synchrony. Earlier inflorescence opening may be associated with higher fruit set compared to later ones as a result of lower competition during the period just following pollination and fertilization.

The data that follow (Table 5-3) are from inflorescences pollinated with the three pollen types in this study. The same combinations of pollen types was used in both female cvs. Fruit set as observed at 50 d.a.p. was chosen as a benchmark time, because early drop has been completed by that time.

Table 5-3 PERCENTAGE FRUIT RETENTION 50 D.A.P., THE STAGE OF DEVELOPMENT INDEX AND TIME FROM THE FIRST UNTIL LAST SPATHE OPENING IN THE TWO CVS IN 1995 AND 1996.

Year *CV*	*Stage index*	*Fruit set at 50 d.a.p. (%)*	*Ave. no. of days between opening of first and last inflorescences*	*Range from first to last opening of inflorescences*
1995				
Khasab	1.0	70.8	15.0	10-19
Khalas	1.0	38.9	6.6	5-8
1996				
Khasab	1.0	69.0	19.3	14-23
Khalas	1.0	37.5	7.6	7-9

Table 5-3 shows for both years that cv Khalas has the shortest period of spathe opening (x) and also the lowest percentage of fertilized ovaries at 50 d.a.p. (y), while cvs like Khasab and Khinaizi, which have inflorescences opening over a more extended period, have a higher set of fruits. Regression analysis, which considers each tree with all its inflorescences as a block, irrespective of cultivar, provides for date palms in general the equations:

In 1995:

- $y = 14.6 + 3.6 \cdot x$, (r^2=0.85, P<0.05).

In 1996:

- $y = 23.2 + 2.3 \cdot x$, (r^2=0.81, P<0.05)

where x = days from first to last inflorescence

and y = fruit set (%) at 50 d.a.p.

No relationship between the day of opening, calculated as the day after the opening of the first inflorescence, and fruit set was observed in either year or cvs.

COMPARISON OF EARLY FRUIT SET AND TIME OF SPATHE OPENING IN THE TWO CVS:

1. The above relationships indicate that the duration of spathe opening influenced fruit set. A shorter duration resulted in lower fruit set, possibly due to competition among inflorescences which had emerged close to each other in time. This may have caused a higher rate of abscission. Accordingly, the regulatory effect which different pollen types may have on fruit set would be influenced by this duration.
2. Time of spathe opening did not influence fruit set.

5.3. Fruit set and fruit and seed weight

The female type has been shown to influence fruit set. Differential fruit set within individual inflorescences would then result in interbunch competition for substrates, which can be expected to affect fresh fruit and seed weight. The aim of the next section is to examine the relationship between fruit set and weight at different stages, so that cultivar specific patterns are understood. This would then provide a background for the later discussion of pollen effects.

Part of the following study will examine the relationship between fruit set percentage and fresh weight at any one time, while another will examine possible relationships between their respective mean rates of change. Each cv is considered in the following separately.

Fruit set, expressed as the percentage of initial ovaries which are retained, is examined in relation to the fresh fruit weight and fresh seed weight. Both were examined at the different stages of fruit growth and development and analyzed for

possible correlations. It was expected that the fruit set percentage at any one time can influence the fresh fruit weight then or later.

CV KHASAB:

Fruit set percentage at 40 d.a.p. and subsequently was correlated with fresh fruit weight from 110 d.a.p. onwards. No correlations were found with seed weight. Since all correlations were negative, a representative correlation between fruit set percentage at 40 d.a.p. and fresh fruit weight at 110 d.a.p. is examined and presented here.

Figure 5-7: *Regression between the percentage of fruits at 40 d.a.p. and fruit fresh weight at 110 d.a.p. in cv Khasab during 1996.*

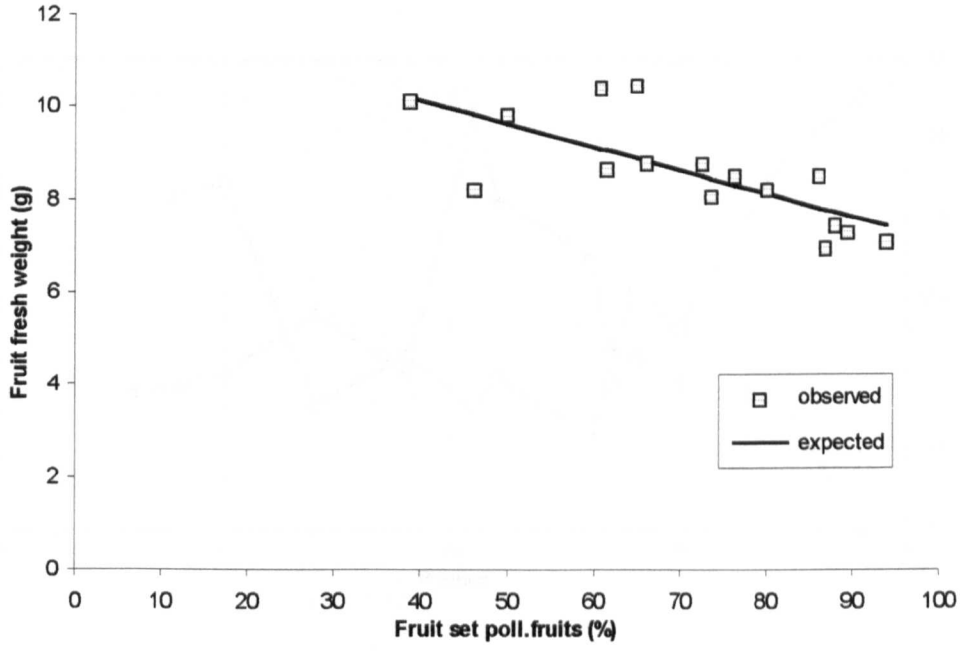


Figure 5-7 shows that a negative linear relationship existed between early fruit set at 40 d.a.p., fruit weights at 110 d.a.p. and afterwards in 1996. This can be described with a highly significant ($p<0.01$, $r^2=0.55$) linear regression equation ($y = 12.2 - 0.051 \cdot x$, x= pollinated fruits at 40 d.a.p. in %, y= fresh fruit weight in g). Such significant correlations continued to exist with the fresh weights of developing fruits until 200 d.a.p.. In contrast, seed weight was at no time linearly related to early or subsequent fruit set. In 1995 the situation was similar.

As indicated in section 5.1., an effect of the rate of growth on fruit abscission is possible. Therefore, the mean rates of change of fruit fresh weight were calculated as

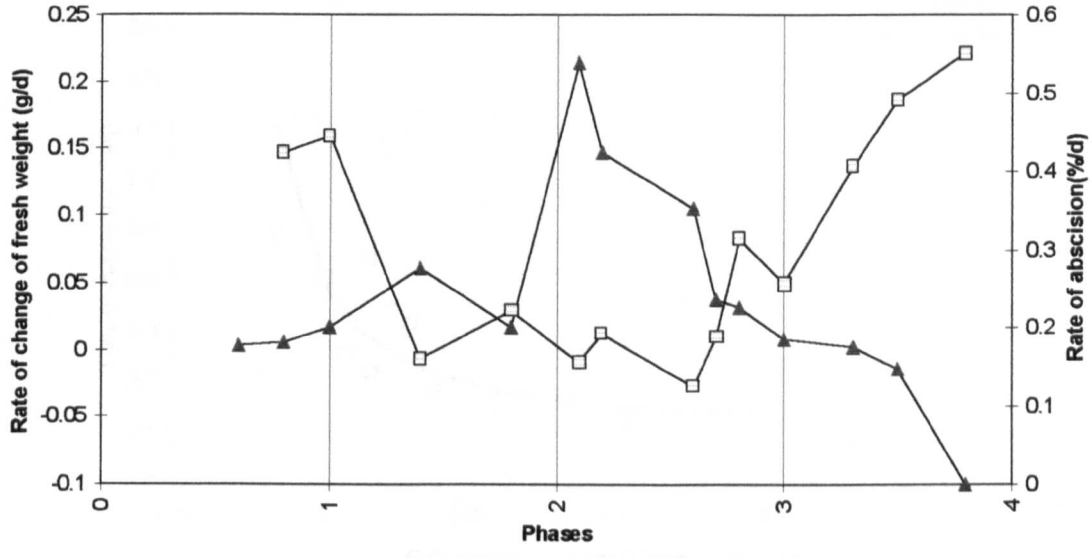
(weight in g at j^{th} d.a.p. - weight in g at i^{th} d.a.p.)/(j - i), where j > i

and the mean rates of abscission of fertilized ovaries as

(fruitset % at j^{th} d.a.p. - fruitset % at i^{th} d.a.p.)/(i - j), where j > i.

Figure 5-8 shows the two mean rates during the entire course of growth and development.

Figure 5-8 *Rate of change of fresh fruit weight (▲) and the rate (as daily change of % fruit set) of abscission (□) during the growth and development of fertilized ovaries of the cv Khasab in 1996.*



Fruit fresh weight increased slowly up to stage 1 and then faster reaching its maximum growth rate at stage 2.0. Thereafter the rate decreased until stage 2.5 from which onwards it dropped critically to nearly zero at about stage 3.0. Afterwards it became negative reflecting loss of fresh weight. Fruit abscission followed a similar but opposite pattern by having been fastest until stage 0.9 to 1.0, followed by a period of slower abscission until stage 2.5. Thereafter abscission increased rapidly.

No simple linear equation could be found to describe the relationship between the mean rates (x) of change of fresh fruit weight during different stages of

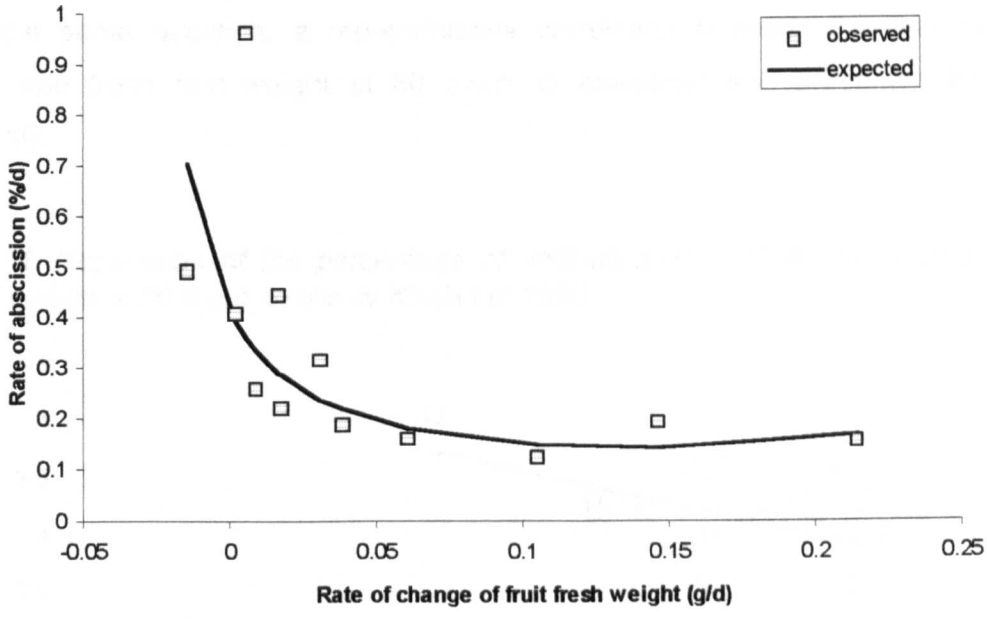
development and the corresponding mean rates (y) of change of fruit abscission (at the same d.a.p.). Data were transformed as follows.

Let $z = y^{-1}$ = 1/ rate (y) of change of fruit abscission,

then the polynomial regression equation $z = -2.422 - 64.88\ x + 225.86\ x^2$ was found to be significant ($P<0.01$).

Substituting z, this is equivalent to $1/y = -2.422 - 64.88\ x + 225.86\ x^2$, which can be written as $y= (-2.422 - 64.88\ x + 225.86\ x^2)^{-1}$. Figure 5-9 shows the observed and expected values of y plotted against x.

Figure 5-9 *Relationship between the mean rate (y) of change of fruit abscission and the mean rate (x) of change of fresh fruit weight in the cv Khasab in 1996.*



It is apparent that the mean rate of change of abscission decreased with an increase in the mean rate of change of fresh fruit weight. A low rate of fruit growth coincided with a high rate of abscission. When the mean rate of change of fruit fresh weight increased, the rate of abscission apparently tended towards a limiting value of 0.1% abscission of fertilized fruits per day. This adequately describes the high rates of abscission during the early and pre-harvest stages of fruit drop during which growth rates are low. In contrast, the intermediate period of fruit abscission is characterized by a low rate of abscission and a high rate of growth. The effect of pollen treatments on this relationship will be examined in later chapters.

Summary:

1. Bunches with a high percentage of fertilized fruits at 40 d.a.p. (stage 0.8) had a low individual fruit fresh weight at 110 d.a.p. and afterwards (stage 2.2 and later).

2. Rates of fruit abscission and fresh weight-gain at any one time were inversely related during the entire course of development.

CV KHALAS:

Correlations between fruit set during the development and fresh fruit and seed weight subsequently were found. Negative relationships were found in 1996, while both negative and positive ones were found in 1995. Since all correlations in 1996 were in the same direction, a representative correlation between fruit set % at 40 d.a.p. and fresh fruit weight at 80 d.a.p. is examined and presented below (Figure 5-10).

Figure 5-10 *Regression of the percentage of pollinated fruits at 40 d.a.p. and the fresh fruit weight at 80 d.a.p. in the cv Khalas in 1996 .*

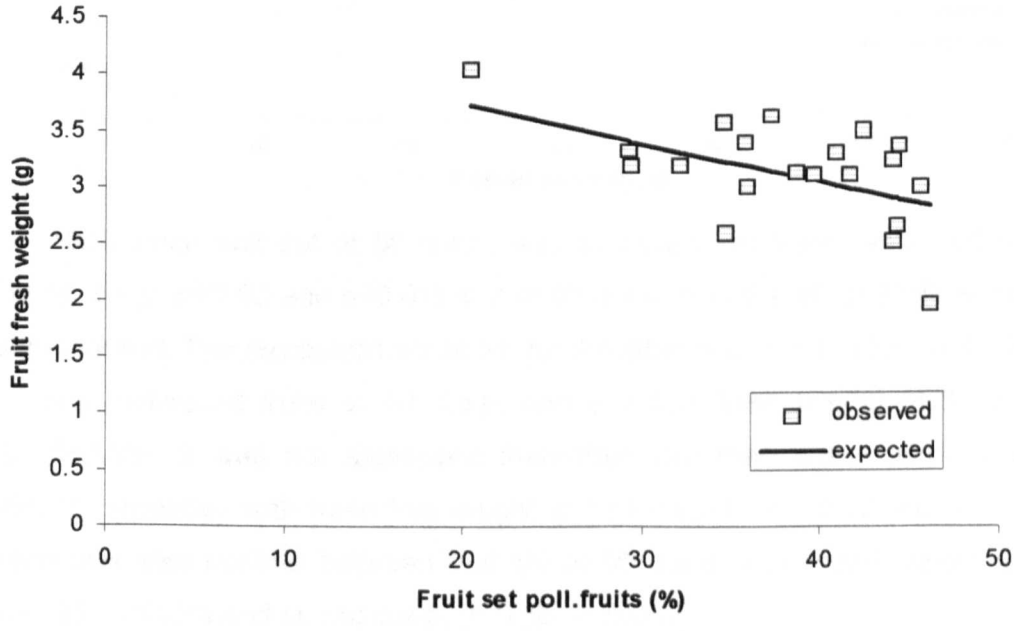
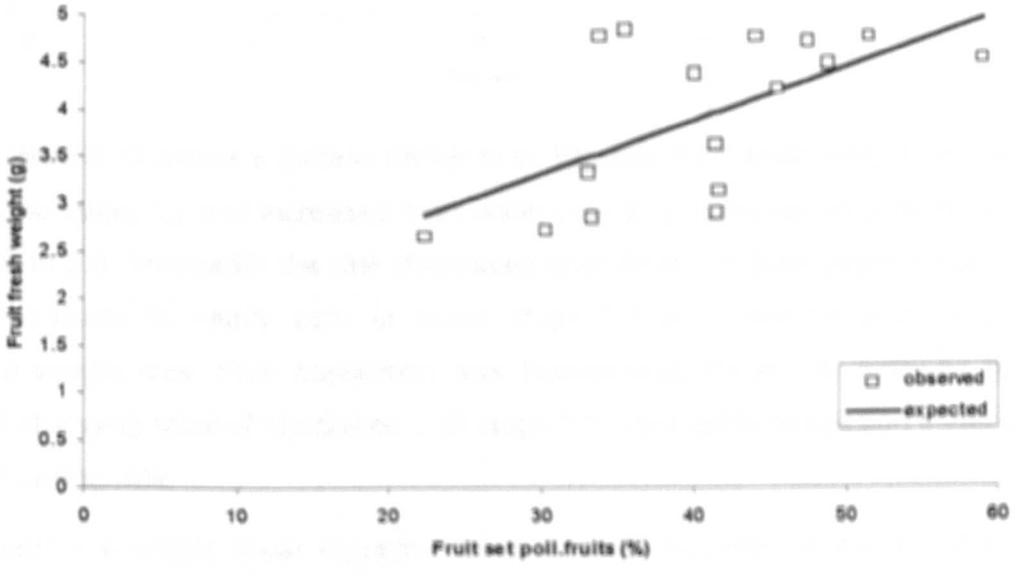


Figure 5-10 shows that in 1996 the earliest significant correlation ($r = -0.65$ and $P<0.001$) was between fruit set of fertilized fruits at 40 d.a.p. and fresh fruit weight at 80 d.a.p. and fresh fruit weight at any time thereafter when all trees were

blocked. Similar significant correlations (P<0.01) existed between any observation on fruit set after 40 d.a.p. and subsequent values of fresh fruit weight. Fruit set at 40 d.a.p. (r = - 0.71 and P<0.001) and 50 d.a.p. (r = - 0.47 and P<0.05) was negatively correlated with fresh seed weight at 80 d.a.p..

Of the significant correlations in 1995, the one between fruit set at 50 d.a.p. and the fresh fruit weight at 80 d.a.p. is presented in Figure 5-11, because it can be compared with the examination of two similar variables in 1996 and because of its unexpected positive direction.

Figure 5-11 *Regression of the percentage (x) of fertilized fruits at 50 d.a.p. with the fresh fruit weight (y) at 80 d.a.p. in cv Khalas in 1995.*



In 1995 initial fruit set at 50 d.a.p. was positively correlated with fruit fresh weight at 50 d.a.p. (r=0.63 and p<0.01) and at 80 d.a.p. (r=0.6 and p<0.05) when all trees were blocked. The regression equation for the latter was y = 1. 629 + 0. 0563 x, with x = nos. pollinated fruits at 50 d.a.p. and y = fruit fresh weight at 80 d.a.p. (P<0.05, r^2=0.36). It was not significant thereafter, but then again when it was negatively (!) correlated with fresh fruit weight at 170 d.a.p.(r = - 0.66 and P<0.01). Correlation was also positive between fruit set at 50 d.a.p. and seed weight at 80 d.a.p. (r=0.62; p<0.05) and at 110 d.a.p. (r=0.58; p<0.05).

Figure 5-12 *Rate of change of fresh fruit weight (▲) and the rate (as daily change of % fruit set) of abscission (□) during the growth and development of fertilized ovaries of the cv Khalas in 1996.*

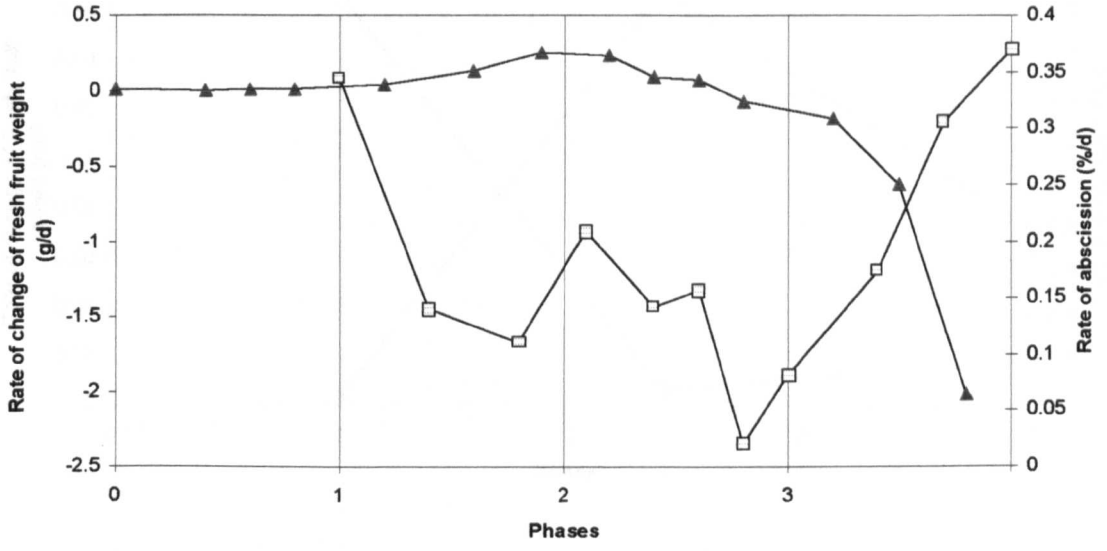


Figure 5-12 shows a pattern similar to cv Khasab. Fruit fresh weight increased slowly up to stage 1.2 and increased then faster reaching its maximum growth rate at stage 1.9 to 2.0. Thereafter the rate decreased until stage 2.6 from which onwards it dropped critically to nearly zero at about stage 2.7 and later became negative indicating weight loss. Fruit abscission was fastest until stage 1.4, followed by a period of changing rates of abscission until stage 2.8. Thereafter abscission increased at an increasing rate.

Neither a simple linear equation nor a binomial equation of the transformed data as was done in case of cv Khasab could be found to describe the relationship between the mean rate (x) of change of fresh fruit weight during different stages of development and the corresponding mean rate (y) of change of fruit abscission (at the same d.a.p.). This suggests that other mechanisms were at work, which added to the complexity of the above described relationship. Possibly, the competition between bunches for resources was so much more due to the narrow period of spathe opening as described in Section 5.2..

Figure 5-13 *Rate of change of fruit fresh weight (▲) and the rate of abscission as daily change of % fruit set (□) during the growth and development of fertilized ovaries of the cv Khalas in 1995.*

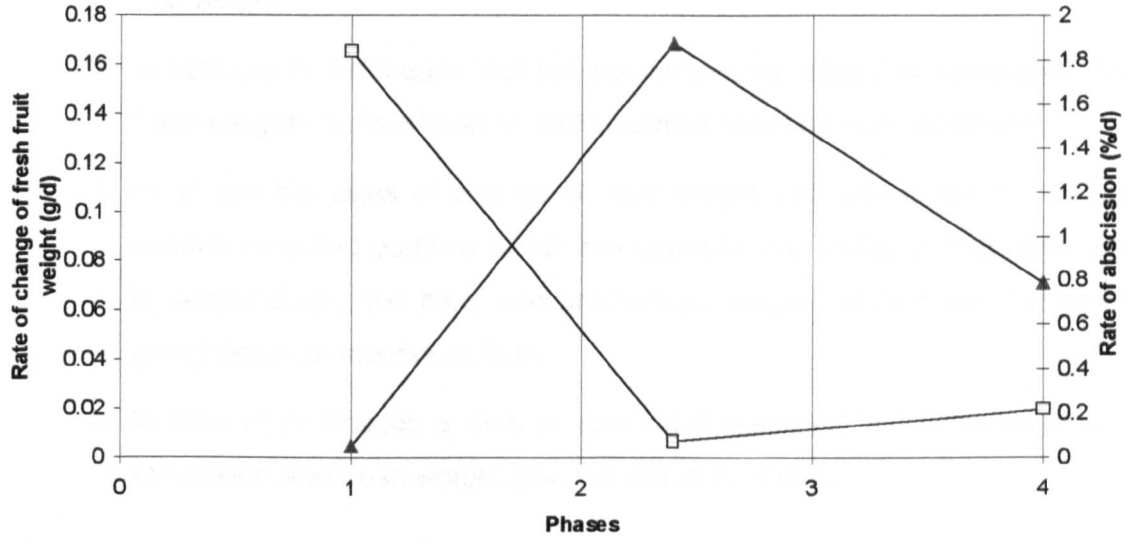


Figure 5-13 indicates a similar pattern of for rates of changes in fresh fruit weight and abscission of fruits for the cv Khalas in 1995 as was observed in 1996. Abscission was fastest during the initial and pre-harvest stages, while fresh fruit weight gain followed an inverse pattern. No linear relationship between these two variables nor any binomial equation describing the relationship of transformed data could be found. The number of data points was also low.

Summary:

1. Rates of change of abscission and weight are clearly defined in the early and late stages of development, while they were irregular in the intermediate stages. Abscission was fastest during the initial and pre-harvest stages, while fresh fruit weight gain followed an inverse pattern.
2. It appears that in cv Khalas relations between early fruit set and fresh weight in the intermediate stages of fruit development varied depending on the year. Different environmental conditions in the two years may have influenced the relationship.
3. While in cv Khasab a relationship between fruit set and fresh weight, which was consistent from year to year, existed, competition between bunches due to the narrower period of spathe opening in this cv possibly modified it.

COMPARISON OF FRUIT SET, FRUIT AND SEED WEIGHT IN THE TWO CVS:

1. In both cvs there were linear relationships between early fruit set and fresh fruit weight.
2. In both cvs in 1996 early fruit set was negatively related to subsequent fruit fresh weights. In cv Khalas in 1995 positive relations were observed.
3. In all cvs the rates of change of fruit weight and abscission of fertilized ovaries exhibited patterns which are opposite but similar in that abscission is fastest during the early and pre-harvest stages, while fresh fruit weight gain follows an inverse pattern.
4. In fruits of cv Khasab a clear inverse relationship existed between rates of abscission and fresh weight gain but not in cv Khalas.

The following chapter will examine the effect of pollen types on the different stages (phases) of fruit growth and development. The following chapters are arranged in the sequence of the major stages of fruit growth and development starting with the earliest stage, which ranges from the day of pollination to the end of the lag phase.

6. Stage One: lag phase

The focus here is on the earliest phase of fruit growth and development which extends from the day of pollination to the end of the lag-phase.

This first phase is characterized by a low rate of growth in comparison to the two subsequent phases. During this phase pollination and fertilization take place. The zygote starts dividing and developing into an embryo after an initial period of dormancy (Plates 4-1 to 4-6). The endosperm consists of syncytia, which start cellularizing towards the end of the phase coincident with the start of rapid growth (Stages 2 and 3). The flower's fertilized carpel starts enlarging and is distinguishable from the other two carpels in the later half of this phase. The unfertilized carpels remain small and eventually fall off.

The following experiments were carried out to examine pollen and growth regulator effects on fruits of different cultivars, particularly the effect of pollen type and of exogenous hormones (BA, Daminozide, GA3, HFCA, NAA and TIBA) on fruit growth and development stages (6.1.). Possible relationships for different pollen types between such variables as fruit weight, fruit size on the one hand and fruit set and thermal time on the other hand (6.2.) will be tested. Seeds were not examined as they were rudimentary during the lag phase.

6.1 Pollen type and plant growth regulator effects on fruit growth and development

The experiments were designed to analyse pollen effects on several physical characteristics of the early fruits and to suggest the underlying mechanisms. It was expected that early differences may be due to substances contributed or stimulated by the pollen type or possibly also due to a contribution of the male genotype. The hormone experiments were designed to explore possible roles for major plant growth substances in regulating fruit growth and development and from there to draw

conclusions about any pollen effects. Two female cvs have been studied during both years of this study. As fruit set is known to influence the growth of the fruit (Chapter 5.3.), pollen effects could be mediated through this as well as through plant growth regulators. Fruit set effects were therefore an important consideration in this study.

6.1.1 Fruit set

CV Khasab:

Pollen effects

Earlier observations (Chapter 5.1.) showed that in 1996 about 23 % of all flowers dropped during the lag phase leaving about 68 % that were pollinated and 9 % that were unpollinated flowers. In 1995 the pattern was similar. This pattern was not influenced by pollen treatment in either year.

Effect of applied PGRs

It is recalled that in 1996 (Chapter 5.1.), fruit set at 40 d.a.p. (poll. fruits) was significantly higher ($P<0.001$) for GA than for control, while NAA resulted in a lower fruit set. No hormone effects were observed in 1995. In that year however, only pollen type Al Arudsabba was used.

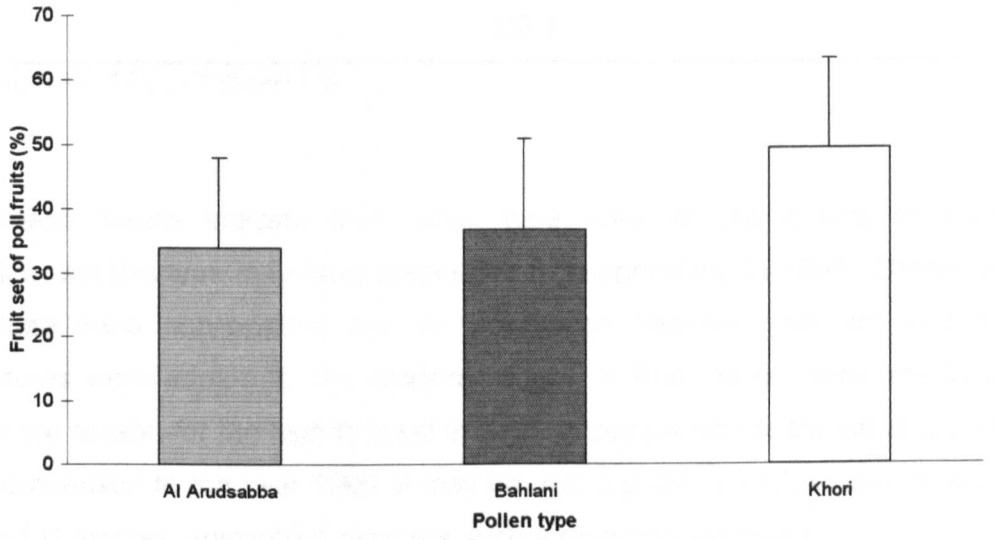
CV Khalas:

Pollen effects

Recalling the general pattern of fruit drop in this cv when pollinated with a number of pollen types, it is noted that in 1996 about 48 % of all flowers dropped during the lag phase, so that at its end 40 % were pollinated and 12 % were unpollinated flowers. In 1995 the pattern was similar (41 % pollinated, 14 % unpollinated).

Treatments with particular pollen types had significant effects by the end of the lag phase (50 d.a.p.) in 1995 as shown in Figure 6-1.

Figure 6-1 *Effect of pollen treatments on fruit set at 50 d.a.p. of pollinated fruits in cv Khalas during 1995. (LSD@P<0.05 bars shown).*



In 1995 set of fruits pollinated with Al Arudsabba and Bahlani was 34 % and 37 %, respectively, whilst with pollen type Khori it was significantly higher ($P<0.001$; LSD @ $P<0.05$= 14%) at 49 % than with Al Arudsabba. In 1996, no differences in fruit set were observed.

Ambient temperature on the day of pollination

In order to investigate the differences in fruit set between the two years, particularly for pollen type Khori, the temperatures on the day of pollination were examined as temperature is known to affect pollen germination *in vitro* (Furr and Ream, 1968). Maximum temperature on the day of pollination (T_{max}-DOP) was considered as it would be indicative of temperature to which pollination events were exposed, given that pollination took place between 10 AM and 3 PM. The results (Table 6-1) reveal that T_{max}-DOP was significantly higher ($P<0.05$) for Khori in 1995. There were no significant differences in 1996. Also, correlation between T_{max}-DOP and the percentage of pollinated fruits at 50 d.a.p. in 1995, indicated a significant ($P<0.05$, $r=0.8$), direct relationship for data blocked by pollen type Khori. Correlations were neither observed for data blocked by the other two pollen types, nor for overall data.

Table 6-1 MAXIMUM TEMPERATURE (° C) AT THE DAY OF POLLINATION FOR GROUPS OF BUNCHES POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN CV KHALAS IN 1995.

Pollen type	*Maximum temperature (° C) at the day of pollination*	
Al Arudsabba	27.2	b
Bahlani	27.6	ab
Khori	28.1	a

LSD @ P<0.05 = 0.7 ° C ; CV(%)=0.1 %.

These results indicate that pollen type Khori or the events involved in fertilization with this type may have responded to temperature. In 1996, differences in temperature were non-existent and no correlation between fruit set and these temperatures were apparent. The responsiveness of Khori to temperatures in 1995 could be the reason for the high fruit set in Khori in comparison to the other two types and in comparison to the year 1996. It may be that a phase threshold temperature of about 28 ° C existed, from which onwards such a response occurred.

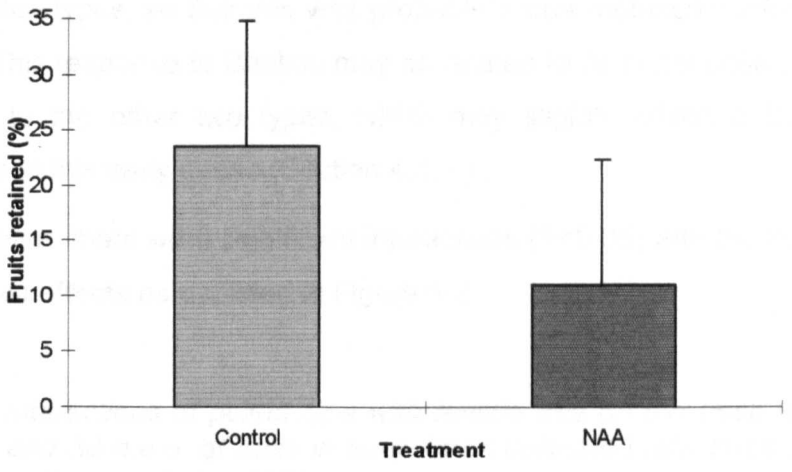
In cv Khasab, correlations of fruit set with temperatures on the day of pollination did neither exist for pollen blocks nor overall data. Though pollination in cv Khasab was in 1995 later than for cv Khalas, mean temperatures for the Khori block were lower than 28 ° C with a coefficient of variation of 8.5 %. This CV (%) indicates that a lot of temperatures were much lower than the assumed threshold temperature in comparison to the Khori block in cv Khalas in 1995. This would imply that for nearly half of the bunches the response of fruit set to temperature did not yet occur.

Effect of applied PGRs

NAA significantly (P<0.05) reduced the percentage of unpollinated fruits at 40 d.a.p. in Khori-pollinated trees as compared to control (Figure 6-2).

In 1995 only Al Arudsabba-pollinated trees were studied, in which no hormone effects on fruit set were observed and in 1996 there was also no response of such trees to plant growth regulators.

Figure 6-2 *Effect of NAA applied 6 d.a.p. on the percentage of unfertilized fruits at 40 d.a.p., which were pollinated with pollen type Khori in 1996.*



6.1.2 Fruit weight

Fruit weight measured in terms of fresh weight is an important characteristic which reflects growth both by cell division and enlargement and so presents also a measure of fruit size. The effect of pollen and plant growth regulators on different varieties will be examined.

CV Khasab:

Pollen effects:

During the lag phase in 1996 pollen type had a significant effect ($P<0.05$) on the fresh fruit weight as shown in Table 6-2, but not on the dry fruit weight of fertilized ovaries of the cv Khasab.

Table 6-2 INCREASE IN FRESH FRUIT WEIGHT BETWEEN 12 AND 30 D.A.P. IN BUNCHES OF CV KHASAB POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

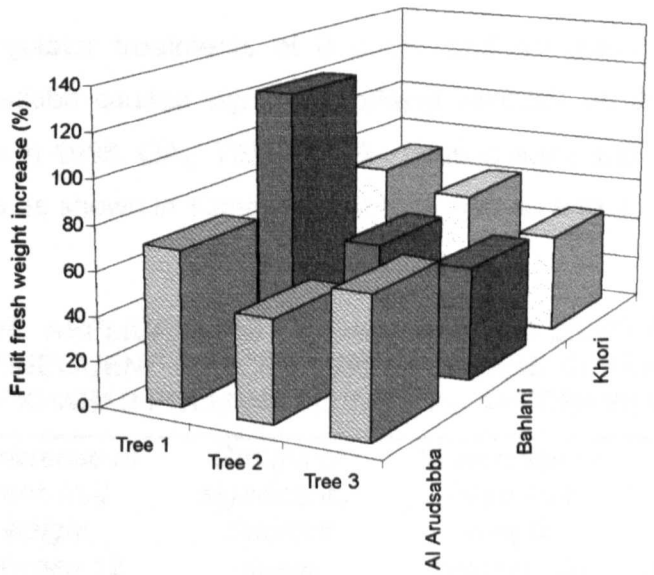
Pollen type	*Mean increase in fruit fresh weight (%) 12 to 30 d.a.p.*	
Al Arudsabba	59.6	b
Bahlani	76.6	a
Khori	59.1	b

LSD @ $P<0.05$ = 14.6 %

Bahlani resulted in a significantly higher increase in fresh fruit weight than the other two pollen types. This occurred in the absence of differences in fruit set between pollen types, so that this was probably a true metaxenic effect independent of fruit set. This response to Bahlani may be related to its faster pollen tube growth in comparison to the other two types, which may slightly advance fruit growth and development in this early phase (Section 4.1.3.).

However, there were significant interactions ($P<0.05$) with the highly significant ($P<0.001$) tree effects as depicted in Figure 6-3.

Figure 6-3 *Interactions of pollen type with female tree on the fresh weight increase between 12 and 30 d.a.p. of fruits in three trees pollinated with three different pollen types in the cv Khasab during 1996.*



Bahlani markedly increased mean fruit fresh weight in Tree No.1, while its effect was on par with Khori's in Tree No.2 and intermediate to the two other pollen types in case of Tree No.3.

In 1995 significant ($P<0.001$) pollen effects were observed in that Al Arudsabba induced the lowest fruit fresh weight at 50 d.a.p. (Table 6-3).

Table 6-3 FRUIT FRESH WEIGHT 50 D.A.P. IN BUNCHES OF CV KHASAB POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1995.

Pollen type	*Fruit fresh weight (g)*	.
Al Arudsabba	0.19	b
Bahlani	0.28	a
Khori	0.30	a

LSD @ P<0.05 = 0.03 g.

Although these effects occurred at equal real time (50 d.a.p.), they must be viewed with caution as thermal time for the Al Arudsabba pollen blocks was 15% lower as compared (P<0.001) to the other blocks.

Effect of applied PGRs

Plant growth regulator treatments at 6 d.a.p. and 40 d.a.p. of bunches pollinated with Al Arudsabba caused significant effects (p<0.05) on the percentage increase in fresh weight in 1996. GA_3, TIBA and BA caused early and TIBA, BA and DZ late inhibitory effects as shown in Table 6-4, but NAA had no effect.

Table 6-4 EFFECTS OF APPLICATIONS OF GA_3, TIBA AND BA AT 6 D.A.P. AND 40 D.A.P. ON THE SUBSEQUENT PERCENTAGE INCREASE IN FRESH WEIGHT OF FRUITS OF THE CV KHASAB POLLINATED WITH AL ARUDSABBA IN 1996

Plant growth regulator	*% increase in fresh fruit weight between 12 and 30 d.a.p.*	*Groups of significantly different means*	*% increase in fresh fruit weight between 40 and 50 d.a.p.*	*Groups of significantly different means (LSD)*
Control	83.1	a	103.8	a
GA3	63.6	bc	93.4	ab
TIBA	63.1	bc	65.3	cd
BA	51.5	c	81.4	bc
DZ	75.1	ab	61.1	d

In 1996, between 12 and 30 d.a.p., applications of GA_3, TIBA and BA caused a reduction in fresh weight increase compared to control. The second application at

40 d.a.p. of TIBA, BA and Daminozide caused inhibitory effects over the period of the next 10 days, while GA_3 had no such effects.

Daminozide caused a significant reduction in fruit fresh weight gain. Applications of GA_3 and BA retarded growth in later phases as well as will be seen later on. None of the growth regulators promoted fruit set. There was no indication from these results of any single growth regulators being responsible for the promoting effect of Bahlani on fruit weight.

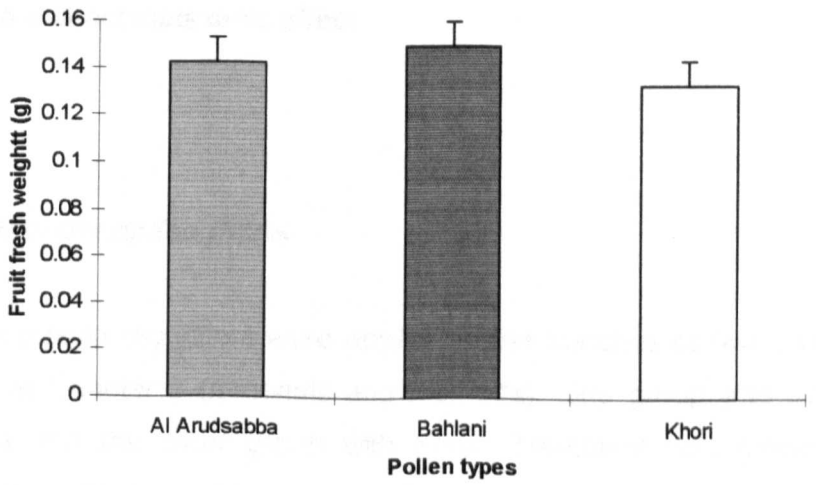
Plant growth regulator applications in 1995 at the day of pollination had no significant effect on fresh fruit weight, rate of fruit growth or on percentage increase at 50 d.a.p..

CV Khalas:

Pollen effects

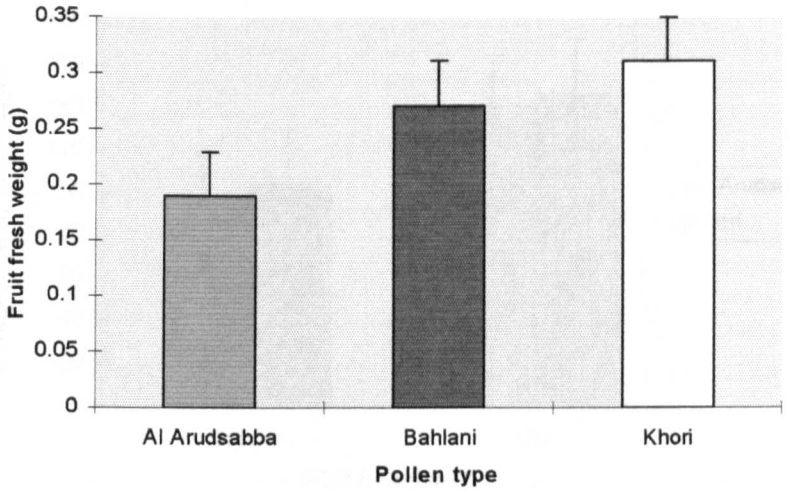
The cv Khalas was also used to investigate effects of pollen type on early fruit growth. Significant pollen effects on fruit weight were observed during the lag phase in cv Khalas during both years of the study (Figures 6-4 and 6-5).

Figure 6-4 *Fruit fresh weight at 40 d.a.p. in cv Khalas pollinated with three different pollen types in 1996. LSD bar @ P<0.05 are shown*



Bahlani again resulted in the highest fruit fresh weight at 40 d.a.p, but dry weight was not affected. As there were no differences in fruit set at any time during the lag phase in 1996, the observed pollen effect on fresh weight was not mediated by different levels of fruit set and so was probably a true metaxenic effect.

Figure 6-5 *Fruit fresh weight at 50 d.a.p. in cv Khalas pollinated with three different pollen types in 1995. LSD-bars at P<0.001 are shown.*



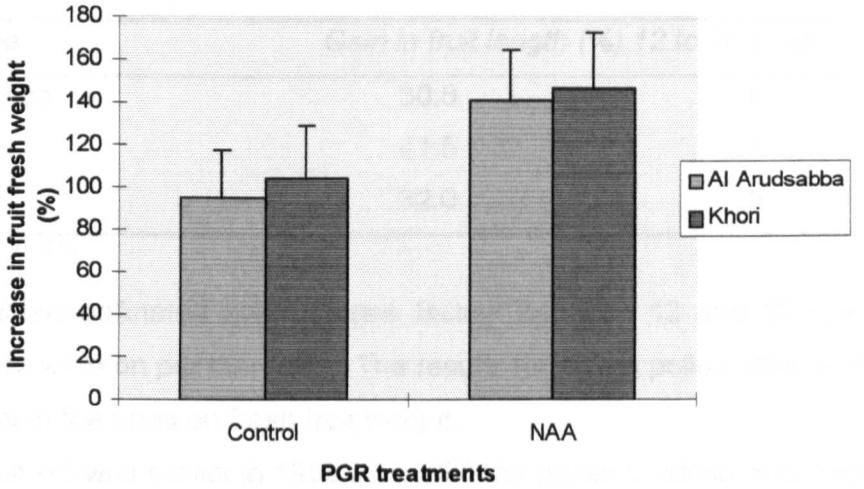
Treatments with pollen types Khori and Bahlani (Figure 6-5) were on par and resulted in the highest fruit fresh weight at 50 d.a.p. ($P<0.001$) when compared to Al Arudsabba. Khori induced a higher fruitset than Al Arudsabba and Bahlani, which were on par (Section 6.1.1). There is a highly significant correlation ($P<0.01$, $r = 0.63$ at $n=16$) between the two variables (Section 6.2.1.), so that the effect observed on fruit weight here were more likely to be a direct result of different levels of fruit set rather than a direct metaxenic effect.

Effect of applied PGRs

Six growth regulators were applied to the bunches of two groups of trees as described in Chapter 3 (materials and methods). One group was pollinated with Al Arudsabba and the other group with Khori. Treatment with growth regulators of bunches of cv Khalas, which were pollinated in 1996 with the two pollen types Al

Arudsabba and Khori, affected fruit fresh weight. Significantly different treatments are shown in Figure 6-6.

Figure 6-6 *Effects of NAA applied 6 d.a.p. on the percentage increase in fruit fresh weight between 12 and 40 d.a.p. in two groups of trees of cv Khalas pollinated with pollen types Al Arudsabba and Khori in 1996 (LSD @ P<0.05 bars for comparison between PGR treatments are shown)*



Pollen types: Al Arudsabba: LSD @ P<0.05 = 22.8 %; Khori LSD @ P<0.05 = 25.5 %.

In comparison to control, NAA resulted in both groups in significant (P<0.05) increases of about 45 % in fresh fruit weight between 12 and 40 d.a.p. However, pollen type and NAA did not interact.

In 1995 no comparison of pollen types with regard to the effect of hormone treatments on fruit weight was possible due to loss of Khori replicates.

6.1.3 Fruit size

Fruit length and width has been reported as affected by pollen type in California (Nixon, 1955). The following study investigates such possible effects with different cultivars under the different environment in the northern Batinah region of Oman.

CV Khasab:

Pollen effects:

Effects on fruit length were observed in this cv during Stage 1 in 1996 (Table 6-5) , but none on fruit width. In 1995 no such effects were observed.

Table 6-5 GAIN IN FRUIT LENGTH BETWEEN 12 AND 30 D.A.P. IN BUNCHES OF THREE TREES OF THE CV KHASAB POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996

Pollen type	*Gain in fruit length (%) 12 to 30 d.a.p.*	
Al Arudsabba	30.6	b
Bahlani	41.5	a
Khori	32.0	b

LSD @ P<0.05 = 8.2 %

Bahlani-pollinated ovaries grew fastest between 12 and 30 d.a.p., while all pollen types were on par thereafter. The results regarding pollen effects on fruit length are parallel to the ones on fresh fruit weight.

Fruit set was similar in 1995 and 1996 for pollen treatments during this stage, so that a direct metaxenic effect independent of fruit set can be assumed.

Effect of applied PGRs:

BA inhibited (P<0.05) gain in fruit length in 1996 as shown in Table 6-6. Other treatments at 6 d.a.p. had no effect with plant growth regulators of bunches pollinated with Al Arudsabba.

Table 6-6 EFFECT OF BA APPLICATIONS AT 6 D.A.P. ON THE SUBSEQUENT PERCENTAGE INCREASE IN FRUIT LENGTH IN CV KHASAB IN 1996

Pollen type	*Gain (%) in fruit length between 12 and 30 d.a.p.*	*Groups of significantly different means*
Control	41.2	a
BA	29.7	b

LSD @ P<0.05 =7.1 %.

Recalling that Bahlani previously caused a significant increase compared to Al Arudsabba, it is speculated that no single growth regulators is responsible for this effect of Bahlani on fruit length.

CV Khalas:

Pollen effects:

Significant pollen effects on fruit length and width were observed during the lag phase in cv Khalas during both years of the study (Tables 6-7 and 6-8).

Table 6-7 LENGTH (CM) AND WIDTH (CM) OF FRUITS AT 12 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996

	Measurement (cm) at 12 d.a.p.			
Pollen type	*fruit length*		*fruit width*	
Al Arudsabba	0.54	a	0.47	a
Bahlani	0.55	a	0.47	a
Khori	0.51	b	0.44	b

Fruit length: LSD @ P<0.05 =0.025 cm; Fruit width: LSD @ P<0.01 =0.02 cm.

Ovaries pollinated in 1996 with Al Arudsabba and Bahlani formed fruits that were the longest (P<0.05) and widest (P<0.01) at 12 d.a.p.. The difference was small but highly significant. After 12 d.a.p. no pollen effects were observed. Because fruit set was not affected by pollen type at any time during this stage, it can be assumed that all effects were direct metaxenic pollen effects.

Table 6-8 LENGTH (CM) AND WIDTH (CM) OF FRUITS AT 50 D.A.P. IN BUNCHES OF TWO TREES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1995.

	Measurement (cm) at 50 d.a.p.			
Pollen type	*Fruit length*		*Fruit width*	
Al Arudsabba	0.82	c	0.64	b
Bahlani	0.94	b	0.78	a
Khori	1	a	0.8	a

Fruit length: LSD @ P<0.05 = 0.05 cm; fruit width: LSD @ P<0.05 = 0.03 cm.

As presented in Table 6-8 pollination with Bahlani and Khori resulted in 1995 in the longest and widest fruits at 50 d.a.p.. Fruit set was also significantly increased by pollen type Khori as shown earlier. However, Bahlani caused longer and wider fruits than Al Arudsabba although levels of fruit set are on par, which possibly indicates a direct pollen effect of Bahlani. Thermal time accumulation for the Khori block was on par with the one for the Bahlani block, but higher than that of the Al Arudsabba block. Khori induced the highest fruit set with the largest fruit, while Bahlani produces large fruits at a low fruit set. It should be noted with a view of results presented later that this is the first result, where Khori is superior to all other treatments.

Effect of applied PGRs:

Growth regulator treatments in 1996 did not interact with pollen type on either fruit length or width during the lag phase. Table 6-9 shows the effect of BA on fruit length.

Table 6-9 EFFECT OF BA APPLICATIONS AT 6 D.A.P. ON FRUIT LENGTH AT 12 D.A.P. IN CV KHALAS IN 1996

Pollen type	*Fruit length (cm) at 12 d.a.p.*	
Control	0.54	a
BA	0.51	b

LSD @ P<0.05 = 0.1 cm.

BA induced a shorter fruit length at 12 d.a.p. than control (P<).05). No PGR effects were found thereafter.

In 1995 no comparison of pollen types with regard to the effect of hormone treatments on fruit length and width was possible due to loss of replicates for pollen type Khori.

6.1.4 Chemical analysis of pollinated ovaries

This experiment was carried out to determine possible differences in a range of endogenous growth regulators and other substances between ovaries pollinated with different types at various times after pollination. The examination focused on 24 hours after pollination, because this would be when the pollen tube would have

reached the ovule (Reuveni, 1986), possibly causing fertilization. At this point any differences would have to be triggered by the pollen grain itself, by the subsequent pollen tube growth or by fertilisation. Genetic effects were not expected as significant syngamous tissues were absent (with the exception of the zygote and the endosperm nucleus).

Fourteen d.a.p. was chosen because

- it was well within the period up to 30-40 d.a.p. during which the zygote remained dormant (Chapter 4) and
- at that time a safe period of 12 days had lapsed, during which all bunches may still have been receptive to unwanted pollination. They were kept covered by paper bags during that period.

Stages of development later than 30-40 d.a.p. may have been under the control of genetic events and were examined using plant growth regulator treatments as presented in the previous sections.

Bunches of the cv Khalas were pollinated with the three pollen types Al Arudsabba, Bahlani and Khori. Ovaries from these bunches were collected 24 hours after pollination and again at the 14 th day after pollination. They were ground in an electric blender and were kept for 48-72 hours in Methanol (50% v/v) at -20 C. This procedure extracted auxins, abscisic acid and cytokinins like zeatin (Davis, 1968). The extract were prepared for injection into a Hewlett Packard High Performance Liquid Chromatograph as described in Chapter 3. The procedure was carried out on pollen types twice in 1996 and once in 1997. This should have produced a range of peaks as a result of the numerous compounds in the samples. As no positive identification of the distinct substances was possible, this HPLC analysis was only preliminary and merits further research. To represent the general plant growth regulator composition, the solvent peaks were disregarded and the remaining peaks were expressed as a percentage of the total area under the curve after the solvent peaks had eluted. This transformation of the data enabled comparison of the curves for different treatments. The general composition for the three lots of ovaries were similar before pollination. Figures 6-7 and 6-8 show the results for 24 hours and 14 days after pollination, respectively.

Figure 6-7 *HPLC analysis of ovules from cv Khalas 24 hours after pollination in 1996 with three different pollen types. The peaks are plotted against the run time and their area expressed as percentage of the total area under the curve. Mobile Phase: methanol: water 60:40, Column: Hypersil ODS; UV detector: 254 nm; Flow rate: 1 ml/minute .*

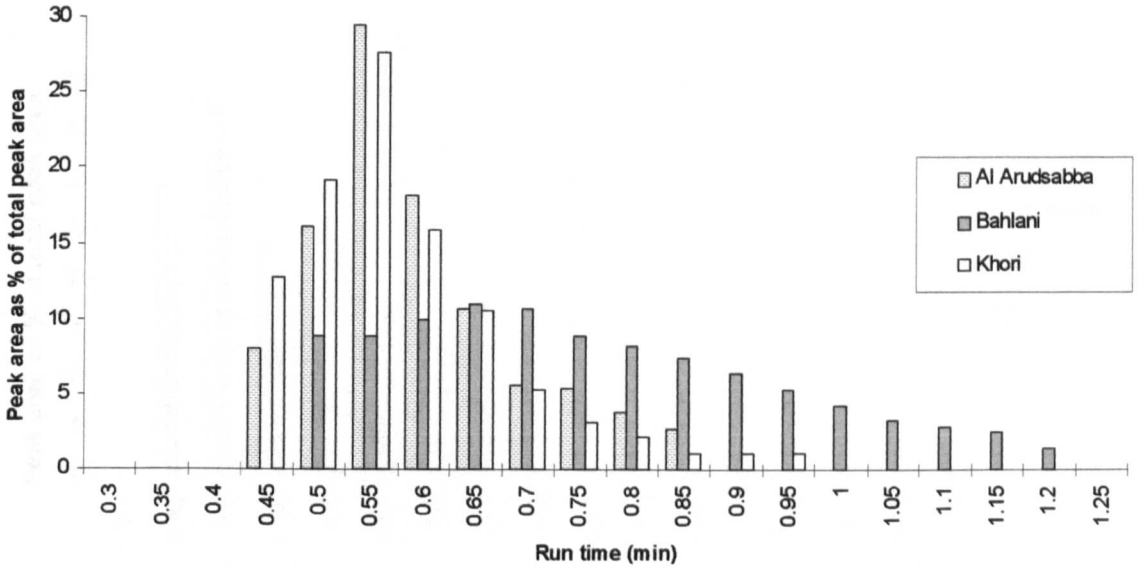


Figure 6-7 shows the HPLC analysis results of three lots of ovaries just after pollination (24 hours) with the three types of pollen. The curves for the types Al Arudsabba and Khori are similar. Starting from 4.5 minutes run time, the eluting peaks increased rapidly in magnitude with the largest peak (about 30 % of the total area) eluting after 5.5 minutes run time. Thereafter the magnitude of peaks declined to zero in both types at 8.5 to 9.5 minutes. In comparison, Bahlani had a distinctly different pattern of peaks, increasing from 9 % at 5 minutes runtime to a maximum peak (12 %) between 6.5 and 7 minutes. Peaks declined thereafter at a comparatively low rate to zero at 12.5 minutes.

The ovaries were again examined by HPLC on the 14th d.a.p. (Figure 6-8).

Figure 6-8 *HPLC analysis of ovaries from cv Khalas 14 days after pollination with three different pollen types in 1996. The peaks are plotted against the run time and their area has been expressed as percentage of the total area under the curve.*

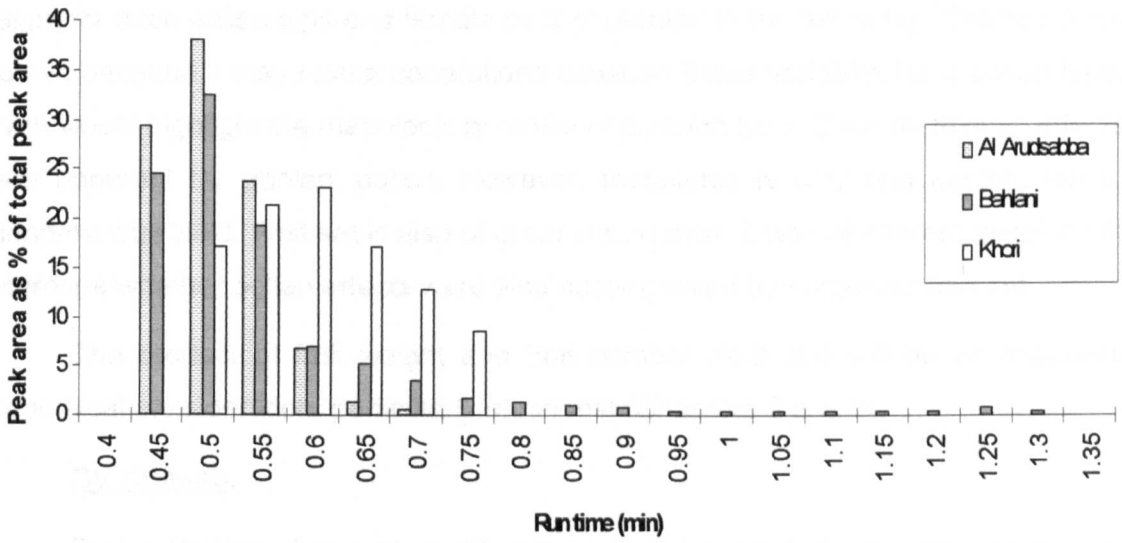


Figure 6-8 shows that Al Arudsabba and Bahlani pollinated ovules eluted a maximum peak (30-40% of total area under the curve) at a run time of 5 minutes and were similar thereafter, although Bahlani pollinated ovules elute peaks long after 7 minutes, when there were no Al Arudsabba peaks. Notably Khori pollinated ovules were distinctly different from the other two types. Here the maximum peak (20-25%) eluted after 6 min and peaks fell to zero at 7.5 minutes. The observed pattern was similar to the response of fruit weight at 40 d.a.p. and fruit size at 12 d.a.p., where Al Arudsabba and Bahlani were also similar and resulted in a larger effect than Khori. It also reflected the similarity of Al Arudsabba and Bahlani in their HPLC profile when the pollen itself was analysed.

6.2 Relationships between different variables

6.2.1 Fruits retained and fruit weight

An examination of possible relationships between fruit set and fresh fruit weight for each pollen type and female cv is presented in the following. This has been studied because it may reveal correlations between these variables for a pollen type, which would highlight the metaxenic potential of a pollen type. Clear metaxenic effects were apparent for Bahlani pollen. However, metaxenia is only one contribution to economic fruit yield. Fruit set is also of great importance. It was of interest therefore to determine whether pollen effects were also accompanied by enhanced fruit set.

The product of fruit weight and fruit number (fruit set) will be an important economical consideration, particularly at harvest (Chapters 8 and 9).

CV Khasab:

During the lag phase no significant correlations existed between fruit weight, increase in fruit weight or rate of change of fruit weight on the one hand and fruit set percentage or rate of abscission, when these variables were blocked according to the pollen type. This may reflect the low competition between spathes emerging in this cv over a long period of time (Chapter 5).

CV Khalas:

Bahlani was consistently superior to at least one of the other two pollen types in promoting fruit growth in this female cultivar. Results presented in Section 5.3 showed that when pollen types were blocked together in 1996, negative correlations existed in 1996 between fruit set in the lag phase and fruit weight in the next stage, while a positive correlation was found in 1995.

In 1996 no relationship existed between any pair of the variables described for cv Khalas..

In 1995 no significant correlation between the percentage of pollinated fruits at 50 d.a.p. and fresh fruit weight at that time was found when data were blocked according to pollen type, although a significant ($r= 0.63$, $n=16$, $P<0.01$) overall correlation exists.

6.2.2 Thermal time and fruit weight

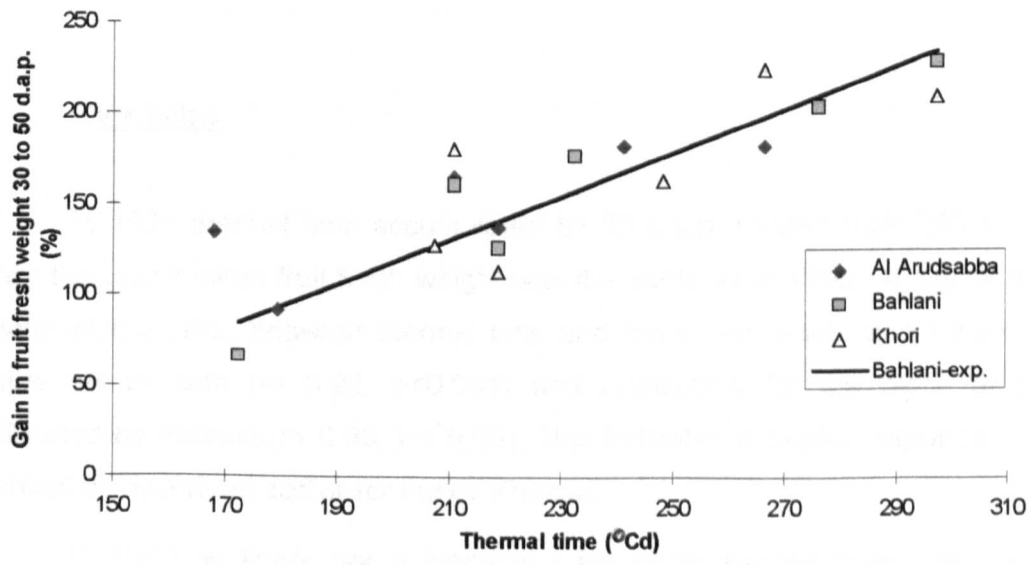
Fruit development did take place during different periods of the annual season. This means that at equal real time (d.a.p.) they may have been exposed to different temperature regimes. Therefore, a comparison of fruit growth and development on a thermal time (°Cd) basis was considered necessary.

Fruit growth in many plants is well correlated with thermal time accumulation. Whilst no rigorous procedure has been yet established, a base temperature of 18 °C has been claimed for growth of date palms (Dowson, 1982). From the earlier sections (6.1.2.) of this chapter, the pollen type Bahlani has been claimed to induce earlier fruit growth than the other two types. If this is true, then for Bahlani it should be possible to correlate early fruit growth with thermal time better than for Al Arudsabba and Khori. The following will examine the relationship of thermal time and fresh fruit weight for each pollen type. This may provide information as to commencement of active growth and may be also useful by providing a common base on which to compare 1995 and 1996.

CV Khasab:

The range of thermal time at 50 d.a.p. was from 170 to 300 degree days, which probably was sufficient variation to account for a response of growth.

Figure 6-9 *Relationship of the increase (%) of fresh fruit weight between 30 and 50 d.a.p. in cv Khasab with thermal time (°Cd; base temp. 18 °C) at 50 d.a.p. for treatments with three pollen types during 1996.*



There was an overall positive correlation (r =0.85, n=18, P<0.001) between these two variables. However, as shown in Figure 6-9, only in case of Bahlani could a similar positive correlation (r =0.94, n=6, P<0.01) be found while there was none for the other two pollen treatments. The relationship between thermal time accumulated at 50 d.a.p. (x) and the fruit weight gain between 30 and 50 d.a.p. (y) can be expressed by the regression equations:

- for Bahlani: $y = -121 + 1.2 \cdot x$, ($P<0.01$, $r^2 = 0.88$)
- for all data points: $y = -63 + 1.0 \cdot x$, ($P<0.001$, $r^2 = 0.72$)

It appears that in Bahlani a high total accumulated thermal time or heat summation up to the 50 d.a.p. coincided with a larger percentage increase in fruit weight between 30 and 50 d.a.p., while there was no evidence that such a relationship existed for the other two types. Furthermore, an examination of the thermal time up to 30 d.a.p. and the corresponding fruit weight increase (%) between 12 and 30 d.a.p. revealed neither an overall linear relationship nor one for any one of the pollen types. As will be seen in later chapters, in later stages a relationship was also found for the other pollen types.

From the above it can be concluded that the growth of fruits (%) pollinated with Bahlani responds earlier than in the other two types in terms of heat summation.

Because, no pollen effects were observed in cv Khasab in 1995, no relationship between thermal time and fruit weight has been examined.

CV Khalas

In 1995 thermal time accumulated by 50 d.a.p. ranged from 220 to 270 °Cd while the grand mean fruit fresh weight was the same as in 1996. A significant linear relationship existed between thermal time and fresh fruit weight at 50 d.a.p. for the entire set of data (r= 0.92, p<0.001) and particularly for the block of bunches pollinated by Bahlani (r= 0.93, P< 0.05). This indicates a similar response pattern to Bahlani as described earlier for the cv Khasab.

In 1996 no linear nor polynomial relationship existed during the lag phase between fresh fruit weight, the fruit weight gain and the rate of fruit growth (fresh

weight) on the one hand and thermal time on the other hand. This holds true for data blocked by pollen type and for the entire set of data. However, the pollination period lasted only 13 days and the thermal time ranged only from 180 to 210 °Cd, which was possibly too low or too less variation to cause any growth response. It should be therefor kept in mind that any pollen-specific thermal time-growth relationship could be masked due to this cv's characteristically narrow range of heat summation..

The existence of the described relationship in 1995 and its absence in 1996 was possibly due to the substantially higher heat summation in 1995, when both the variation and the mean of heat summation were higher. A comparison of the means of fruit weight and heat summation for individual pollen treatments in 1996 and 1995 revealed that in case of Bahlani and Khori the fruit weight attained by 50 d.a.p. in 1995 was higher than in 1996 as shown in Table 6-10.

Table 6-10 FRUIT FRESH WEIGHT AND THERMAL TIME AT 50 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996 AND 1995.

Pollen type	*1996*		*1995*	
	Fruit fresh weight at 50 d.a.p. (g)	*Thermal time at 50 d.a.p. (°Cd)*	*Fruit fresh weight at 50 d.a.p. (g)*	*Thermal time at 50 d.a.p. (°Cd)*
Al Arudsabba	0.26 a	188 a	0.19 b	226 b
Bahlani	0.24 a	194 a	0.28 a	264 a
Khori	0.24 a	194 a	0.30 a	268 a

1995- Fruit fresh weight: LSD @ P<0.001 = 0.06 g; Thermal time: LSD @ P<0.05 = 12 °Cd.

The results (Table 6-10) suggests that in 1995 differences in heat summation at 50 d.a.p. were associated with the pollen effects on fruit weight. However, considering the significant (P<0.05) differences in fruit length (Section 6.1.3) between any two treatments, a true metaxenic effect is still indicated as it bears no similarity to response patterns of effects on fruit set and to thermal time. In any case, a true metaxenic effect of pollen type on fruit weight in cv Khalas in 1995 can not be proved at this stage, while the significant difference (P<0.05) between the fruit length caused by treatment with Khori and Bahlani was likely due to a superior metaxenic effect.

6.3. Summary and discussion

Effects on fruit set:

1. Pollen treatments had significant effects on fruit set in cv Khalas only in 1995 with Khori resulting in the highest fruit set possibly due to incompatibility mechanisms inactivated by higher temperatures at the time bunches were pollinated with Khori in 1995. It is known (Townsend, 1971) that relatively high temperatures can inactivate incompatibility mechanisms acting on the style, not the pollen.
2. Plant growth regulator treatments had a significant effect on fruit set of fertilized and the retention of unfertilized ovaries only in Khori pollinated Khalas bunches but not in those pollinated with Al Arudsabba in 1996 only. Notably, NAA reduced unfertilized fruits in cv Khalas and fertilized fruits in cv Khasab. As no syngamy had yet occurred this suggested physiological, non-hereditary mechanisms.

Effects on fruit fresh weight

1. Pollen type Bahlani increased fruit fresh weight in cv Khasab during 1996. In case of cv Khalas Bahlani increased fruit fresh weight in both years, while Khori did so only in 1995. As different levels of fruit set for each pollen treatment were absent in 1996, unlike in 1995, a true metaxenic effects can be assumed.
2. GA_3 inhibited very early and TIBA, BA and DZ later fruit growth in cv Khasab, while NAA promoted it in cv Khalas. As reported by Looney (1984), GA applications to seeded fruits at blossom time may inhibit development, possibly by reducing fruit set and he suggests that supra-optimal levels of GA may be responsible. He further reports that GA effects on fruit growth appear to decline in importance as the season progresses, which would be consistent with the results presented here.
3. It is noteworthy that Bahlani increased fruit fresh weight in both cvs. In view of the data presented in section 4.1.4., similarity between Al Arudsabba and Bahlani reflecting compositional similarities revealed by HPLC, was expected with regard to pollen effect. In cv Khalas this was the case, but not in cv Khasab. As, however, AAS examination revealed that Bahlani differed from the other pollen types by its low Cu-content, a possible role for Copper during this stage of cv Khasab-fruit

growth and development is implicated. Also, the effect caused in particular by Bahlani may be due to faster *in vivo* growth of the pollen tube in cv Khasab ovaries, which was observed *in vitro* and reported in 4.1.3.. This may result in cv Khasab in earlier fertilization and subsequently faster development.

Effect on fruit size:

1. Pollen type Bahlani increased fruit size early on in both cvs during 1996, while in 1995 Bahlani and Khori induced larger fruits than Al Arudsabba in cv Khalas only at 50 d.a.p., while no such effect was observed in the following year. A direct metaxenic effect of Bahlani over Al Arudsabba and Khori may have existed as fruit set was unaffected by Bahlani.
2. For the first time Khori caused a stronger effect than both other two types in case of fruit length in cv Khalas at 50 d.a.p. in 1995.

Chemical analysis of pollinated ovaries

24 hours after pollination Al Arudsabba and Khori pollinated ovaries had a similar general PGR composition, but Bahlani was different, while fourteen days after pollination Al Arudsabba and Bahlani pollinated ovaries had a similar general PGR composition, but Khori was different. However, at that time Bahlani pollinated ovaries contained the widest range of substances.

Relationship between fruit weight and thermal time

Bahlani pollinated fruits are responsive earlier to heat summation in case of both cvs Khasab and Khalas.

This response appears after zygote division and cellularization of the endosperm has started, while it is absent during the early stage of the dormant zygote. However, it is recalled that Bahlani caused a faster growth (fruit weight and fruit length) between 12 and 30 d.a.p. indicating that possibly a comparatively more advanced stage of development is reached in Bahlani pollinated ovaries earlier than in others. This could be the reason why these ovaries are able to respond linearly with increasing heat summation.

Viewing these results it appears likely that pollen effects on fresh weight may have been indirectly due to substances contributed by pollen or formed due to pollination. For example, Wang (1996) reports that ethylene accentuates signal molecules for pollination-induced mRNA and ONeill (1997) mentions interorgan signalling following pollination involving the regulation of ethylene-biosynthetic gene expression and interorgan transport of hormones and their precursors. Also Hetherington (1991) suggests that a role of ABA in preparing tissue for entry into a new and different physiological state. It is possible that different pollen types carry different complements and quantities of inducing compounds, which would also contribute to the differences in the HPLC analysis and the bioassay of pollen types reported on earlier. Devic (1996) reported that genes get promoted by signal molecules, possibly hormones, already in the stages preceding morphogenesis, which in this study would during the zygote stage. Bahlani differed from the other two pollen types by having the longest pollen tube after 24 hours' *in vitro* growth, which leads to the speculation that its tubes may have reached the ovary earlier. This would imply that biochemical pathways triggered by pollination events, were more advanced in case of Bahlani when compared to the other two types. As no growth observation in 1996 had a pattern similar to the one depicted in Figure 6-7, it may be speculated that it reflected differences in pollen tube growth rate. A wider range of peaks had eluted in the HPLC analysis of ovaries pollinated with Bahlani, which would have also been expected if the biochemical processes triggered by pathways caused by pollination were more advanced. The role of pollen tube growth in fruit set was also described by Bassiri (1967) , who observed that seed set failure in *Cicer* could be attributed to the slowness of pollen tube growth and the collapse of fertilized ovules. In this study, the possibility of an early genetic effect triggered by a signalling zygote and/or endosperm can not be conclusively ruled out. However, the pre-meiosis differences for Bahlani pollen strengthen the argument for a biochemical, non-hereditary mechanism.

The HPLC characteristics of the pollen type was not reflected in the physical and chemical characteristics of pollinated ovaries immediately after fertilisation, which suggests that pollen composition *per se* did not cause a response in ovules after the formation of the zygote and endosperm nucleus. It is anyhow unlikely that the differences in the HPLC analysis (Figure 6-7) were due to the mere addition of substances by the pollen grains as only a few pollen grains landed and adhered to the

stigma, which would have contributed an insignificant quantity of substances, insufficient to explain the substantial differences observed. The cause of these differences was probably substances formed following an interaction between pollen grain and stigma/style.

It appears that early effects on physical variables in cv Khalas were in 1996 under the control of the rate of pollen tube growth and of compositional or physiological characteristics of the pollen type that trigger complex biochemical reactions. Looking at the results of Sections 6.1.2. and 6.1.3. it appears that pollination triggered various biochemical processes, first in Bahlani, slower in Al Arudsabba and slower still in Khori.

It appears that the metaxenic effect of Bahlani is initiated very early after pollination and during the subsequent days and it results, in comparison with the other two types, in an advanced state of development which lasts for a long time up to the end of the lag phase.

7. Stage Two: first rapid growth stage

Overall fruit growth takes place at a rate that increases from the end of the lag phase up to its maximum at the end of this stage. This corresponds with cellularization of the endosperm and embryo differentiation as shown in Chapter 4. Fruit growth is mainly by cell enlargement along the longitudinal axis (Reuveni, 1986; Long, 1943). Any pollen effects due to a genetic interaction of the male and female genomes is expected at this stage as most syngamous tissue develops during this stage. An interaction of pollen type and fruit set on fruit growth is likely.

Experiments were carried out to examine pollen and growth regulator effects on fruits of different cultivars as was the case in the previous chapter. They examine the effect of pollen type and of exogenous hormones (BA, Daminozide, GA3, HFCA, NAA and TIBA) on fruit growth and development stages (7.1.) looking for relationships between such variables as fruit and seed weight and size on the one hand and fruit set and thermal time on the other hand (7.2.) for each of the pollen types as these would be expected to vary with the metaxenic potential of a pollen type.

7.1 Pollen type and plant growth regulator effects on fruit growth and development

The experiments were designed to analyse pollen effects on several physical characteristics of the rapidly growing fruits and to suggest the underlying mechanisms. Differences due to a contribution from the male genotype were expected. The hormone experiments were designed to explore possible roles of major plant growth substances in regulating fruit growth and development and from there look for parallels with any pollen effects. As fruit set is known to influence the growth of the fruit (Chapter 5), pollen effects could be mediated through this as well as through plant growth regulators. Fruit set effects were therefore an important consideration in this study.

7.1.1 Fruit set

Fruit set as influenced by pollen type is examined here. Fruit drop occurred as the last event in a series of biochemical and physiological events. Therefor fruit set at 110 d.a.p., which was just after the rapid growth phase, was likely to be the result of events occurring earlier on during that stage. Pollen effects were measured in two female cvs: Khalas and Khasab.

CV Khalas:

Pollen effects:

About 5 % of all ovaries dropped during this stage. Pollen effects were observed in 1995 at 110 d.a.p. as shown in Table 7-1. None were observed in 1996.

Table 7-1 FRUIT SET AT 110 D.A.P. IN CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1995.

	Fruit set (%)	
Pollen type	*110 d.a.p.*	
Al Arudsabba	30	b
Bahlani	29	b
Khori	44	a

LSD @P<0.05 = 12.2

Fruit set in Khori pollinated bunches was 46 % higher (P<0.05) than in bunches pollinated with Al Arudsabba and Bahlani, which were on par. It may be recalled that a similar response pattern was observed at 50 d.a.p.. It was expected that this would affect fruit growth and development.

Effect of applied PGRs:

NAA significantly (P<0.05) reduced the percentage of unpollinated fruits to zero at 65 d.a.p. in Khori-pollinated trees (Table 7-2) in 1996. The auxin inhibitor, HFCA, increased (P<0.05) the percentage of unpollinated fruits by 111 %.

Table 7-2 EFFECT OF NAA AND HFCA APPLIED 6 AND 40 D.A.P. ON THE PERCENTAGE OF UNFERTILIZED FRUITS IN CV KHALAS AT 65 D.A.P., WHICH WERE POLLINATED WITH POLLEN TYPE KHORI IN 1996.

	Unfertilized fruits (%)	
Pollen type	*65 d.a.p.*	
Control	5.8	b
HFCA	12.4	a
NAA	0	c

LSD @ P<0.05 = 5.8 %

Neither treatment affected the percentage of pollinated or total number of fruits. It should be noted that in Al Arudsabba-pollinated bunches of the same experiment no such effects were observed. Furthermore, no interactions with pollen type were observed and none of the pollen treatments caused similar effects. In 1995, only Al Arudsabba-pollinated trees were studied, in which no hormone effects on fruit set were observed, as was also the case in 1996.

CV Khasab:

About 9 % of all ovaries dropped during this stage. No pollen effects were observed during this stage or at 110 d.a.p..

7.1.2 Fruit and seed weight

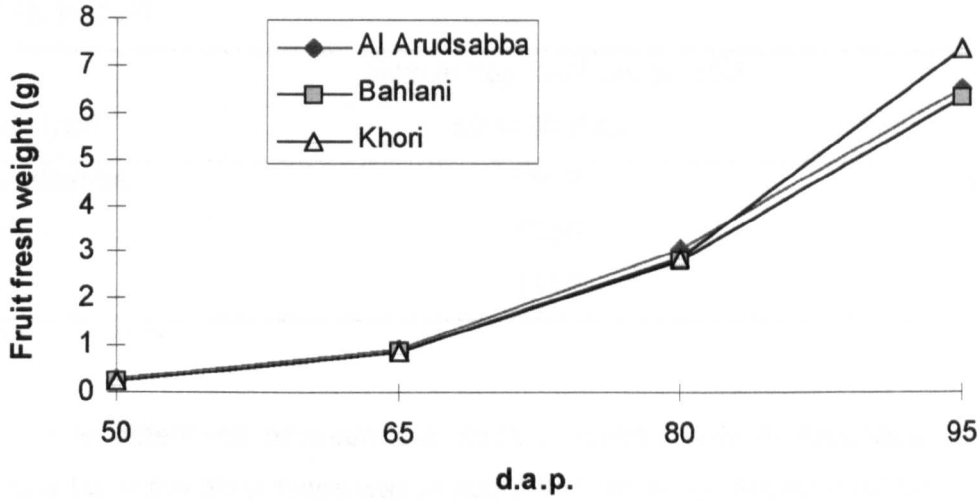
CV Khalas:

Pollen effects:

Pollen effects on fruit weight could be observed in both years, but on seed weight only in 1995.

Figure 7-1 shows pollen effects in 1996 , particularly between 80 and 95 d.a.p.

Figure 7-1 *Fresh fruit weight (g) during the first rapid growth phase in bunches of cv Khalas pollinated with three different pollen types in 1996.*



Apparently Khori pollinated fruits grew fastest. Further detailed examination of the fresh weight gain during this period is presented in Table 7-3.

Table 7-3 GAIN IN FRUIT FRESH WEIGHT BETWEEN 80 AND 95 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

	Gain in fruit weight (%)	
Pollen type	*80 to 95 d.a.p.*	
Al Arudsabba	115	b
Bahlani	127	ab
Khori	167	a

LSD @ P<0.05 = 40 %.

Khori pollinated fruits grew 52 % more than Al Arudsabba. As this occurred in the absence of fruit set effects, these were probably true metaxenic effects.

In 1995 several pollen effects were observed.

- on the gain of fruit fresh weight (Table 7-4),
- on the fruit fresh weight as shown in Table 7-5 and
- on the seed fresh weight as shown in Table 7-6.

Table 7-4 GAIN (%) IN FRUIT FRESH WEIGHT BETWEEN 50 AND 80 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1995.

	Gain in fruit fresh weight (%)	
Pollen type	*50 to 80 d.a.p.*	
Al Arudsabba	1530	a
Bahlani	1360	b
Khori	1390	b

LSD @ P< 0.01 = 127 %.

The difference between the block pollinated with Al Arudsabba and those pollinated with the other types was at about 8 % highly significant (P<0.01).

Table 7-5 FRUIT FRESH WEIGHT AT 80 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1995.

	Mean Fruit weight (g)	
Pollen type	*80 d.a.p.*	
Al Arudsabba	3.1	c
Bahlani	4.0	b
Khori	4.5	a

LSD @ P<0.05= 0.3 g.

Table 7-6 shows that treatment with Khori resulted in heavier seeds followed by Bahlani, then Khori. Treatments with Khori and Bahlani resulted in heavier fruits, about 50 % and 30 % respectively, than Al Arudsabba (Table 7-6). The pattern was similar to that observed 50 d.a.p..

Table 7-6 SEED FRESH WEIGHT AT 80 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1995.

	Seed fresh weight (g)	
Pollen type	*80 d.a.p.*	
Al Arudsabba	0.15	c
Bahlani	0.24	b
Khori	0.3	a

LSD @ P<0.05 = 0.03 g.

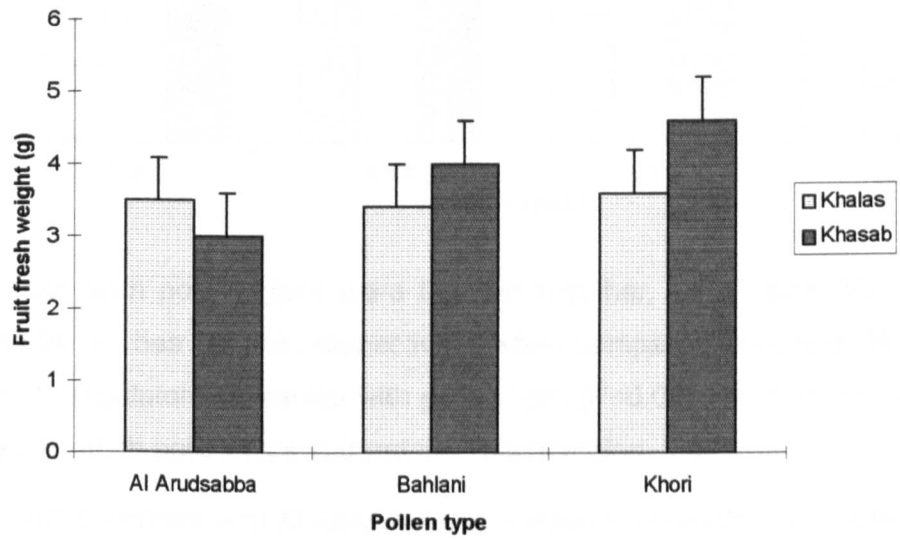
Table 7-6 shows that here also treatment with Khori resulted in heavier seeds followed by Bahlani, then Khori. Khori and Bahlani treated fruits had seeds about 100 % and 50 % heavier, respectively, than Al Arudsabba.

As fruit set was affected by pollen type at 50 d.a.p in both years and at 110 d.a.p. in 1995, it was necessary to examine the described pollen effects on fruit growth and development against this background. This will be presented in the Section 7.2.1. (Correlations).

Interaction of cv and pollen type:

Fruit fresh weight was only in 1995 significantly affected (LSD @ $P<0.05$ = 0.6 g) by the interaction effect of pollen type x cv as shown in Figure 7-2.

Figure 7-2 *Interaction effect of pollen type x cvs on fruit fresh weight (g) at 80 d.a.p. in 1995. Bars for LSD @ P<0.05 = 0.6 g are shown.*



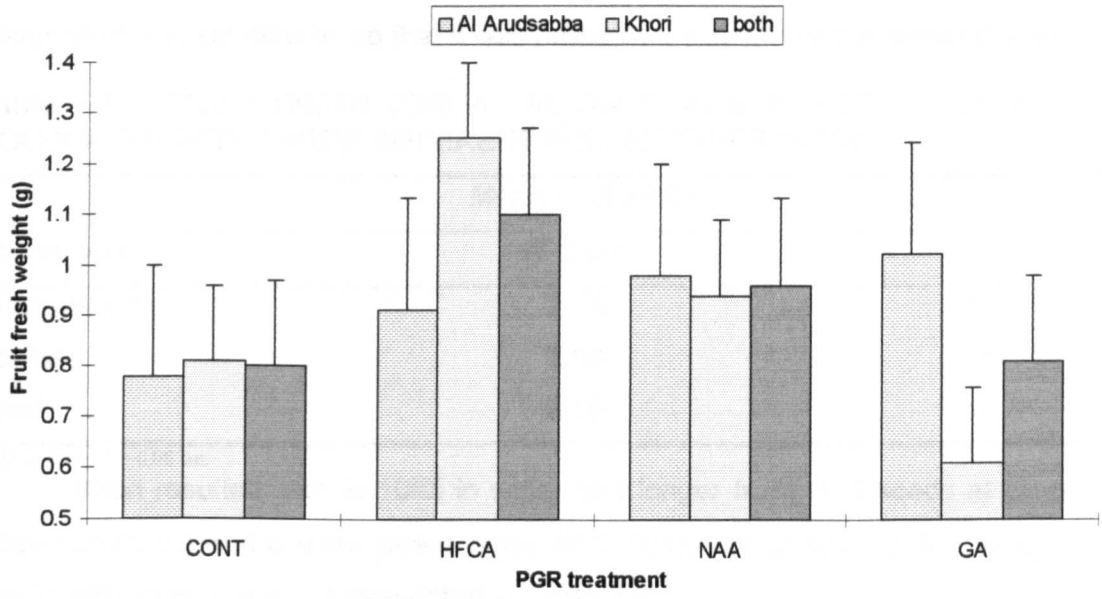
The effect of Al Arudsabba was on par in both cvs.. Bahlani and Khori induced 18 % and 28 % more fruit weight in cv Khasab than in cv Khalas, respectively. Compared to Bahlani, Khori induced a similar fruit fresh weight in cv Khasab, but 15 % higher fruit fresh weight in cv Khalas.

The above probably reflects genetic effects.

Effect of applied PGRs:

The plant growth regulator experiment in 1996, in which six growth regulators in addition to control were applied to bunches pollinated with the pollen types Al Arudsabba and Khori, revealed significant effects on fruit weight at 65 d.a.p. in the absence of pollen effects. However, an interaction with pollen type existed. The effects of these growth regulators were therefore examined separately for the two pollen types (Figure 7-3).

Figure 7-3 *Interaction of plant growth regulator with pollen type on fruit weight at 65 d.a.p. in the cv Khalas in 1996. LSD bars for comparisons between PGR treatments are shown.*



When both pollen types were blocked together, HFCA and NAA resulted in 35 % and 20 % heavier fruit, respectively, when compared to control. However, the plant growth regulators interacted with pollen type ($P<0.001$), so that the results were examined for each pollen type separately. This revealed, that

1. GA treatment with Al Arudsabba increased fruit weight, but decreased it with Khori, compared to respective controls and that
2. HFCA treatment increased fruit weight only with Khori, while NAA treatment increased fruit weight with both pollen types.

In 1995 no comparison of pollen types with regard to the effect of hormone treatments on fruit weight was possible due to loss of replicates in pollen type Khori.

CV Khasab:

No pollen effects on fruit and seed fresh and dry weight were observed.

7.1.3 Fruit and seed size

CV Khalas:

In 1996 Khori resulted in slightly wider fruits than Al Arudsabba and Bahlani at 95 d.a.p.. The difference is only 5%, but significant ($P<0.05$) and occurred in the absence of fruit set effects, so that it was probably a true metaxenic effect (Table 7-7).

Table 7-7 FRUIT WIDTH (CM) AT 95 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

	Mean Fruit width	
Pollen type	*95 d.a.p.*	
Al Arudsabba	2.05	b
Bahlani	2.04	b
Khori	2.15	a

LSD @ P< 0.05 = 0.08 cm.

Khori resulted also in 1995 in wider and longer fruits and seeds at 80 d.a.p. when compared to the other pollen types ($P<0.001$). The effects on fruit length and seed width at 80 d.a.p. are presented in Table 7-8.

Table 7-8 FRUIT LENGTH (CM) AND SEED WIDTH (CM) AT 80 D.A.P. IN BUNCHES ON CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1995.

	Fruit size at 80 d.a.p.			
Pollen type	*Fruit length (cm)*		*Seed width (cm)*	
Al Arudsabba	2.0	c	0.44	c
Bahlani	2.3	b	0.55	b
Khori	2.4	a	0.58	a

Fruit length: LSD @ P< 0.05= 0.1 cm ; Seed width: LSD @ P< 0.05=0.014 cm.

Fruits treated with Khori were 20% longer and had 32% wider seeds than fruits treated with Al Arudsabba. Khori caused also slightly but significantly ($P<0.05$) wider

seeds than Bahlani. These effects occurred coincident with fruit set and thermal time effects, so that a true metaxenic effect cannot be assumed without further examination as presented in the following sections.

Growth regulator treatments had no effects on fruit size in cv Khalas.

CV Khasab:

No pollen effects on fruit and seed size were observed in either years.

7.2 Relationships between different variables

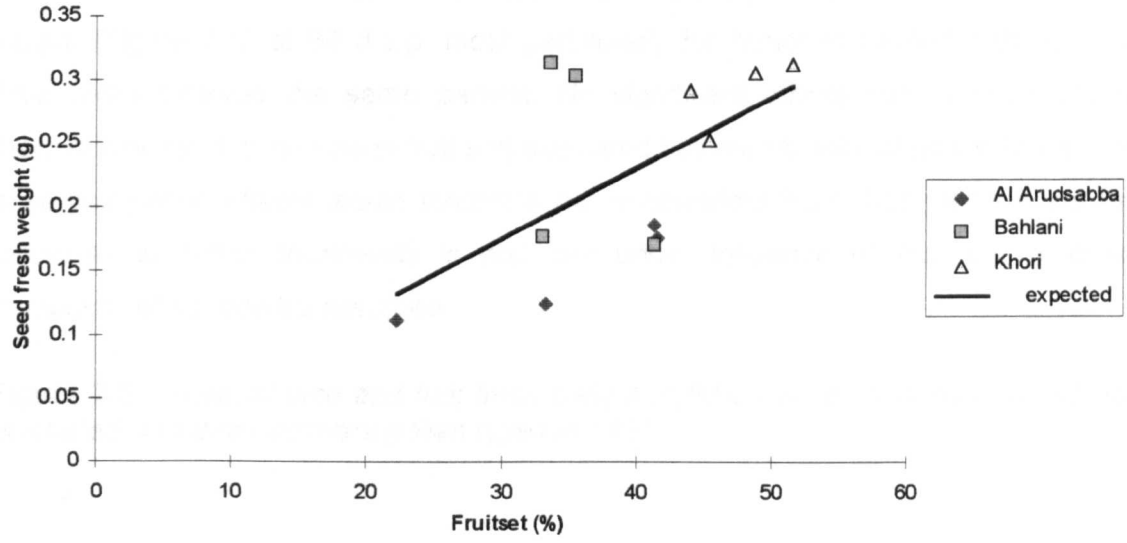
7.2.1 Fruits set and weight of fruits and seeds

Possible correlations are examined here to determine whether pollen effects on fruit and seed weight were direct or mediated through the effect on fruit set. Interest was also attached to whether fruit set varied with the metaxenic potential of pollen types. A pollen effect on fruit set was observed only in 1995 in cv Khalas (Section 7.1.1.).

CV Khalas:

Although a significant positive correlation ($r= 0.59$, $P=0.045$) was observed between individual seed fresh weight at 80 d.a.p and fruit set at 50 d.a.p. in 1995 when all data were looked at (Figure 7-4), none was found to be pollen specific.

Figure 7-4 *Relationship between seed fresh weight at 80 d.a.p and fruit set at 50 d.a.p. in bunches of cv Khalas pollinated with three different pollen types in 1995.*



Regression analysis (y = 0.0062 + 0.0056*x; with x=fruit set at 50 d.a.p. (%), y=seed fresh weight (g) at 80 d.a.p.) shows a significant overall relationship ($P<0.05$) with seed weight increasing with an increasing fruit set. No relationship existed for data blocked by pollen type. As the relationship is positive, it can be concluded that a higher fruit set does not cause a reduction in the weight of individual seeds and that pollen type affects both in the same direction of response (Sections 7.1.1. and 7.1.2.).

In 1996 no fruit set effects were observed and so, if no thermal time differences are found, the pollen effects on seed weight observed then were probably direct metaxenic effects.

CV Khasab: No correlations were observed.

7.2.2 Thermal time and weight of fruits and seeds

Fruit development did take place during different periods of the annual season. This means that at equal real time (d.a.p.) they may have been exposed to different temperature regimes. Therefore, a comparison of fruit growth and development on a thermal time (°Cd) basis was considered necessary.

CV Khalas:

In 1996 thermal time at 80 d.a.p. was positively correlated with overall fruit weight (Figure 7-5) at 80 d.a.p. most particularly for bunches treated with Bahlani. Fruit width followed the same pattern. No significant differences in accumulated thermal time (and also none in fruit set) appeared between blocks of pollen types. Any observed pollen effects would therefore be independent from thermal time. As the response to pollen treatments is also not under influence of fruit set, a direct metaxenic effect can be assumed.

Figure 7-5 *Thermal time and fruit fresh weight at 80 d.a.p. in bunches of cv Khalas pollinated with three different pollen types in 1996.*

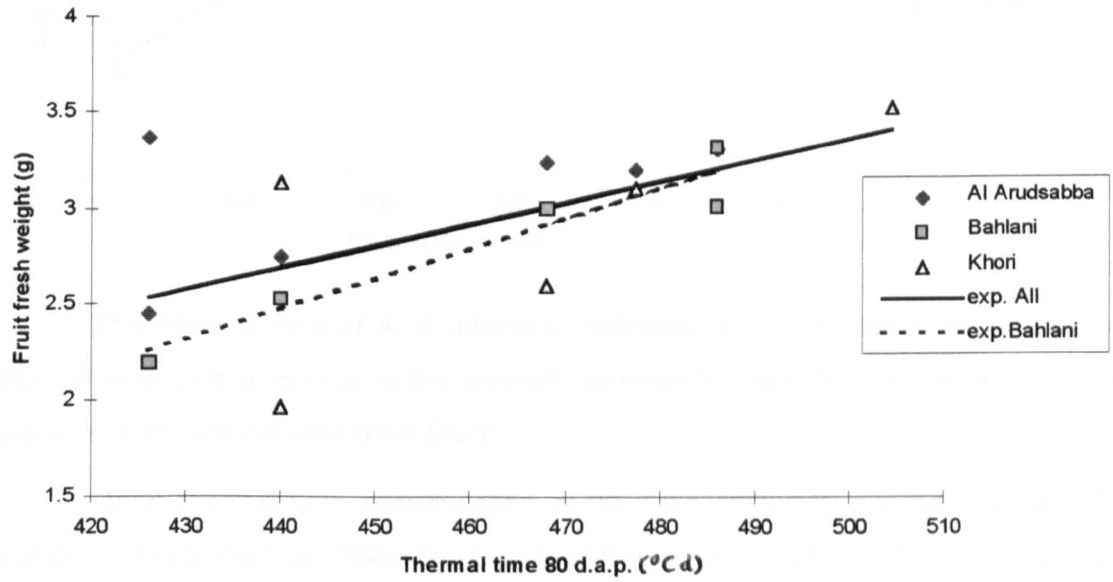
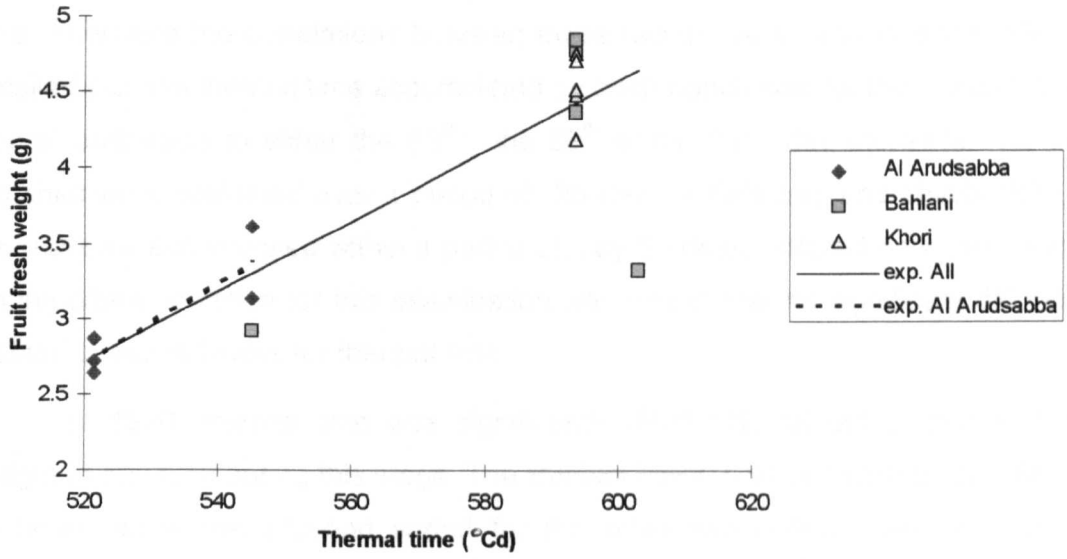


Figure 7-5 illustrates the peculiar response of Bahlani-pollinated fruits, which could be predicted to increase their weight (y) by 42 % in response to a thermal time (x) increment of 60 °Cd ($y = -4.42 + 0.0157*x$, $r^2 = 0.92$, $P<0.01$), whilst no such relationship could be found for the other pollen types. This increment is larger (slope = 0.016) than that of the overall fruit weight (slope = 0.011) and indicates a possible response of fruit fresh weight to pollen type Bahlani on the basis of thermal time, which in itself would constitute a pollen effect.

In 1995 thermal time accumulated by 80 d.a.p. was positively correlated with overall fruit and seed fresh weight at 80 d.a.p. and particularly for bunches treated with Al Arudsabba (Figure 7-6). Although significant differences (K, B>A) existed

between thermal time blocked by pollen type, it was only about 10 % less for Al Arudsabba than for the other pollen types.

Figure 7-6 *Thermal time and fruit fresh weight at 80 d.a.p. in bunches of cv Khalas pollinated with three different pollen types in 1995.*



The fresh weight of Al Arudsabba pollinated fruits can be clearly rrelated to thermal time and is similar to the overall correlation, whilst for the other two pollen types no such correlations were found.

Mean thermal time accumulation at 80 d.a.p. was 110 degree days or 24 % higher in 1995 than in 1996, so that a comparison of pollen effects at 80 d.a.p. between years is of limited value. However, the difference is possibly the reason for the later appearance of pollen effects in 1996 (fruit fresh weight increase 80 to 95 d.a.p.) and probably for the higher fruit fresh weight in 1995.

The effect of Al Arudsabba on fruit weight at 80 d.a.p. in 1995 (K>B>A) may be a reflection of shorter thermal time rather than a direct pollen effect. This response in addition to the influence of fruit set, indicate a complex relationship, whereby fruit set and thermal time influenced fruit weight in the same direction. As no correlation between fruit set (110 d.a.p.) and thermal time (80 d.a.p.) existed, a relationship between these variables can be excluded. Considering the other two pollen types, the significant differences in weight between Bahlani and Khori were not reflected in thermal time differences and may have been therefore true metaxenic effects. However, as differences on fruit set (Sections 6.1.1. and 7.1.1.) with these two pollen

types existed, no clear conclusion can be drawn whether the pollen effects on fruit weight were direct effects.

CV Khasab:

Although no direct pollen effects on fruit or seed weight were observed in cv Khasab, pollen type may affect the responsiveness of growth in terms of thermal time. Therefore the correlations between these factors were examined for 1996. It is recalled that the thermal time accumulated by each bunch was for the period from the day of pollination to either the 65th , the 80th or the 95th day thereafter. As these bunches were pollinated over a period of 28 days in February and March 1996, the thermal time accumulated within a period of, say 80 days, differed between bunches. An important condition for this examination was met in that no significant differences existed between blocks for thermal time.

In 1996, thermal time was significantly ($P<0.001$) related to fruit and seed weight at any time during this stage. The Bahlani block was consistently correlated at all times, while the situation varied for the other two pollen types as shown in Table 7-9.

Table 7-9 CORRELATION DURING THE RAPID GROWTH PHASE BETWEEN THERMAL TIME AND FRUIT- AND SEED FRESH WEIGHT IN BUNCHES OF THE CV KHASAB POLLINATED WITH THREE DIFFERENT TYPES IN 1996.

	65 d.a.p.		*80 d.a.p.*		*95 d.a.p.*	
Blocks	*Corr.(r)*	*level of sign.*	*Corr.(r)*	*level of sign.*	*Corr.(r)*	*level of sign.*
Fruit fresh weight						
Al Arudsabba	0.14	ns	0.96	**	0.59	ns
Bahlani	0.96	**	0.98	***	0.96	**
Khori	0.90	*	0.96	*	0.83	ns
ALL	**0.74**	***	**0.95**	***	**0.84**	***
Seed fresh weight						
Al Arudsabba	0.63	ns	0.85	*	0.83	*
Bahlani	0.86	*	0.92	**	0.97	**
Khori	0.94	**	0.91	*	0.88	ns
ALL	**0.77**	***	**0.86**	***	**0.86**	***

Levels of significance: ns= not significant at 5% level, * = 5 % level, **= 1% level, ***= 0.1% level.

Before the linear growth response curves for pollen blocks as shown in figures 7-8 and 7-9 could be related to each other, it is first necessary to examine the general response for all bunches.

It appears that overall growth was positively related to thermal time and can be represented by linear equations as shown in Table 7-10.

Table 7-10 REGRESSION EQUATIONS DESCRIBING THE RELATIONSHIP BETWEEN THERMAL TIME (X) AND FRUIT FRESH WEIGHT (Y_1) AND SEED FRESH WEIGHT (Y_2) FOR ALL BUNCHES IN CV KHASAB IN 1996.

	Regression equation			
d.a.p.	*Fruit weight (y_1)*	*sig.*	*Seed weight (y_2)*	*sig.*
65	$y_1 = 3.593 - 0.0174 \cdot x$	***	$y_2 = 0.184 - 0.0011 \cdot x$	***
	$+ 0.000029 \cdot x^2$	*	$+ 0.0000017 \cdot x^2$	***
80	$y_1 = -1.264 + 0.0083 \cdot x$	***	$y_2 = 0.484 - 0.0021 \cdot x$	***
			$+ 0.0000027 \cdot x^2$	*
95	$y_1 = -0.842 + 0.0099 \cdot x$	***	$y_2 = 1.491 - 0.0039 \cdot x$	***
			$+ 0.0000034 \cdot x^2$	*

sig.) indicates level of significance of 1. and 2. degree terms, respectively;

***=0.001 %, **=0.01, *=0.05.

Figure 7-7 depicts the above equations graphically.

Figure 7-7 *Relationship between thermal time (x) and fruit fresh weight (y_1) and seed fresh weight (y_2) for all bunches in cv Khasab in 1996.*

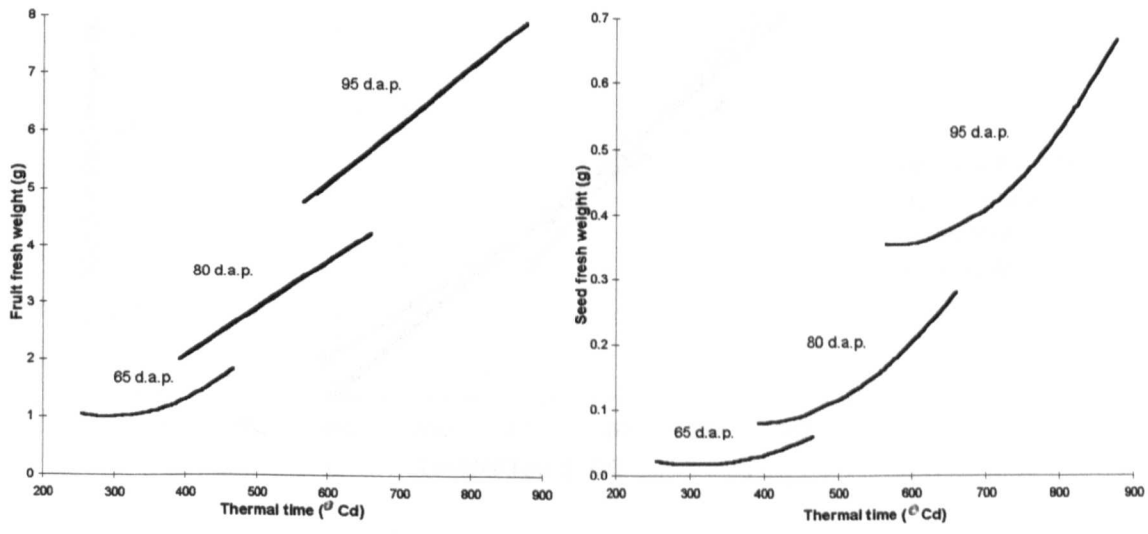
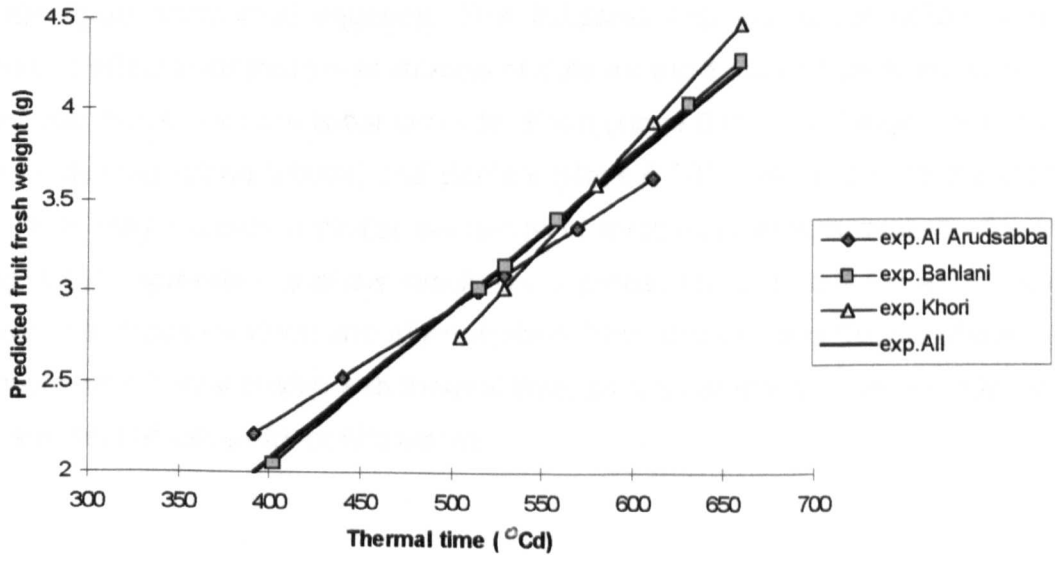


Figure 7-7 shows that fruit fresh weight relates to thermal time linearly except for 65 d.a.p., while seed weight relationships are better described by second-degree polynomial equations. Comparison of the models for fruit fresh weight, first requires transformation of the predicted values for 65 d.a.p. into a linear equation, i.e.: $y = -0.147 + 0.0039 \cdot x$. It can now be seen that responsiveness to increasing thermal time according to the linear equations more than doubles from a slope of 0.0039 to 0.0083 between 65 and 80 d.a.p., while it increases only by about 20% until 95 d.a.p.. The response of seed weight to thermal time follows a second degree polynomial equation and upon transformation into linear equations, slopes of 0.00019, 0.00077 and 0.0099 for 65, 80 and 95 d.a.p., respectively are found, which reveal that responsiveness of seed weight quadruples between 65 and 80 d.a.p and thereafter increases by about 30 % until 95 d.a.p.. It is peculiar that a non-linear relationship between growth and thermal time existed. This reflects that more than one process influenced growth, possibly the pollen treatments.

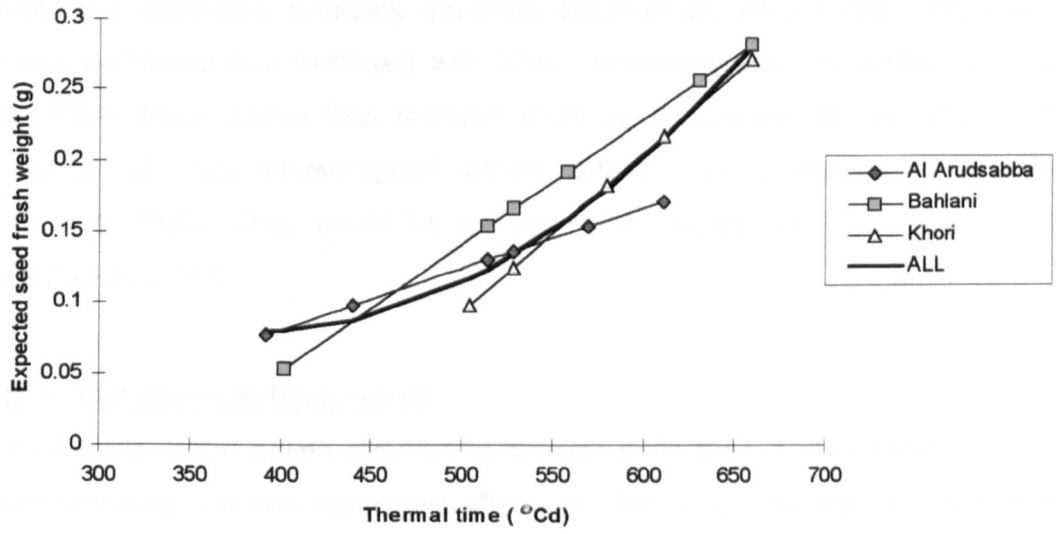
Because only for Bahlani correlations exist during the entire period (Table 7-9), the data for 80 d.a.p. of fruit (Figure 7-8) and seed weight (Figure 7-9) are examined and are modelled using linear equations. No significant second degree terms could be found for fruit weight, but well for seed weight. No correlations existed for Al Arudsabba except at 80 d.a.p. and Khori treated bunches exhibit this correlation all during the stage except at its end (Table 7-9).

Figure 7-8 *Model of fruit fresh weight in relation to thermal time at 80 d.a.p. in bunches of cv Khasab pollinated by three different pollen types in 1996.*



From Figure 7-8 for fresh fruit weight it can be seen that Khori caused the fastest response (slope 0.011), which is 38 % higher than the overall rate (slope 0.008). Bahlani (slope 0.009) caused almost the same response as the overall response while the response for Al Arudsabba (slope 0.006) was about 25% slower. Regression analysis using a generalised linear model confirms that the difference in slopes for Khori and Al Arudsabba was significant ($P<0.05$). This indicated a superior metaxenic effect by Khori over Al Arudsabba.

Figure 7-9 *Model of seed fresh weight in relation to thermal time at 80 d.a.p. in bunches of cv Khasab pollinated by three different pollen types in 1996.*



In Figure 7-8, the predicted curve for seed weight for all bunches follows a second-degree polynomial equation. This indicates that the factor pollen type is exerting an effect such that linear subsets of data for each pollen type together create a non-linear curve., i.e.: the linear curve for Khori (slope 0.0011) is tangent and those for Al Arudsabba (slope 0.0004) and Bahlani (slope 0.007) are secant to the overall curve. This may indicate a similar sequence of metaxenic effects as seen for fruit weight. GLM regression analysis results in a probability of 0.053 for a difference between the slopes for Khori and Al Arudsabba. This also explains the peculiarity of a non-linear growth relationship with thermal time, as the parabolic curve is made up of linear sub sets of values for pollen blocks.

7.3. Summary and discussion

Effects on fruit set

1. Pollen treatments had significant effects on fruit set in cv Khalas only in 1995 with Khori again resulting in the highest fruit set.

2. NAA and HFCA treatments had a significant effect on fruit set only on Khori-pollinated bunches in 1996, but not in those pollinated with Al Arudsabba. Work in the present section indicates that the effect continued from the last stage until 65 d.a.p. and that NAA treated bunches pollinated with Khori lost their unfertilized fruits faster. The opposite effect was caused by the auxin-inhibitor, HFCA applied at 40 d.a.p.. The absence of this response on unfertilized fruits in Al Arudsabba pollinated bunches indicates biochemical differences compared to ovaries pollinated (not fertilized) with Khori. Assuming that no fertilization would have taken place, rather than fertilized fruits being aborted, this would imply the existence of truly physiological pollen effects acting during siphonogamy (Browning, 1989). They would have been non-hereditary as no syngamy would have had occurred.

Effects on fruit and seed fresh weight

1. In cv Khalas, Khori pollen resulted in heavier fruits than Al Arudsabba in 1996, which probably is a true metaxenic effect. In 1995, Khori resulted in the heaviest fruits and seeds followed by Bahlani then Al Arudsabba possibly through effects on fruitset. No effects were observed in cv Khasab. This indicates a possible genetic interaction between parental types supporting the theory that pollen type effects are due to genetic causes during this stage, particularly because much syngamous tissue is formed in this stage, which would account for most of the growth This is also confirmed by an examination of fruit fresh weight at 80 d.a.p. in an 2-factor experiment with three pollen type and two cvs in 1995 revealing a significant interaction ($P<0.05$).

   No differences in dry fruit weight or its increase existed during this stage, so that the pollen effect on fruit fresh weight may have been due to cell enlargement rather than cell division.

2. GA may have been responsible for this effect of Khori in cv Khalas in 1996. The differences between pollen treatments in response to PGRs indicated biochemical differences between them. As the fruits alone were treated with GA_3, it is unlikely that competing growth had been elsewhere induced thereby, so that it is possible that the application of GA_3 resulted in supra-optimal levels (Looney, 1986) in Khori, thereby inhibiting growth, while in Al Arudsabba suboptimal endogenous levels may have been brought to near optimal levels by GA_3. Accordingly, endogenous GA_3-levels may have been *a priori* higher in Khori than in Al Arudsabba pollinated fruits and could have caused the superior performance of Khori pollinated fruits in the pollen experiments. Furthermore, it should be noted that HFCA had a promoting effect on fruit fresh weight with Khori but not with Al Arudsabba. This promotive effect was also observed with regard to retention of unpollinated fruits at the same time. The above possibly indicates differences in induced hormonal activity between treatments. A direct effect of pollen through imported substances cannot be responsible, firstly because the described effects were observed more than two months after pollination, and secondly because they were different from the ones observed during the lag phase when Khori was inferior.

Effect on fruit size

The response of fruit size to pollen treatments was similar to that of fruit fresh weight in 1996, but Bahlani was on par with Khori in 1995.

Relationship fruit set and weight

The absence of any pollen specific relation ship supports that pollen effects described in Section 7.1.2 were truly metaxenic.

Relationship thermal time and fruit weight

1. Khori caused in cv Khalas in 1996 a true metaxenic effect on fruit growth in comparison with Al Arudsabba in that thermal time and fruits set differences were absent.
2. In cv Khasab (1996), a metaxenic effect of Khori over Al Arudsabba was indicated by the thermal time relationship with fruit weight and seed weight at 80 d.a.p..

3. Another observation, possibly indicating a pollen effect, maybe metaxenic, were the continuous relationship of the fruit and seed weight of Bahlani pollinated bunches to thermal time in cv Khasab as well as in cv Khalas at 80 d.a.p in 1996. No correlations existed for Al Arudsabba except at 80 d.a.p. and Khori treated bunches exhibited this correlation all during the stage except at its end.

8. Stage Three: second rapid growth stage

This stage is characterized by a fruit growth rate which decreases from its maximum at the inversion point to zero at the end of this stage. The fruit reaches maximum fresh weight and physiological maturity at the end of the stage, whereas the seed with its embryo reach their final size near the middle of the stage. Both seed and fruit colour mature (Khimri to Khalal) and the fully mature fruit (Bissr) can be consumed. Any pollen effects due to a genetic interaction are expected at this stage as the seed with its syngamous tissues would influence overall fruit growth by cell expansion (Reuveni 1984; Schroeder, 1958). An interaction of pollen type and fruit set on fruit growth is likely.

Experiments were carried out to examine pollen and growth regulator effects on fruits of different cultivars. They examine the effect of pollen type and of applied PGRs (BA, Daminozide, GA_3, HFCA, NAA and TIBA) on fruit growth and development stages (8.1.) looking for relationships between such variables as fruit and seed weight, size and maturity as indicated by colour change on the one hand and fruit set and thermal time on the other (8.2.) for each of the pollen types. These would be expected to vary with the metaxenic potential of pollen type.

8.1. Pollen type and plant growth regulator effects on fruit growth and development

The experiments were designed to analyze pollen effects on several physical and chemical characteristics of the fruits and to suggest the underlying mechanisms. Differences due to a contribution from the male genotype were expected. The hormone experiments were designed to explore possible roles of major plant growth substances in regulating fruit growth and development and, from there, look for parallels with any pollen effects. As fruit set is known to influence the growth of the fruit (Chapter 5), pollen effects could be mediated through this as well as through

plant growth regulators. Fruit set effects were therefore an important consideration in this stage as well. In cv Khalas, this stage lasted from 95 to 150 d.a.p. and from 95 to 200 d.a.p. in cv Khasab.

8.1.1. Fruitset

Effects of pollen type on fruit set are examined here in two female cvs Khalas and Khasab.

CV Khalas (95 to 150 d.a.p.):

About 7.5 % of all ovaries dropped during this stage. Pollen effects were observed in 1995 at 110 d.a.p. as presented in the previous chapter. Table 8-1 shows these effects again. In 1996, no pollen effects on fruit set (%) were observed.

Table 8-1 FRUIT SET AT 110 D.A.P. IN CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1995.

	Fruit set (%)	
Pollen type	*110 d.a.p.*	
Al Arudsabba	30	b
Bahlani	29	b
Khori	44	a

LSD @ P< 0.05 = 12 %.

Fruit set in Khori pollinated bunches was 46 % higher (P<0.05) than in bunches pollinated with Al Arudsabba and Bahlani, which were on par. A similar response pattern was observed at 50 d.a.p.. It was expected that this would affect fruit growth and development. Plant growth regulator treatments had no effect on fruit set in 1996.

CV Khasab (95 to 200 d.a.p.):

No pollen or plant growth regulator effects on fruitset were observed in either years.

8.1.2. Fruit and seed weight

CV Khalas (95 to 150 d.a.p.):

Pollen effects on fruit fresh weight at 140 d.a.p. (Table 8-2) and seed fresh weight at 110 d.a.p. (Figure 8-1) were observed in 1996, but none in 1995. No pollen effects on the total dry weight nor the dry weight of the pericarp were observed in 1996.

Table 8-2 FRUIT AND PERICARP FRESH WEIGHT (g) AT 140 D.A.P. IN CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

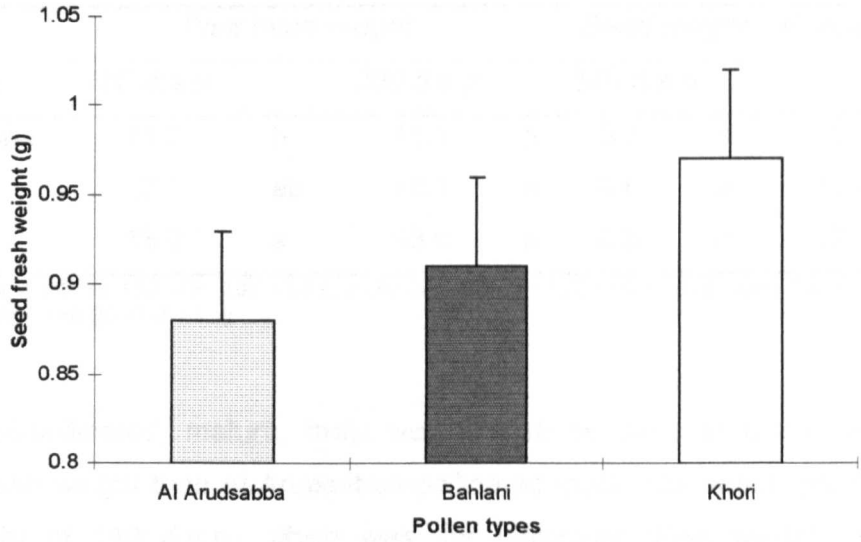
	Fruit fresh weight (g)				*Pericarp fresh weight (g)*	
Pollen type	*130 d.a.p. (interpolated)*		*140 d.a.p.*		*140 d.a.p.*	
Al Arudsabba	12.3	b	12.2	b	11.4	b
Bahlani	12.3	b	12.6	b	11.6	b
Khori	14.4	a	14.8	a	13.8	a

Fruit fresh weight: LSD @ P< 0.05 = 1.4 g at 130 d.a.p and LSD @ P<0.05= 1.7g at 140 d.a.p..; Pericarp FW: LSD@P<0.05=1.7g.

Khori resulted (P<0.05) in mature fruits (140 d.a.p.), which were about 20 % heavier in terms of total and pericarp fresh weight than Al Arudsabba and Bahlani . The same pattern of differences (P<0.05) was found when the fruit fresh weight at 130 d.a.p. was interpolated.

As many fruits are in the consumable "Bissr" stage at 140 d.a.p., this has considerable economic significance with regard to fruit quality. Later sections (8.1.4. and 8.1.8.) will examine the proportion of such fruits and the total yield as influenced by pollen type.

Figure 8-1 *Seed weight (g) at 110 d.a.p. in cv Khalas pollinated with three different pollen types in 1996 (LSD @ P<0.05 bars are shown).*



The seeds of fruits pollinated with Khori were at 110 d.a.p. about 10 % heavier than those pollinated with Al Arudsabba, with which Bahlani was on par (Figure 8-1). These differences were small, but significant (P<0.05). The fruit/seed ratio is about 14:1 without differences between treatments. No correlations between entire fruit/pericarp and seed fresh weight was observed.

Possible metaxenic effects in 1995 may have been obscured by the differences then in fruit set, when Khori pollinated bunches showed the heaviest fruit set (110 d.a.p.) with 44 % compared to a mean of 29.5 % for the other pollen types (Section 8.1.1.). This relatively high fruit set may have caused relatively stronger intrabunch competition for resources thereby counteracting any metaxenic effect. This will be examined more closely by correlation analysis in Section 8.2.1.. No plant growth regulator effects were observed.

CV Khasab (95 to 200 d.a.p.):

Pollen effects:

Significant pollen effects (P<0.05) on fruit fresh weight at 180 and 200 d.a.p. and seed fresh weight at 140 d.a.p. were observed in 1996 (Table 8-3). No effects on the dry weight of the entire fruit or of the pericarp were apparent.

Table 8-3 FRUIT FRESH WEIGHT (g) AT 180 AND 200 D.A.P. AND SEED FRESH WEIGHT (g) AT 140 D.A.P. IN CV KHASAB POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

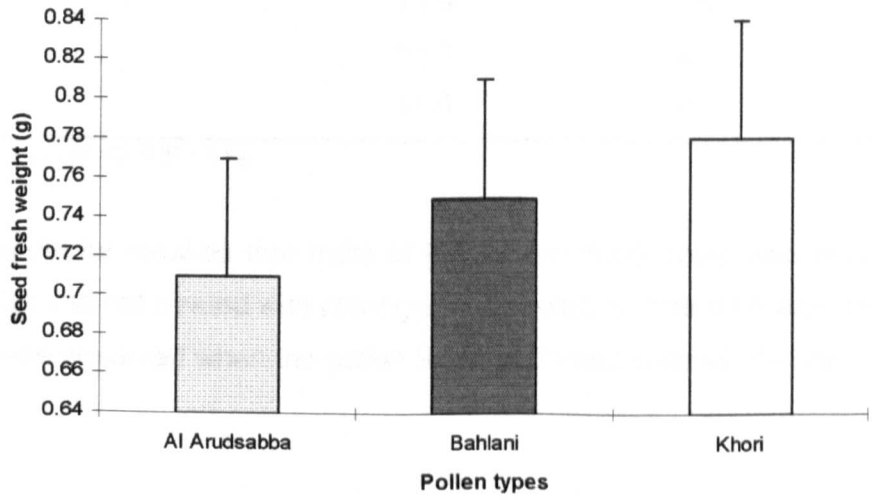
	Fruit fresh weight				*Seed weight*		*Pericarp weight*	
Pollen type	*180 d.a.p.*		*200 d.a.p.*		*140 d.a.p.*		*180 d.a.p.*	
Al Arudsabba	11.2	b	11.1	b	0.7	b	10.5	b
Bahlani	12.1	ab	12.3	a	0.8	a	11.4	ab
Khori	13.0	a	13.0	a	0.8	a	12.2	a

Fruit fresh weight at 180 dap: LSD @P< 0.05 = 1.8 g, at 200 dap: LSD @P< 0.05 =1.2 g ; Seed weight: LSD @P<0.05 = 0.1 g.; Pericarp fresh weight: LSD @P<0.05 = 1.1g.

Khori-pollinated, mature, fruits weighed 16 % more in terms of total and pericarp fresh weight than Al Arudsabba-pollinated fruits. The same was true for the seed weight at 140 d.a.p., which was the maximum fresh weight, except that Bahlani- and Khori-treated seeds were on par in this regard. The mean fruit/seed ratio was about 17:1 and similar for all treatments. As many fruits of this cv were in the consumable "Bissr" stage at 200 d.a.p., this has considerable economic significance regarding fruit quality. Section 8.1.4. and 8.1.8. will examine the proportion of such fruits and the total yield as influenced by pollen type.

Pollen effects (P<0.05) on seed fresh weight of immature fruits were observed at 140 d.a.p. in 1995 (Figure 8-2). No effects on fresh fruit weight were observed in 1995.

Figure 8-2 *Seed weight (g) at 140 d.a.p. in cv Khasab pollinated with three different pollen types in 1995 (LSD @P< 0.05 bars are shown).*



Khori resulted in 10 % heavier seeds than Al Arudsabba. This can be considered a xenic effect in the absence of fruit set effects. No effects on the weight of fruits in the "Bissr" stage (180 d.a.p.) were observed. The relationship with thermal time will be looked at in Section 8.2.3.. This was the first time a pollen effect had been observed in Khasab since 12 to 30 d.a.p., when Bahlani was superior to the other two pollen types. This suggests that different mechanisms are at work at these different times. As will be seen in Section 8.1.3. this effect was also reflected in the whole fruit with regard to fruit size.

Effect of applied PGRs:

Plant growth regulator effects ($P<0.01$) were observed in 1996 in trees pollinated with Al Arudsabba, where NAA treatment (40 d.a.p.) resulted in fruits which were about 11 % heavier than untreated fruits, as shown in Table 8-4.

Table 8-4 PLANT GROWTH REGULATOR EFFECTS ON THE FRESH WEIGHT AT 180 D.A.P. OF FRUITS OF CV KHASAB POLLINATED WITH AL ARUDSABBA IN 1996.

Plant growth regulator	*Fruit fresh weight (g)*	
Control	11.9	bc
NAA	13.2	a
TIBA	12.2	ab
DZ	11.4	bc
HFCA	11.3	bc
GA_3	11.1	c
BA	11.0	c

LSD @P< 0.05 = 1 g; LSD @P<0.01 = 1.4 g

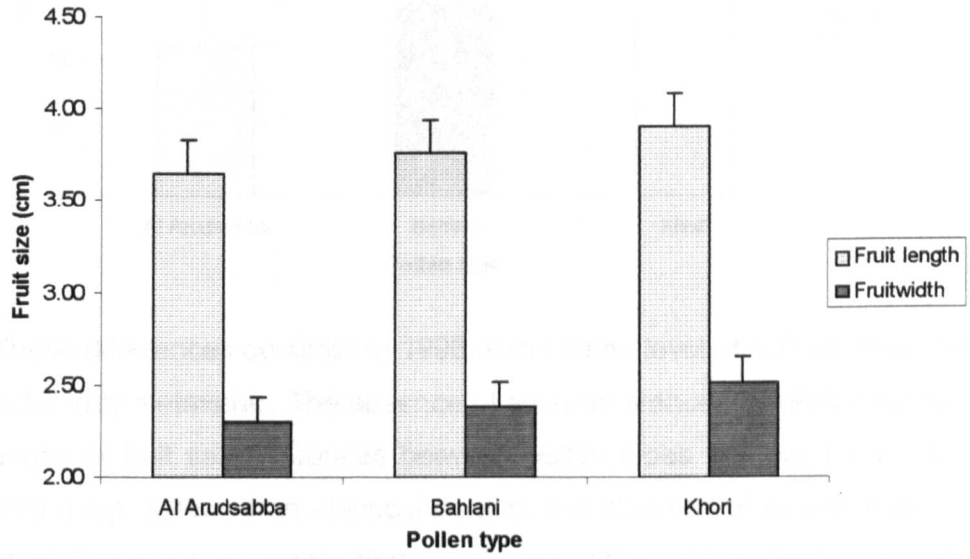
It should be recalled that fruits of the control block were also pollinated with Al Arudsabba, but not treated with plant growth regulators. The NAA effect was similar to the increase observed when the pollen Khori was used instead of Al Arudsabba.

8.1.3. Fruit and seed size

CV Khalas (95 to 150 d.a.p.):

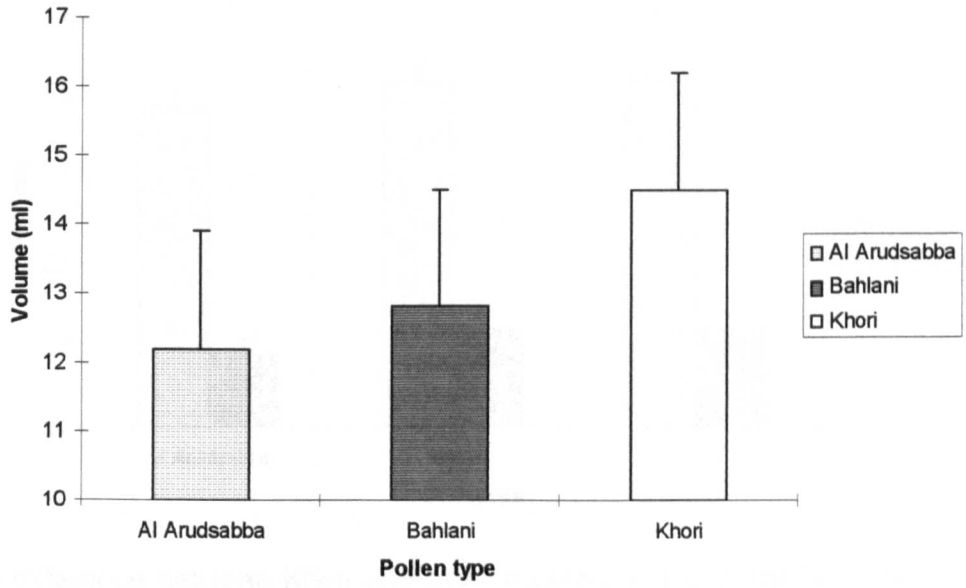
Both length and width of mature fruits (140 d.a.p.) were influenced by pollen type ($P<0.05$) in 1996 (Figure 8-3), while in 1995 no such effects were observed.

Figure 8-3 *Length (cm) and width (cm) of mature fruits (140 d.a.p.) in cv Khalas pollinated with three different pollen types in 1996. (LSD @P<0.05-bars are shown)*



Fruits pollinated with Khori were 7 % longer and 9 % wider than those pollinated with Al Arudsabba. This small difference was reflected more substantially in the significant differences ($P<0.05$) in volume of the fruits, where Khori pollinated fruits were about 19 % larger by volume than for Al Arudsabba as shown in Figure 8-4.

Figure 8-4 *Volume (ml) of mature fruits (140 d.a.p.) in cv Khalas pollinated with three different pollen types in 1996. (LSD @P<0.05-bars are shown)*

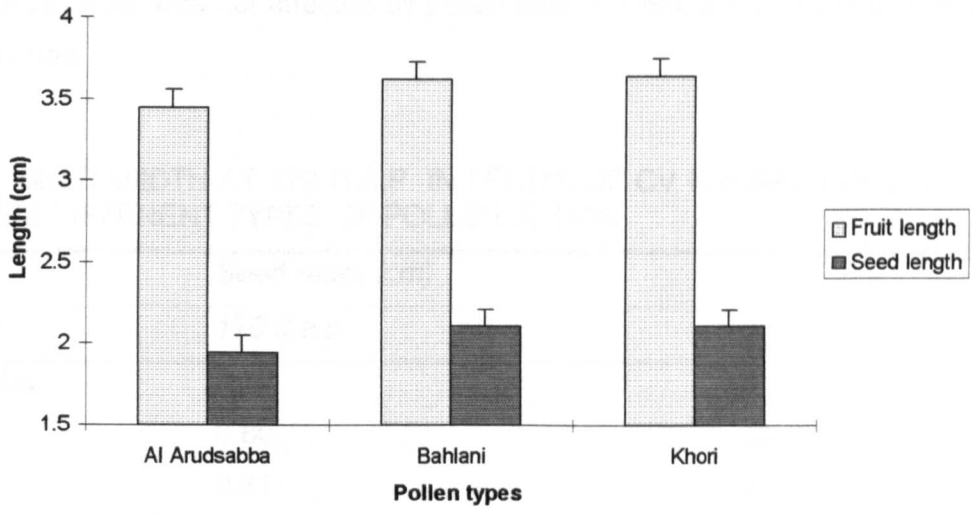


These differences occurred in 1996 at the same level of fruit set and can be assumed to be truly metaxenic. The absence of such differences in 1995 may be due to the influence of fruit set differences between pollen types. Although seed weight effects at 110 d.a.p. followed an identical pattern, the absence of its correlation with fruit volume at 140 d.a.p. suggests that the volume effect did probably not entirely originate from the seed. This would imply a possible separate metaxenic effect.

CV Khasab (95 to 200 d.a.p.):

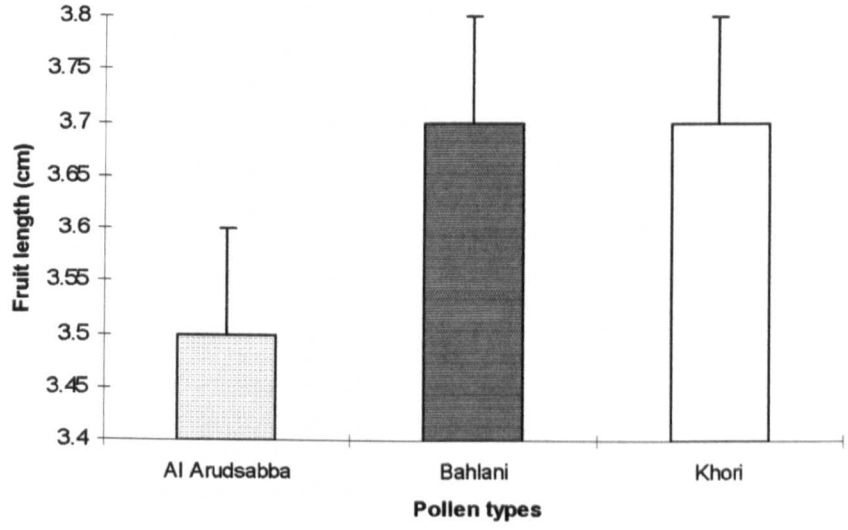
In 1996, pollination with Khori and Bahlani resulted in slightly longer fruits ($P<0.01$) and seeds ($P<0.05$) at 140 d.a.p. as shown in Figure 8-5 and longer fruits ($P<0.05$) at 180 d.a.p. (Figure 8-6), which is a desirable quality feature. No effects on fruit set were observed in cv Khasab during this stage, so that these are probably true metaxenic and xenic effects, respectively.

Figure 8-5 *Length of fruit and seeds of cv Khasab at 140 d.a.p. pollinated with three different pollen types in 1996. (LSD @P< 0.05-bars are shown)*



The difference between Khori and Al Arudsabba was 6 % for fruit length and 8 % for seed length.

Figure 8-6 *Length of fruits of cv Khasab at 180 d.a.p. pollinated with three different pollen types in 1996. (LSD @P<0.05-bars are shown)*



Khori and Bahlani pollinated fruits were 6 % longer than those pollinated with Al Arudsabba.

In 1995 Khori resulted in wider seeds ($P<0.05$) in nearly mature fruits (170 d.a.p.) than Al Arudsabba, while Bahlani was intermediate, as shown in Table 8-5. As fruit set was not affected by pollen type in 1995, a true metaxenic effect can be assumed.

Table 8-5 SEED WIDTH AT 170 D.A.P. IN FRUITS OF CV KHASAB POLLINATED WITH THREE DIFFERENT TYPES OF POLLEN IN 1995.

	Seed width (cm)	
Pollen type	*170 d.a.p.*	
Al Arudsabba	0.77	b
Bahlani	0.80	ab
Khori	0.81	a

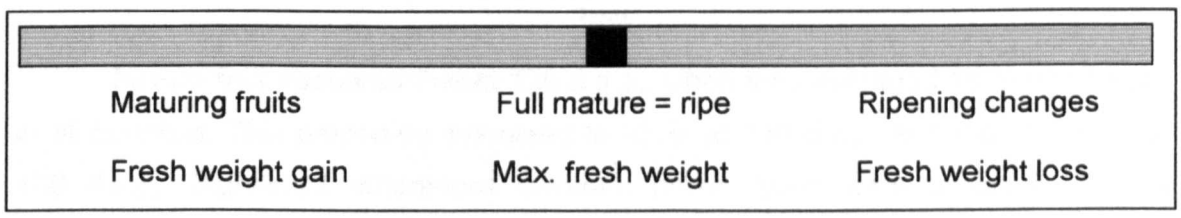
LSD @P<0.05 = 0.04 cm

The difference in seed width between Khori and Al Arudsabba was 6 %, which coincided with their effect on seed weight (Section 8.1.2.). No effects on fruit size (Section 8.1.3.) were apparent.

8.1.4. Maturity as indicated by fruit colour

Fruit colour is an indicator of maturity and ripening. During this stage, the change from Khimri (green) to Khalal (mature) takes place. In cv Khalas, this is the change from green to yellow and in cv Khasab from green to magenta. The Khalal colour then gradually darkens until the fruits reach full physiological maturity, here called 'full mature', at which time they are ripe. In terms of consumable stage, the darkest yellow and magenta corresponds to the Bissr stage. While fruits approach full maturity, they pass through a series of tones of colour which reflect what is here called 'mature'. The point of full maturity and the transition from there to a series of ripening changes are well indicated by colour. These principal changes are schematically shown in Figure 8-7. The following sections will examine the proportion of fruits in treated bunches reaching maturity as indicated by colour. Graf's horticultural colour chart (1985) was used, which allocates codes to different colours.

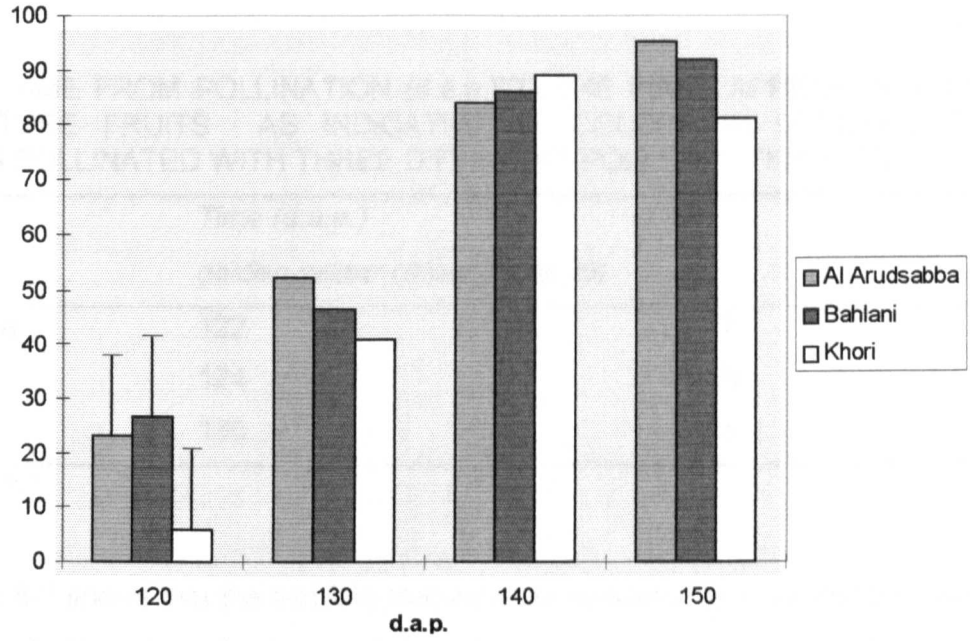
Figure 8-7 Maturity, ripening and fresh weight changes in dates (schematic).



CV Khalas (95 to 150 d.a.p.):

Bissr fruits were first observed at 120 d.a.p. and reached a maximum number at 140 and 150 d.a.p. (Figure 8-8). It should be noted that Bissr fruits are available up to 170 d.a.p., which will be discussed in detail in the next chapter. In the present stage, the proportion of yellow (code C04) and golden-yellow (code C05) corresponds to the proportion of Bissr fruits. As presented in Table 8-6 it was much higher ($P<0.05$) in Bahlani and Al Arudsabba-pollinated fruit bunches at 120 d.a.p. than in those pollinated with Khori. This was also reflected in the time to full maturity (indicator: colour code 05) as shown in Table 8-7. Furthermore, pollination with Bahlani caused the most uniform maturity as indicated by the lowest coefficient of variation (Table 8-6). There were no differences in the percentage of green Khimri fruits, lighter green fruits or the sum total of the two. The results for maturing plus full mature fruits are also shown.

Figure 8-8 *Percentage of the total of yellow (maturing) and golden-yellow fruits (full mature) between 120 and 150 d.a.p. in bunches of cv Khalas pollinated with three different types of pollen in 1996. (LSD @P<0.05-bars are shown)*



Mature fruit appeared first at 120 d.a.p., when they averaged 18 % of all fruits in all bunches. This proportion increased to 47 % at 130 d.a.p. and then to 89 % at 150 d.a.p.. Significant differences between pollen types were observed only at 120 d.a.p., as detailed in Table 8-6, when Al Arudsabba and Bahlani resulted in about 4 times as many mature and fully-mature fruits as Khori.

Table 8-6 PERCENTAGE AND COEFFICIENT OF VARIATION (CV) OF MATURE-COLOURED FRUITS AT 120 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT TYPES OF POLLEN IN 1996.

	Colours at 120 d.a.p.				
Pollen type	*% mature C04*	*% full mature C05*	*% total C04+C05*	*sig. C04+C05*	*CV (%) C04+C05*
Al Arudsabba	18.6	4.6	23.2	a	71
Bahlani	24.3	2.3	26.6	a	19
Khori	5.1	0.9	6.0	b	74

LSD @P< 0.05 = 16.6, for % total (C04+C05)

Table 8-6 shows that variation of mature and fully mature fruits as indicated by a CV that was 3-4 times higher between bunches pollinated by Al Arudsabba and Khori at 120 d.a.p. than by Bahlani.

Table 8-7 TIME FROM POLLINATION (d.a.p.)TO THE FIRST APPEARANCE OF FULLY MATURE FRUITS AS INDICATED BY COLOUR IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

	Time (d.a.p.)	
Pollen type	*golden-yellow colour (code 05)*	
Al Arudsabba	122	b
Bahlani	124	b
Khori	130	a

LSD @P<0.05 = 6 days

Table 8-7 shows that the first fully mature fruits appeared in Al Arudsabba- and Bahlani pollinated bunches about one week earlier than in those pollinated with Khori.

Effects on fruit size (Section 8.1.4.) occurred in the absence of fruit set effects and would therefore be true metaxenic effects or the result of metaxenic effects on fruit weight. It is recalled that Khori caused the heaviest and largest fruits at 140 d.a.p., which may be due to growth, which possibly continued, while maturity changes were delayed in comparison with fruits pollinated with the other pollen types. Section 8.2.2. will examine the relationship between fruit weight and maturity.

In 1995, at 140 d.a.p., Al Arudsabba pollinated bunches contained immature, maturing and fully mature fruits, while the other two pollen types resulted in fruits with only mature colours. This is different from 1996, when even at 140 d.a.p. all three colours were present for all three pollen types. A comparison is shown in Table 8-8. No counts were taken in 1995.

Table 8-8 IMMATURE (GREEN) AND MATURE COLOURS (YELLOWS) IN FRUITS OF CV KHALAS (140 d.a.p.) POLLINATED WITH THREE DIFFERENT TYPES OF POLLEN IN 1996 AND 1995.

Pollen types	*1996*			*1995*		
	immature colours	*mature colour*	*°Cd 140 dap*	*immature colours*	*mature colour*	*°Cd 140 dap*
Al Arudsabba	yes	yes	1276	yes	yes	1371
Bahlani	yes	yes	1296	no	yes	1440
Khori	yes	yes	1296	no	yes	1446

The absence of immature colours at 140 d.a.p. in 1995 shows that in Bahlani- and Khori-, but not in Al Arudsabba pollinated bunches, maturity occurred earlier than in 1996. This difference in the response pattern may be due to differences in thermal time or due to the influence of differential fruit set for different pollen types and possibly the absence of fruit weight differences in 1995. Assuming that true metaxenic effects appear only if fruitset and heat summation are uniform, then these results would suggest that the metaxenic potential arises from mechanisms causing Khori and Bahlani to mature later as was the case in 1996 rather than mechanisms causing Al Arudsabba to mature earlier. It is recalled that in 1996 neither fruit set nor thermal time differences existed between pollen blocks, although fresh weight effects existed.

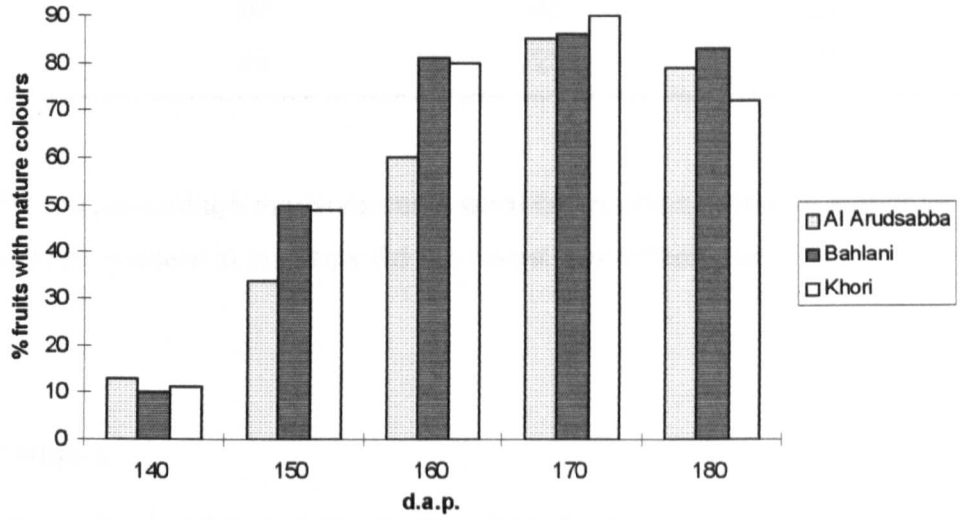
CV Khasab (95 to 200 d.a.p.):

In this cv the range of changing colours is wider than in cv Khasab, so that colour changes are examined in the following for Khalal colour (maturing fruits) and Bissr colour (fully mature fruits), separately.

Khalal-coloured fruits (Figure 8-9) were observed first at 140 d.a.p. and reached a maximum at 180 d.a.p.. The first Bissr fruits (code C42=very dark magenta, almost black colour) were observed from 180 d.a.p. without a pollen effect on the time

until their first appearance. Only late into the next stage were the majority of fruits entering the Rutab stages observed.

Figure 8-9 *Percentage of the total of Khalal fruits between 140 and 180 d.a.p. in bunches of cv Khasab pollinated with three different types of pollen in 1996.*



The proportion of Khalal-coloured fruit (codes C26 and C28) and Bissr fruits (code 42) was not affected by pollen type in 1996.

Khori pollinated bunches matured most uniformly. The CV (%)for the percentage of Khalal coloured fruits blocked by pollen type between 160 and 180 d.a.p. was consistently lowest for Khori (Table 8-9). This was also the case for Bissr fruits between 180 and 200 d.a.p. (Table 8-10).

Table 8-9 COEFFICIENT OF VARIATION (%) OF KHALAL-COLOURED FRUITS IN BUNCHES OF CV KHASAB POLLINATED WITH THREE DIFFERENT TYPES OF POLLEN IN 1996.

	CV (%) of Khalal-coloured fruits (%) at		
Pollen types	*160 d.a.p.*	*170 d.a.p.*	*180 d.a.p.*
Al Arudsabba	45	11	18
Bahlani	22	13	19
Khori	13	6	14

Table 8-10 COEFFICIENT OF VARIATION (%) OF BISSR-COLOURED FRUITS IN BUNCHES OF CV KHASAB POLLINATED WITH THREE DIFFERENT TYPES OF POLLEN IN 1996.

	CV % of Bissr-coloured fruits (%) at		
Pollen types	*180 d.a.p.*	*190 d.a.p.*	*200 d.a.p.*
Al Arudsabba	119	52	35
Bahlani	94	40	37
Khori	49	23	21

In 1995, no percentage measurements were taken and a record of immature and mature colours present in bunches did not reveal any differences.

8.1.5. Total sugars

The amount of total sugars in the fruit flesh was measured using a refractometer and is given as °Brix. This is also an indicator of the sweetness of the fruit. In both cvs this value reached about 28 °Brix at the end of this stage.

CV Khalas (95 to 150 d.a.p.):

In 1996 the mean of total sugars was 27.8 % in mature fruits at 150 d.a.p.. Pollen effects on the total sugars in the fruit flesh (pericarp) were observed already at 110 d.a.p. (Table 8-11).

Table 8-11 TOTAL SUGARS AT 110 D.A.P. IN THE FLESH OF FRUITS OF CV KHALAS POLLINATED WITH THREE DIFFERENT TYPES OF POLLEN IN 1996.

	Total sugars (°Brix)	
Pollen type	*110 d.a.p.*	
Al Arudsabba	8.7	b
Bahlani	9.3	a
Khori	8.5	b

LSD @P< 0.05 = 0.3 °brix

Bahlani pollinated fruits contained about 8 % more total sugars than the other pollen treatments at 110 d.a.p. in 1996. Their was no consistent effect of pollen on °Brix. In 1995 no pollen effects were observed.

CV Khasab (95 to 200 d.a.p.):

No pollen effects on total sugars (mean of 42.5 % at 200 d.a.p.) were observed in either years.

8.1.6. Acid, sugar and tannin content of mature fruits

These constituents are important aspects of fruit quality. Acidity and the content of sucrose and reducing sugars are indicative of the degree of ripening and maturity (Reuveni, 1986). The dry matter of the fruit flesh at the Bissr stage contained about 80 % reducing sugars, tannins 1.3 % (0.4% on fresh weight basis) and acidity about 0.4 % (as malic acid) in both cvs. The fruit flesh in cv Khalas contained about 2 % sucrose on dry matter basis, which was double the sucrose content observed in case of cv Khasab.

A pollen effect only on the sucrose content was observed and then also only in cv Khalas in 1995 (Table 8-12).

Table 8-12 SUCROSE CONTENT (% OF DRY WEIGHT) IN THE FLESH OF BISSR FRUITS (140 D.A.P.) OF CV KHALAS POLLINATED WITH THREE DIFFERENT TYPES OF POLLEN IN 1995.

	Sucrose content (%), dry wt.basis	
Pollen type	*Bissr fruits*	
Al Arudsabba	0.9	b
Bahlani	2.8	a
Khori	2.6	a

LSD @P< 0.05 = 1.2%

Al Arudsabba pollinated fruit contained only about a third of the sucrose contained in the pericarpal dry matter of fruits pollinated with other types. This was

consistent with the results of the earlier section that Al Arudsabba pollinated fruits matured latest and it indicates that the sucrose accumulation was lagging behind in these fruits compared to fruits pollinated with the other two types.

8.1.7. Uniformity of fruit and seed size

Another important aspect of fruit quality is uniformity of fruit and seed size. Uniformity can be assessed by calculation of the coefficient of variance (CV(%)). To asses uniformity, the CV(%) is calculated by taking all six observations on a variable into consideration. The resulting CV(%)'s are calculated for each block of six samples from a bunch and are called 'CV(%)$_{bunch}$'. The CV(%)$_{bunch}$ values can be blocked by pollen type and analysed by ANOVA. This analysis is discussed as it indicates whether there are pollen effects on the CV(%) of fruit and seed size.

CV Khalas (95 to 150 d.a.p.):

In 1995, pollination by Khori and Bahlani gave more uniform fruits ($P<0.05$) in terms of fruit length and width (Bissr stage at 140 d.a.p.) than Al Arudsabba (Table 8-13). In 1996, Al Arudsabba and Bahlani resulted in more uniform seeds ($P<0.05$) than Khori (Table 8-14).

Table 8-13 COEFFICIENT OF VARIATION (%) THE LENGTH OF BISSR-STAGE FRUITS IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1995.

	CV_{bunch} (%) for Bissr fruit size			
Pollen type	$CV_{Fruit\ length}$ (%)		$CV_{Fruit\ width}$ (%)	
Al Arudsabba	5.4	a	4.4	a
Bahlani	3.7	b	3.1	b
Khori	3.1	b	3.0	b

CV_{bunch} Fruit length LSD @$P<0.05$ = 1.6 %; CV_{bunch} Fruit width LSD @$P<0.05$ = 1 %.

Uniformity of fruit length for pollen type Al Arudsabba was 46 % and 74 % higher than for Bahlani and Khori, respectively. For fruit width the corresponding differences were 32% and 42%.

Table 8-14 COEFFICIENT OF VARIATION (%) OF THE SEED WIDTH OF BISSR-STAGE FRUITS IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

	$CV(\%)_{bunch}$ at Bissr stage	
Pollen type	*$CV_{Seed\ width}$ (%)*	
Al Arudsabba	4.6	b
Bahlani	4.4	b
Khori	7.6	a

CV_{bunch} Seed width LSD @$P<0.05$ = 2.9 %.

Khori induced 69 % more variation in seed width than the other two pollen types in 1995.

It may be recalled that, in 1995, fruit set differences were significant, with Khori inducing 44 % fruit set as compared to about 30 % for the other two pollen types and 21 % for Khori in 1996, at which time no significant differences were observed. This suggests that fruit set in addition to pollen type influenced uniformity, which is confirmed by regression analysis in Section 8.2.4., which will examine the relationship between these two variables for pollen effects.

CV Khasab (95 to 200 d.a.p.):

No pollen effects on uniformity of fruits and seeds were observed in either years for this cultivar.

8.1.8. Yield

Total yield (y) is taken here as the total fresh weight of fruits per bunch at the end of this stage. It is calculated by multiplying the total number of pollinated fruits (n) with their fresh weight (w).

- $y = n \times w$

This indicates the total potential Bissr yield, which could be obtained if all fruits were to be harvested when they attain that stage.

Bissr yield (z_i) is the total weight of Bissr fruits per bunch at different times (i) and is estimated for the 1996 data by multiplying the number of Bissr fruits (b_i) with the mean fruit fresh weight (w_i) at day "i" after pollination.

- $z_i = b_i \times w_i$,

where $b_i = p_i \times m_i$, with p_i = percentage of Bissr fruits (%) per bunch and m_i =the total number of fruits per bunch.

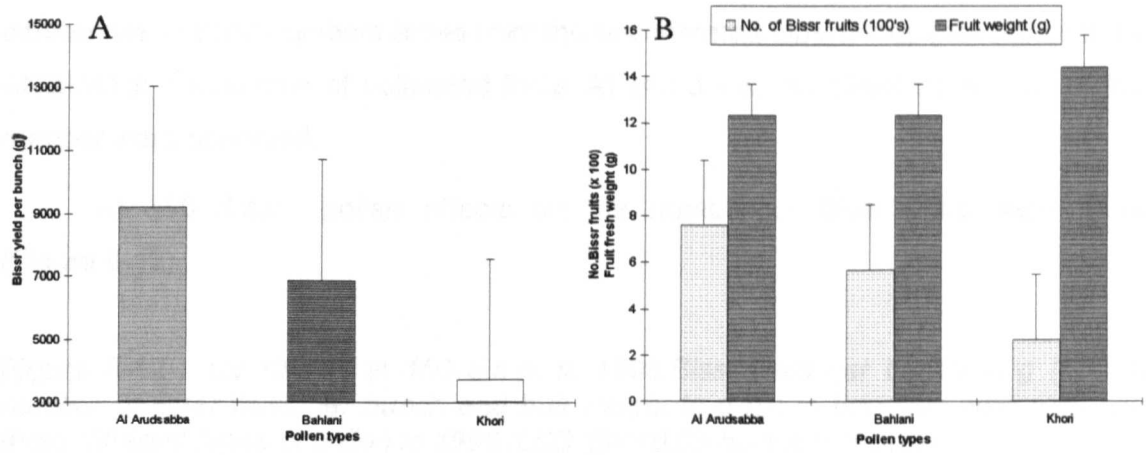
This would give an indication of pollen effects on the period of availability.

The concept of yield as presented above assesses the entire bunch directly. This is a system on a higher level of complexity than the single fruit, which was examined in previous sections. It derives from combining variables on lower levels of complexity, which are probably affecting each other, e.g.: fruit number and fruit set as directly observable and simple characteristics of the bunch on the one hand and fruit fresh weight as a simple characteristic of the single fruit on the other. It may also use means as multiplicators, which cannot be confirmed to be statistically different, but which have a large leverage on yield. It is therefore necessary to view yield with caution when discussing pollen effects.

CV Khalas (95 to 150 d.a.p.):

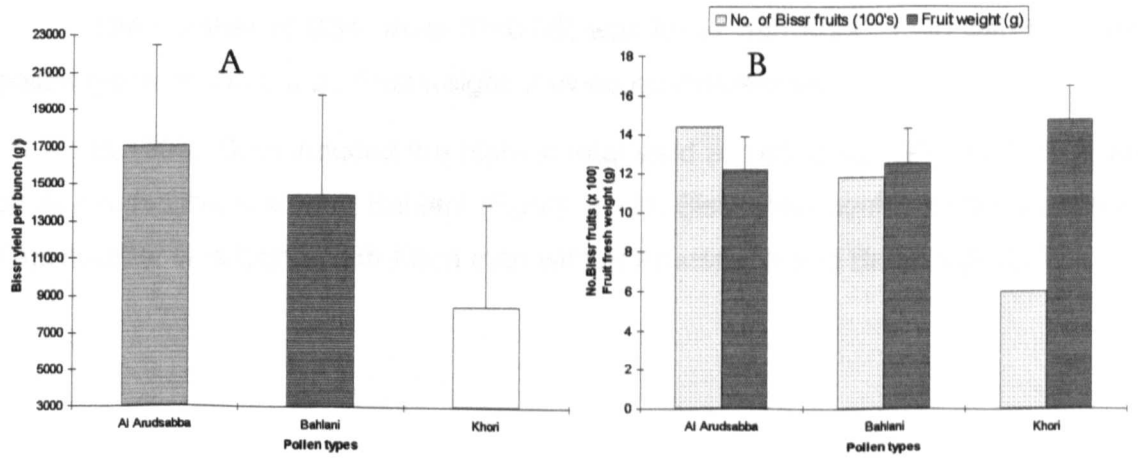
In 1996, Al Arudsabba resulted in a much higher Bissr yield than Khori ($P<0.05$) at 130 d.a.p. (Figure 8-10). Al Arudsabba and Bahlani resulted in a higher Bissr yield per bunch than Khori ($P<0.05$) at 140 d.a.p. as shown in Figure 8-12 and at 150 d.a.p. as shown in Figure 8-12. Mean total bunch yield was 14.8 kg, but not affected by pollen type.

Figure 8-10 *Cv Khalas at 130 d.a.p. in 1996: Bissr yield per bunch in g (A) and number of Bissr fruits per bunch and fruit fresh weight in g (B) in bunches pollinated with three different types of pollen in 1996 (LSD @P<0.05 bars are shown).*



Bissr yield of Khori pollinated bunches was about 2.5 times lower than that of Al Arudsabba pollinated bunches. Although Khori induced heavier fruits than Al Arudsabba, in the same bunches the number of fruits in the Bissr stage was significantly lower, exerting a relatively stronger leverage than fruit weight when both are multiplied to estimate this yield.

Figure 8-11 *Cv Khalas at 140 d.a.p. in 1996: Bissr yield per bunch in g (A) and number of Bissr fruits per bunch and fruit fresh weight in g (B) in bunches of cv Khalas pollinated with three different types of pollen (LSD @P<0.05 bars are shown).*

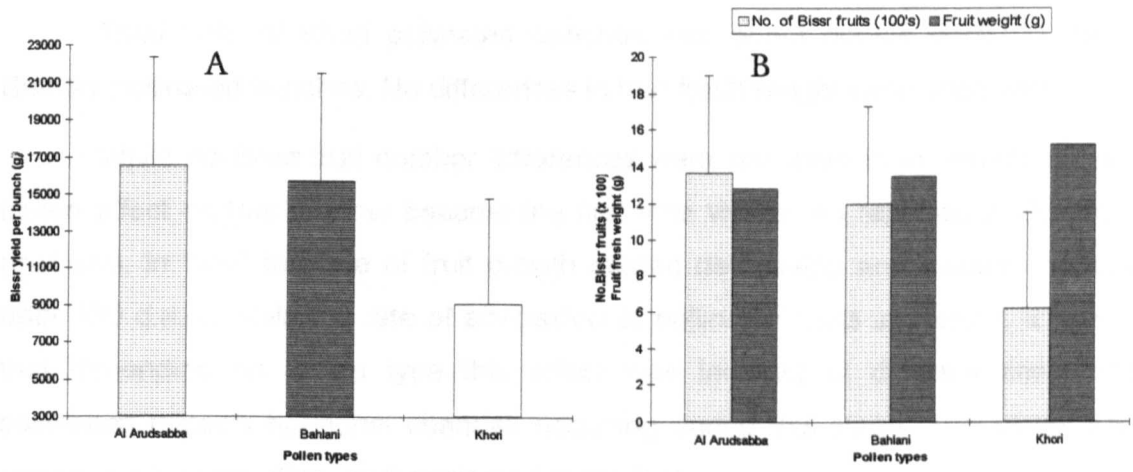


The Bissr yield of bunches pollinated with Al Arudsabba and Bahlani was about twice as high as those pollinated with Khori (Figure 8-11). The multiplicators used to calculate this yield were fruit weight, which was 19 % lower with Al Arudsabba

than with the other pollen types, and number of Bissr fruits, which was with Khori about 2.5 times and 2 times lower than with Al Arudsabba and Bahlani, respectively. This demonstrates the leverage of Bissr fruit number on the Bissr yield. The differences in Bissr numbers arose from the unconfirmed differences (not significant in ANOVA) in the number of pollinated fruits. At 140 d.a.p., no effect on fruit set or fruit number were observed.

At 150 d.a.p., pollen effects on the number of Bissr fruits were found (Figure 8-12).

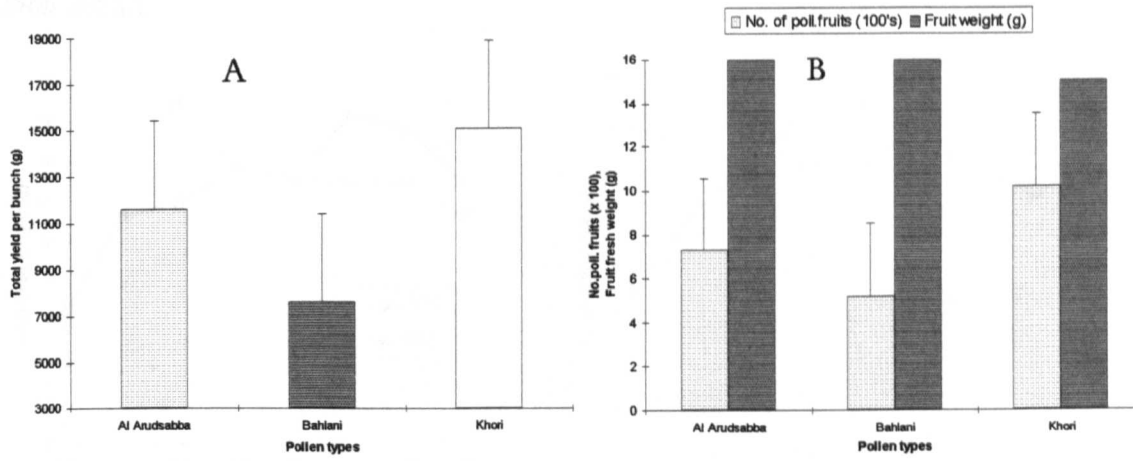
Figure 8-12 *Cv Khalas at 150 d.a.p. in 1996:Bissr yield per bunch in g (A) and number of Bissr fruits per bunch and fruit weight in g (B) in bunches pollinated with three different types of pollen in 1996 (LSD @P<0.05 bars are shown).*



The number of Bissr fruits (P<0.05) was lower with Khori than with the other pollen types at 150 d.a.p.. Fruit weight showed no differences.

In 1995, Khori induced the highest total yield at 140. d.a.p. (P<0.001) followed by Al Arudsabba and then Bahlani (Figure 8-13). Bissr yield could not be examined. Fruit number was higher with Khori than with Al Arudsabba and Bahlani (P<0.05).

Figure 8-13 *Total yield per bunch in g (A) and number of pollinated fruits per bunch and fruit weight in g (B) at 140 d.a.p. in bunches of cv Khalas pollinated with three different types of pollen in 1995.*



LSD @P< 0.05 bars shown

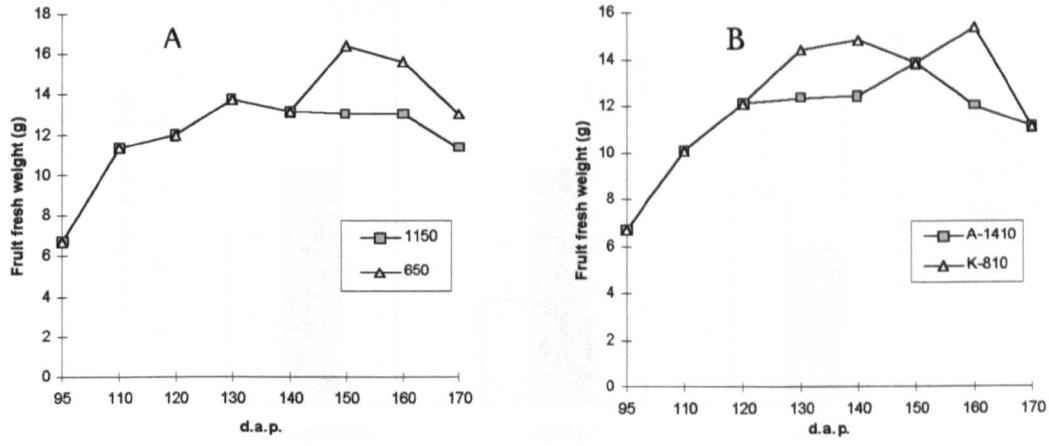
LSD @P<0.05 bars shown

Total yield of Khori pollinated bunches was about double (P<0.01) that of Bahlani pollinated bunches. No differences in fruit fresh weight were observed.

While no Bissr fruit number differences were observed in an earlier stage, a pollen effect on fruit number became the first time visible. As reported in Chapter 5 (fruit set), in 1996 the rate of fruit growth started decreasing and became negative after 130 d.a.p., while the rate of abscission of pollinated fruits increased. It may be that depending on pollen type this effect was induced at different times after pollination through hormonal changes occurring during this stage. This would be a metaxenic or xenic effect as it originated in the fruit.

A question arising here was, whether the differences between pollen blocks in fruit weight in 1996 were due to pollen type or only due to different fruit numbers (Figure 8-14).

Figure 8-14 *Fruit fresh weight (g) of bunches of cv Khalas blocked by two levels of pollinated fruit numbers at 120 d.a.p. (A) and of bunches of cv Khalas blocked by two pollen types (B) in 1996. Observations without significant differences are presented by their mean.*



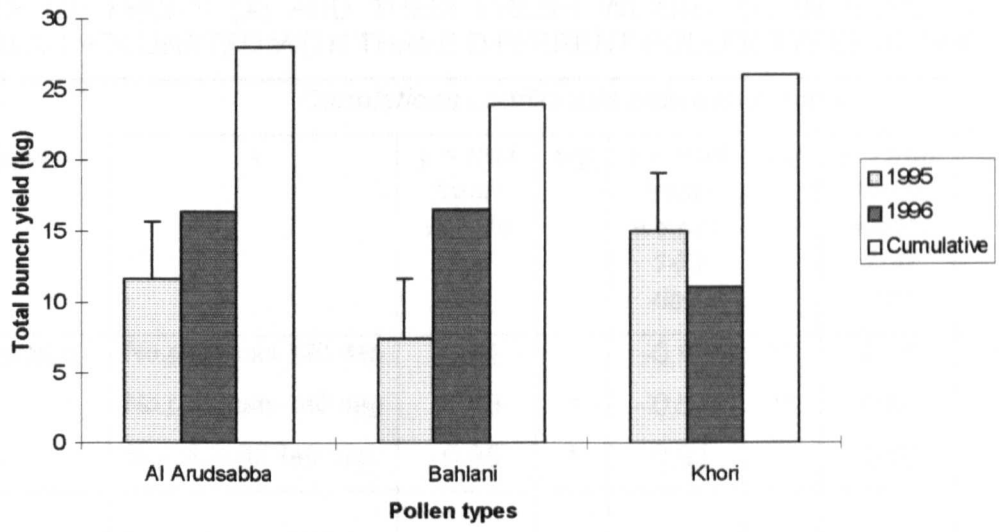
Effects on fruit fresh weight became apparent when firstly (Figure 8-14A) the data were blocked by levels (orthogonal to pollen type) of pollinated fruit numbers at 120 d.a.p. irrespective of pollen type and secondly (Figure 8-14B) by pollen type using only such replications which made the difference in fruit number levels between blocks similar to that in the first blocking. While in the first case differences in fruit weight became apparent only after 140 d.a.p., i.e.: when fruit ripening had started, they appeared in the second case already during the lag phase (not shown in Figure 8-14B) and appeared again after 120 d.a.p., i.e.: when fruits had started to mature. This comparatively earlier appearance of fruit fresh weight effects between pollen blocks is evidence of a pollen effect independent of fruit numbers.

The total yield in 1995, reflects the same significant fruit set differences, which in that year existed already at 50 d.a.p. and may have affected fruit growth. This would have masked the superior effect of Khori on fruit fresh weight, which has not been observed after 80 d.a.p.. No measurements on Bissr yield were taken in 1995.

Statistical analysis of yield taking the two years as replicates reveals no pollen effects.

The cumulative total yield per bunch can be calculated for the two years and is shown in Figure 8-15. As fruits matured earlier in 1995 than in 1996 the 1995 yield is calculated for the 140th d.a.p. and the 1996 yield for the 150th d.a.p.. On a thermal time basis about 1430 °Cd (mean) had been accumulated by the respective d.a.p.'s.

Figure 8-15 *Annual and cumulative total bunch yield (kg) of cv Khalas pollinated with three different pollen types. (LSD @ P<0.05 bars are shown for significantly different pollen treatments).*



Mean cumulative total bunch yield for all pollen blocks was 26 kg and there was an indication that Al Arudsabba induced 17 % more yield than Bahlani and 8% more than Khori. However, given the inconsistency of the annual yield and because only two years were considered, no predictive conclusions were drawn from this.

CV Khasab (95 to 200 d.a.p.):

No effects on yield were observed in either year.

8.2. Relationships between different variables

8.2.1. Fruits retained and fruit weight

CV Khalas (95 to 150 d.a.p.):

In 1996, correlation between fruitset and fruit number on the one hand (x) and fruit fresh weight (y) on the other suggest pollen effects on the influence of one on the

other (Table 8-15). It may be recalled that no pollen effects on fruit set or number were observed (8.1.1.).

Table 8-15 COEFFICIENT OF CORRELATION BETWEEN THE SET (%) AND NUMBER OF FRUITS (X) AND THEIR FRESH WEIGHT (Y) IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

	Correlations coefficients between x and y						
Pollen type	*x*	*y = fruit fresh weight 110 dap*	*sig*	*y = fruit fresh weight 140 dap*	*sig*	*y = fruit fresh weight 150 dap*	*sig*
Al Arudsabba	No.poll.fruits 120 dap	-0.91	*	-0.95	**	-0.96	**
	No.poll.fruits 140 dap	-0.89	*	-0.95	**	-0.92	**
	% poll.fruits 140 dap	-0.85	*	-0.91	*	-0.96	**
Bahlani	No.poll.fruits 120 dap	-	ns	-	ns	-	ns
	No.poll.fruits 140 dap	-	ns	-	ns	-	ns
	% poll.fruits 140 dap	-	ns	-	ns	-	ns
Khori	No.poll.fruits 120 dap	-	ns	-	ns	-0.87	*
	No.poll.fruits 140 dap	-	ns	-	ns	-	ns
	% poll.fruits 140 dap	-	ns	-	ns	-	ns

In Al Arudsabba pollinated bunches, strong and consistent negative correlations were found between all x- and y-variables. It is remarkable that this was not the case for Bahlani as Al Arudsabba and Bahlani were on par with regard to fruit weight, fruit set and fruit number. If causation between the x- and y-variables is assumed, then it would be apparent only for the pollen type Al Arudsabba, while it would have been compensated for in case of the other two pollen types. This in itself would constitute a pollen effect. No such correlations were found with the seed weight.

In 1995, no pollen-specific correlations existed, but an overall correlation existed ($r = -0.8$ @ $P<0.01$) between the number of pollinated fruits at 110 d.a.p. and the fruit fresh weight at 140 d.a.p.. This supports the suggestion made in

Section 8.1.2., that possible pollen effects were obscured or compensated by the influence of differences in fruit set/number or in thermal time.

CV Khasab (95 to 200 d.a.p.):

In 1996, significant negative correlations were observed between the percentage of pollinated fruits and the fruit fresh weight at 180 d.a.p. for all bunches ($r = -0.6$ @ $P<0.05$), and particularly for pollen types Al Arudsabba ($r = -0.9$ @ $P<0.05$) and Bahlani ($r = -0.8$ @ $P<0.05$). However, in 1995 no correlations for all or bunches blocked by pollen types were observed at 170 d.a.p., while there were highly significant negative correlations (overall $r = -0.5$ @ $P<0.01$, for Al Arudsabba $r= -0.7$ @ $P<0.05$) still apparent between fruitset and fresh weight at 110 d.a.p.

8.2.2. Fruit weight and fruit maturity

CV Khalas (95 to 150 d.a.p.):

The suggestion made in section 8.1.4., that in 1996 Khori-pollinated fruits kept on growing with the end of maturity and beginning of ripening being delayed, is supported by correlation analysis. A significant, negative correlation ($r = -0.94$ @ $P<0.05$) between the fruit fresh weight at 140 d.a.p. and the percentage of mature fruits at 120 d.a.p. as indicated by fruit colour, was only found in bunches

pollinated with type Khori. This implied that Khori-pollinated fruits became heavier while maturing later, while a similar covariation did not exist for the other two pollen types. This implication is supported when the increment of fruit fresh weight between 110 and 140 d.a.p. for the three pollen types was examined (Table 8-16).

Table 8-16 INCREMENT IN FRESH WEIGHT BETWEEN 110 AND 140 D.A.P. OF FRUITS IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

	Fresh weight increment (g) between 110 and 140 d.a.p.	
Pollen type		
Al Arudsabba	2.2	b
Bahlani	2.5	b
Khori	3.9	a

LSD @P<0.05 = 1.7 g.

Pollination with Khori resulted in a 80 and 55 % larger absolute increment in fruit fresh weight than pollination with Al Arudsabba and Bahlani, respectively.

The above described correlation was in itself a pollen effect, which was probably metaxenic or which may have been mediated through a xenic effect on the seed weight at 110 d.a.p. (Section 8.1.2.).

Although it is not possible to draw definite conclusions about causal effects, i.e.: heavy weight causing delayed maturity or vice versa, it can be speculated that endogenous substances, which bring about maturity and ripening changes, acted later than in the other two pollen types, so that Khori-pollinated fruits could continue to grow thereby becoming heavier.

CV Khasab (95 to 200 d.a.p.):

No correlations between fruit weight at the Bissr stage (200 d.a.p.) and the proportion of such fruits were observed.

8.2.3. Relationships of different variables with thermal time

Observations blocked by pollen type were examined for correlations between thermal time on the one hand and fruit fresh weight, fruit size, total sugars (°Brix) and the percentage of Bissr fruits as indicated by colour on the other.

CV Khalas (95 to 150 d.a.p.):

In 1996, thermal time was overall positively correlated with fruit and seed fresh weight at 80 d.a.p. and 95 d.a.p. ($P<0.01$) and only with fruit fresh weight at 110 d.a.p. ($P<0.05$). There were no pollen specific correlations of thermal time with any of the above mentioned variables, except for total sugars (°Brix). In that case, a significant ($P<0.05$) correlation coefficient of $r = 0.86$ was observed at 150 d.a.p. for fruits pollinated with Al Arudsabba. It may be recalled from Section 8.1.5., that there were no pollen effects on total sugar content at 150 d.a.p..

It appeared, that the more thermal time accumulated at 150 d.a.p. by fruits pollinated with Al Arudsabba, the more total sugars accumulated. This was neither the case with the other two pollen types, nor for the data of all three blocks taken together. As the observations were on the same day after pollination (150 d.a.p.) , this may have also reflected the response to the actual date of pollination, i.e.: late pollinated flowers, which accumulated more thermal time units in 150 days, responded more than earlier ones, which accumulated less thermal time units in 150 days. This phenomenon is due to the increasingly larger heat unit increments as the season progresses . The described correlation may be a pollen effect, possibly metaxenic. It was not an experimental artifact, as there were no significant differences between the thermal time accumulated by the different treatment blocks at 150 d.a.p..

The absence of thermal time differences also lend support to earlier claims (Sections 8.1.1. to 8.1.8) of metaxenic effects in cv Khalas in 1996, because, apart from fruit set differences, these differences could have also masked or imitated "pollen effects" if they had existed.

In 1995, no correlations between the above variables were observed within treatment blocks .

CV Khasab (95 to 200 d.a.p.):

Thermal time correlations with the variables, for which pollen effects occurred, and with the °Brix at 180 and 200 d.a.p. were examined for the year 1996. Variables were blocked by pollen type.

Positive correlations with thermal time (x) were found only for Bahlani pollinated fruits with

- y= °Brix at 200 d.a.p. (r^2 = 0.72 @ P<0.01), y= -37+0.04 • x
- y= seed weight at 140 d.a.p. (r^2= 0.88 @ P<0.05), y=-0.11+6.5 • x

The above shows that total sugar content and seed growth in Bahlani pollinated fruits increased linearly over a range of thermal time, which in itself may be a pollen effect.

8.2.4. Uniformity of size and fruit set

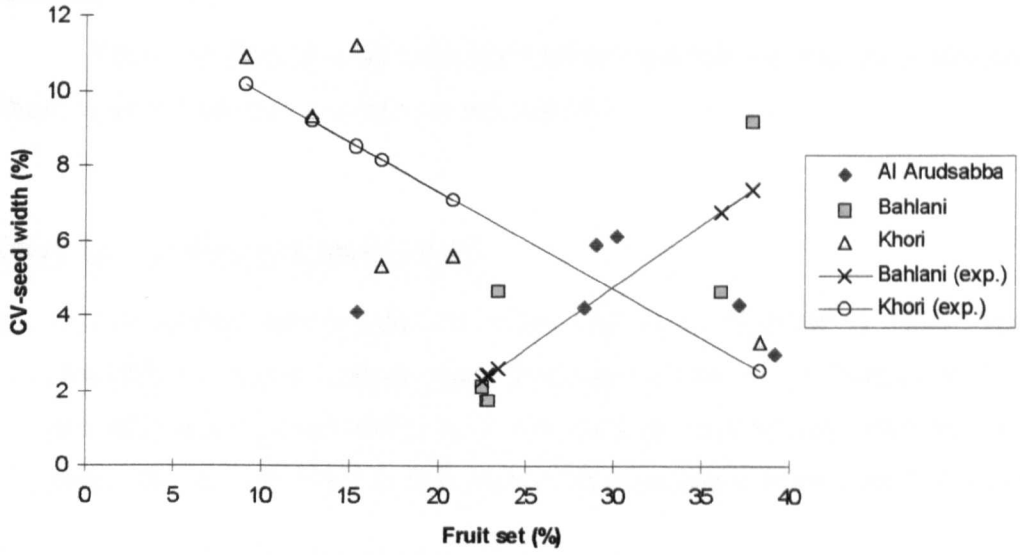
In cv Khalas, pollen effects on uniformity of fruit and seed size have been observed in both years of the study as presented in Section 8.1.7..

Figure 8-16 shows that in 1996 the $CV(\%)_{seed\ width}$ of Bahlani and Khori pollinated fruits at 140 d.a.p. behaved very differently. While for Bahlani $CV(\%)_{seed\ width}$ increased, i.e.: uniformity decreased, with increasing fruit set (r^2=0.69 at P<0.05), it decreased, i.e.: uniformity increased, with increasing fruits set (r^2= 0.66 at P<0.05). This relationship can be represented by the following regression equations:

- for Bahlani: y = -5.1 + 0.33 • x
- for Khori: y = 12.5 - 0.26 • x ,

where x = fruit set (%)and y = $CV(\%)_{seed\ width}$ at 140 d.a.p..

Figure 8-16 *Relationship between fruit set (%) and CV(%) of seed width in fruits of cv Khalas pollinated with three different pollen types in 1996.*



In the Bahlani block the CV increased three times when fruit set increased by 15% whilst in the Khori block the CV was reduced to one quarter when fruit set increased from 38 to 9 %.

In 1995, no pollen specific, but a negative overall correlation at 140 d.a.p. between fruit set (x) and $CV(\%)_{Fruit\ length}$ (y) was observed, which can be described by the regression equation:

- $y = 7.1 - 0.1 \cdot x$

8.3. Summary and discussion

Effects on fruit set

Pollen treatments had significant effects on fruit set only in cv Khalas. In 1995 Khori again resulted in the highest fruit set (%).

Effect on fruit and seed fresh weight

1. In cvs Khalas and Khasab in 1996 and in cv Khasab in 1995, Khori pollen resulted in heavier mature fruits and seeds than Al Arudsabba in 1996, which probably are true metaxenic and xenic effects, respectively. Bahlani was in some cases on par with Khori and in others intermediate to Khori and Al Arudsabba.

   Total fruit fresh weight effects in 1996 can be considered true metaxenic effects as pollen did not affect fruit set. The seed effects can not be called metaxenic, as the results would reflect embryo or endosperm weight, which by definition would be a xenic and probably genetic effect. Pollen type elicited similar, but separate, responses in the fresh weight of seed and pericarp. The seed effect would be xenic. The pericarp fresh weight effect would be largely due to the seed effect but at the same time some other factors influenced it, such as due to the metaxenic effect of pollen type on other apparent characteristics like stage of maturity and ripeness (Section 8.1.4. and Chapter 9).

2. In cv Khasab in 1996, with NAA caused heavier fruits. This effect is of similar magnitude as that due to pollen type Khori and suggests that possibly genetic causes may have brought about a higher auxin-level in case of Khori.

Effects on fruit and seed size

1. Khori induced in cv Khalas only in 1996 slightly longer, wider and more voluminous fruits (180 d.a.p.) than Al Arudsabba. The effects are probably true metaxenic or mediated through a xenic effect on seeds.

2. Khori and Bahlani had a true xenic effect on seeds and metaxenic effect fruits in cv Khasab in 1996 resulting in longer seeds and fruits at 140 d.a.p. and longer mature fruits at 180 d.a.p. In 1995 Khori resulted in wider seeds at 170 d.a.p..

Effects on maturity

1. In 1996, pollen effects, which are probably truly metaxenic, occurred in cv Khalas with Al Arudsabba and Bahlani pollinated bunches containing more mature-coloured fruits at 120 d.a.p.. Maturity, as indicated by colour, was the most uniform in Bahlani pollinated fruits. Khori pollinated bunches matured latest.

2. In 1995, pollination with Bahlani and Khori caused earlier maturity in bunches of cv Khalas than in 1996. Generally fruits had matured about 10 days earlier in 1995 than in 1996 but at equal thermal time.

3. Khori treated Khasab bunches showed in 1996 the lowest variation between 160 and 200 d.a.p.. indicating that they matured more uniformly.

Effects on sugars

In cv Khalas in 1995, less sucrose had accumulated in fruits pollinated with Al Arudsabba as compared to Bahlani and Khori indicating delayed maturity. The measurement of total sugars (°brix) was not a reliable indicator of maturity as no differences were found at the time of maturity, when colour clearly indicated differences in maturity.

Effects on the uniformity of fruit and seed size

1. Pollination with Khori and Bahlani resulted in cv Khalas in 1995 in the most uniform fruit length and width. This is probably influenced by fruit set differences.
2. Pollination with Al Arudsabba and Bahlani resulted in cv Khalas in 1996 in the most uniform seed width. which may be a true metaxenic effect as no differences in fruit set existed.

Effect on yield

1. In 1996 Khori pollinated bunches of cv Khalas yielded between 130 and 150 d.a.p. about half the Bissr yield of bunches pollinated with the other two pollen types, while in 1995 Khori pollinated bunches of cv Khalas yielded a total bunch yield double that of Bahlani pollinated bunches

2. Cumulative yields appeared to be highest for Al Arudsabba, lower for Khori and lowest for Bahlani.

Relationship between fruit retention and weight

1. In cv Khalas in 1996, in cv Khasab at 180 d.a.p. in 1996 and at 110 d.a.p. in 1995, Al Arudsabba specific negative correlations between fruit set and mature fresh weight existed. The underlying mechanism can be only speculated on. It may be that Al Arudsabba-pollinated fruits are under the influence of limiting factors, which made fruits in bunches with a higher fruit set grow to a smaller fresh weight. However, it could be also, that in Bahlani and Khori pollinated bunches, particular types or levels of hormones, have offset the commonly occurring tendency of high fruitset to cause low fruit weight.

2. No pollen specific correlations were found in cv Khalas in 1995, possibly because such relationships would have been masked or compensated by differential fruit set. Recalling that no pollen effects on fruit set at 180 d.a.p. were observed in either year, it could be reasoned that in 1995 the comparatively high fruit set in all bunches (51 %) had passed beyond a critical level, at which some or all substrates (photosynthates, water, etc.) would have just met the demand of their sinks. The entire tree system could have been affected by this, so that individual bunches were no longer independent of each other. This would be also supported by observations, firstly that a clear overall correlation still existed at 100 d.a.p., and secondly that the overall mature fruit fresh weight was about 0.5 gm lower in 1995 than in 1996. In 1996, the overall fruit set mean was much lower at 43 % and pollen specific correlations could be observed, possibly because supply of substrates was still below critical level. Consequently competition and differential distribution of resources between fruits in different bunches would have taken place, which resulted in the observed fruit weight differences. In either years

specific levels of hormones may have been active in bunches pollinated with different pollen types, but their effect appears to have been obscured in 1995, while becoming apparent in 1996.

Relationship between fruit weight and maturity

Khori pollinated fruits in cv Khalas in 1996 grew heavier while maturing later.

Relationship between total sugar content and thermal time

In 1996 total sugar content at 150 d.a.p. in Al Arudsabba-pollinated fruits of cv Khalas and in Bahlani-pollinated fruits at 200 d.a.p. of cv Khasab increased with advancing thermal time indicating advancing maturity. The observation here, that the total soluble solid content of Al Arudsabba pollinated fruits increased with thermal time, supports the findings of earlier sections that cv Khalas fruits, and for the first time also cv Khasab fruits which were pollinated with this type, matured earlier. The nature of the described pollen effect, i.e.: pollen specific correlation of the total sugar content with thermal time, rather than a direct pollen effects on total sugar content, suggests that Al Arudsabba pollinated fruits are characterized by pollen specific biochemical or physiological processes, which are time and temperature dependent.

Relationship between uniformity and size of fruits and seeds

In cv Khalas in 1996 uniformity of seed width increased with increasing fruit set in the Khori block, but decreased in the Bahlani block.

Bahlani (and also Al Arudsabba) induced more uniform seeds and maturity than Khori, which may be due to different levels of heterozygosity (Osman, 1974) in that Khori induces a wider spread in these variables, which indicates genetic effects. However, the diametrically different response of seed uniformity to fruit set may be due to physiological processes acting on seeds which have a different genome. This may explain the different response. Whether this is the cause or consequence of the late onset of maturity in Khori pollinated bunches and the early onset in Bahlani pollinated ones can not be clarified.

9. Stage Four: beginning of ripening to harvest of the product

This stage started when the fruits had reached full maturity as indicated by maximum size and the development of the full Khalal colour. Ripening began immediately thereafter and was characterized by a reduction in fruit weight and size, ending with the harvest of full Rutab fruits. Differences in fruit growth and development due to pollen were likely, but they may have been also under the influence of fruit set. For most variables, this influence could not be reliably assessed at the end of this stage, because fruit set was highly variable (over ripe fruits tended to drop and humidity, insects and birds led also to fruit loss). Results are presented therefore until observations became impossibly erratic, which was 170 d.a.p. in cv Khalas and 245 d.a.p. in cv Khasab.

Experiments were carried out to examine pollen effects on fruits of different cultivars. They examined fruit growth and development (Sections 9.1.), looking particularly for correlations between such variables as fruit and seed weight, size and the degree of ripeness as indicated by colour change on the one hand and fruit set, thermal time and pericarp weight on the other (Sections 9.2.) for each of the pollen types. These were expected to vary with the metaxenic potential of pollen type. As effects in this last stage were likely to be influenced by effects in previous growth stages, correlation between variables in earlier stages may have to be examined as well.

9.1. Effect of pollen type on growth and development of ripening fruit

The experiments were designed to analyse pollen effects on several physical and chemical characteristics of the ripening fruits and to suggest their underlying mechanisms. Effects of pollen type on fruit set were examined here in two female cvs Khalas and Khasab. Differences due to a contribution from the male genotype were expected. Fruit set effects were therefore an important consideration in this stage as well. In cv Khalas, this stage extended from 150 d.a.p. to 170 d.a.p. and from 200 d.a.p. to 245 d.a.p. in cv Khasab.

9.1.1. Fruit set

CV Khalas (150 d.a.p. to 170 d.a.p.):

About 10 % of all ovaries dropped during this stage. Pollen effects were observed at 160 d.a.p. and 170 d.a.p. in 1996 and at 170 d.a.p. in 1995 (Table 9-1). This was the first time a pollen effect on fruit set was observed in this cv in 1996. Al Arudsabba pollinated bunches retained 8 % and 10 % more of the initial number of ovaries than Khori pollinated ones at 160 and 170 d.a.p., respectively. This effect of pollen type Khori on fruit set could have been related to the high fruit weight at 160 d.a.p., which will be examined in Section 9.2.1..

Table 9-1 FRUIT SET AT 160 AND 170 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996 AND 1995.

	1996: Fruit set (%)				*1995: Fruit set (%)*	
Pollen type	*160 d.a.p.*		*170 d.a.p.*		*170 d.a.p.*	
Al Arudsabba	25	a	23	a	16	b
Bahlani	24	ab	19	ab	21	b
Khori	17	b	13	b	31	a

1996: LSD @ P< 0.05 = 7.5% at 160 d.a.p and LSD @ P<0.05= 9.5% at 170 d.a.p..
1995: LSD @ P< 0.001 = 7 %.

In 1995 Khori pollinated bunches retained 15 % more of the initial number of ovaries than Al Arudsabba pollinated ones at 170 d.a.p.. Fruit set in this stage followed the same response pattern to pollen treatments, which was observed in Stage 1 and Stage 2 and it is likely that this effect originated and continued from Stage 1 onwards. Its influence on other variables was expected and examined by correlation in Sections 9.2.1. and 9.2.3..

CV Khasab (200 d.a.p. to 245 d.a.p.):

About 20 % of all ovaries dropped during this stage. No pollen effects on fruitset were observed in either years.

9.1.2. Fruit fresh weight

CV Khalas (150 d.a.p. to 170 d.a.p.):

Pollen effects were observed on the fruit fresh weight at 160 d.a.p. in 1996 and at 170 d.a.p. in 1995 (Table 9-2). No effects on dry weight were observed.

Table 9-2 FRESH WEIGHT (g) OF FRUITS AT 160 D.A.P. AND 170 D.A.P. IN CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996 AND 1995.

	1996: Fruit fresh weight (g)		*1995: Fruit fresh weight (g)*	
Pollen type	*160 d.a.p.*		*170 d.a.p.*	
Al Arudsabba	12.1	b	16.1	a
Bahlani	12.2	b	14.1	b
Khori	14.7	a	13.3	b

1996: LSD @ P< 0.05 = 2.3 g.
1995: LSD @ P< 0.001 = 1.5 g.

In 1996 Khori pollinated fruits were 21 % heavier than fruits developing after pollination with the other two male types. This is an advantageous quality feature of Khori pollinated fruits. The effect appears to be a continuation of the response on fruit fresh weight at 140 d.a.p., and was unlikely to be due to fruit set differences between pollen blocks, which did not exist until 170 d.a.p. (Section 9.1.1.). This will be examined further in Section 9.2.1..

In 1995, the response pattern was different. The degree of the differences caused by pollen type was similar to the one in 1996, but Al Arudsabba pollinated fruits were 21 % heavier than the ones pollinated with either Bahlani or Khori. Common to both years was, that Bahlani pollinated fruits were among the lightest, while Khori was superior in 1996 and Al Arudsabba in 1995.

The above will be examined on a thermal time basis in Section 9.2.2..

CV Khasab (200 d.a.p. to 245 d.a.p.):

No pollen effects were observed in either year.

9.1.3. Fruit size

CV Khalas (150 d.a.p. to 170 d.a.p.):

Significant pollen effects on the width and length of fruits were observed at 160 d.a.p. in 1996 and on the width of at 170 d.a.p. in 1995 (Table 9-3). They followed a response pattern similar to fruit fresh weight (Section 9.1.2.).

Table 9-3 SIZE (cm) OF FRUITS AT 160 D.A.P. AND 170 D.A.P. IN CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996 AND 1995.

	1996: Fruit size at 160 d.a.p.				*1995: Fruit width at 170 d.a.p.*	
Pollen type	*Length (cm)*		*Width (cm)*		*Width (cm)*	
Al Arudsabba	3.6	b	2.3	b	2.5	a
Bahlani	3.6	b	2.3	b	2.4	b
Khori	3.9	a	2.4	a	2.4	b

1996: LSD @ P< 0.05 = 0.2 cm for length and LSD @ P<0.05= 0.1 cm for width.
1995: LSD @ P< 0.05 = 0.1 cm. Interaction between tree and pollen.

Fruit size in 1996 was largest in Khori pollinated fruits, which were about 9 % longer and 4 % wider than those pollinated with the other two pollen types. Fruit width in 1995 was 4 % larger in Khori pollinated fruits than those pollinated with the other two pollen types.

This was consistent with the findings on fruit weight and the causes were assumed to be similar.

CV Khasab (200 d.a.p. to 245 d.a.p.):

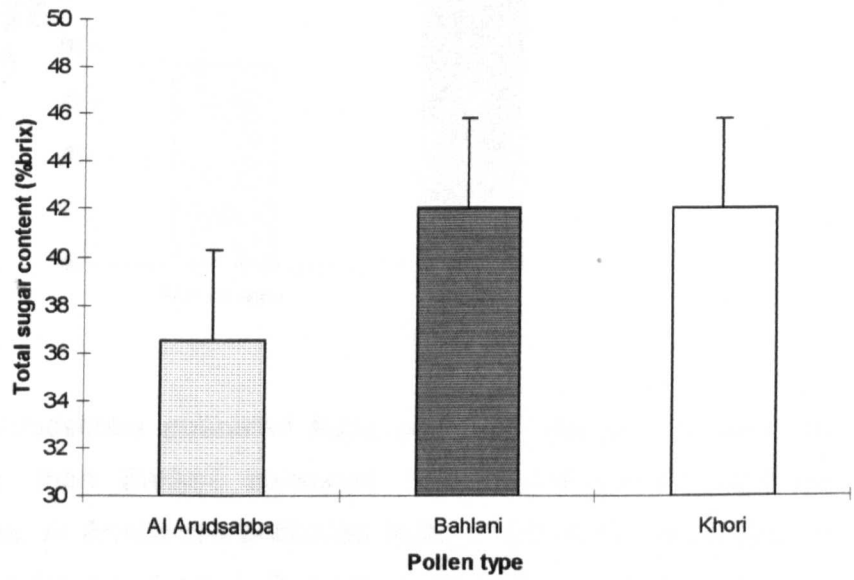
No pollen effects were observed.

9.1.4. Total sugars

CV Khalas (150 d.a.p. to 170 d.a.p.):

In cv Khalas, pollen significantly ($P<0.05$) affected the total sugar content of the pericarp at 170 d.a.p. in 1995 (Figure 9-1).

Figure 9-1 *Total sugars content (°Brix) in the pericarp of fruits in cv Khalas pollinated with three different pollen types in 1995 (LSD @ P<0.05 bars are shown).*

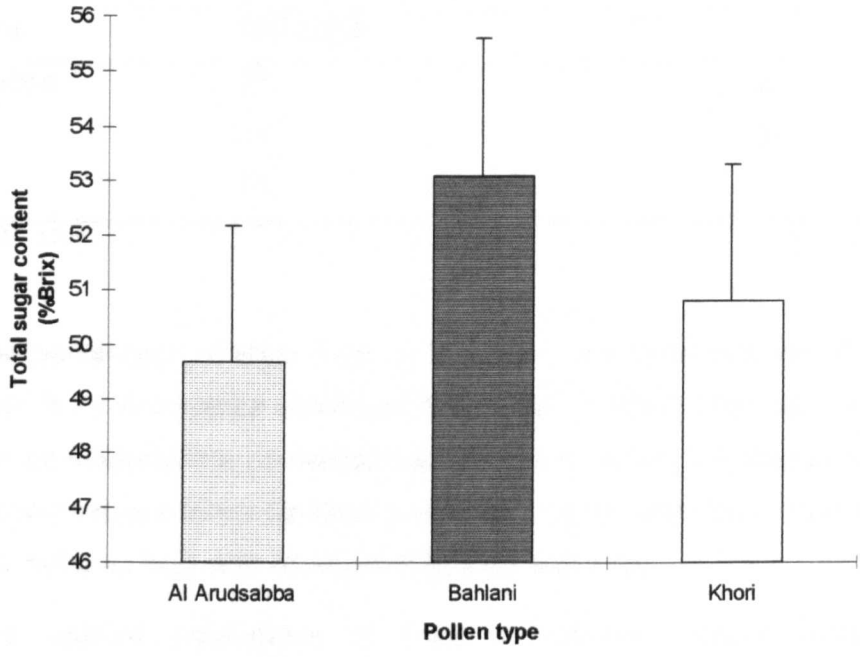


Al Arudsabba pollinated fruits contained 6 % less total sugars at 170 d.a.p. in 1995 than fruit pollinated with the other two pollen types. This indicated delayed ripening in these bunches in comparison to Bahlani and Khori pollinated ones, which ripened together. This was consistent with results on maturity as reported in Section 8.1.4..

CV Khasab (200 d.a.p. to 245 d.a.p.):

Pollen significantly ($P<0.05$) affected the total sugar content of the pericarp in cv Khasab fruits at 215 d.a.p. in 1996 as shown in Figure 9-2.

Figure 9-2 *Total sugars content (°Brix) at 215 d.a.p. of the pericarp of fruits in cv Khasab pollinated with three different pollen types in 1996 (LSD @ P<0.05 bars are shown).*



Al Arudsabba pollinated fruits contained about 3 % less total sugars at 215 d.a.p. than Bahlani pollinated ones, while Khori pollinated fruits were intermediate. Al Arudsabba pollinated fruits, which were the lightest (Section 9.1.2.) and smallest (section 8.1.3) in Stage 3, contained also the least total sugars.

9.1.5. Harvested products

CV Khalas (150 d.a.p. to 170 d.a.p.):

The percentage of Bissr fruits at 160 d.a.p. in relation to the initial number of ovaries (Table 9-4) and the relative proportions of Bissr, half-Rutab and Rutab fruits in a bunch (Figure 9-3 and Table 9-5) at different times in this stage were significantly affected (P<0.05) by pollen type in 1996.

Table 9-4 PERCENTAGE OF BISSR FRUITS IN RELATION TO THE INITIAL NUMBER OF OVARIES AT 160 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

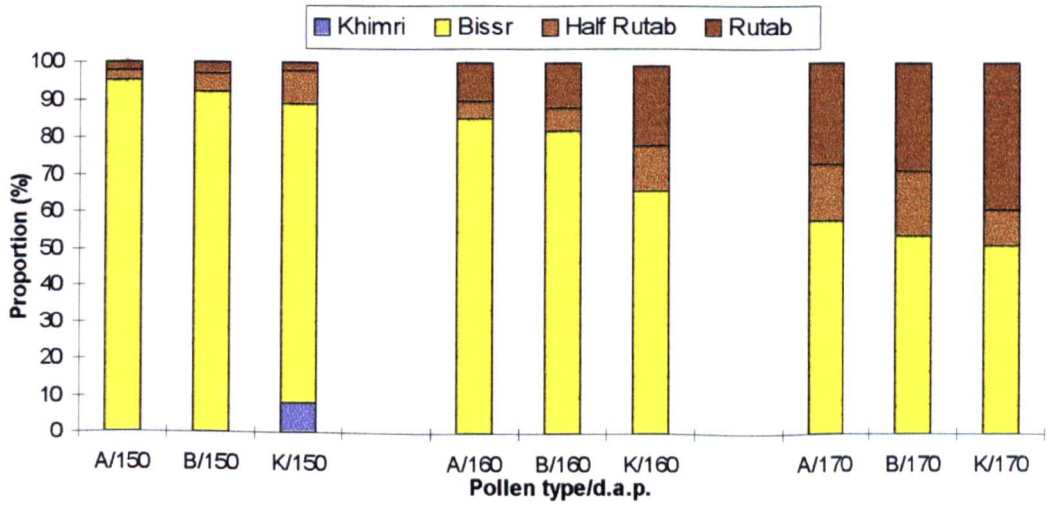
	Bissr fruits (%)	
Pollen type	*160 d.a.p.*	
Al Arudsabba	23	a
Bahlani	21	ab
Khori	14	b

LSD @ P< 0.05 = 8.5 %.

The percentage of Bissr fruits in relation to the initial number of ovaries was 9 % higher in Al Arudsabba pollinated fruits than in Khori pollinated ones. Bahlani resulted in an intermediate percentage at 160 d.a.p. in 1996. It should be noted that this is of commercial interest for Bissr production, as the total Bissr yield at 150 d.a.p. was nearly twice as high with Al Arudsabba than with Khori.

The relative proportions of fruits in different stages were examined (Figure 9-3). This was to provide information firstly about the earliness of maturity as indicated by the relative proportion of Bissr fruits at the beginning of this stage and secondly about the progress or 'speed' of ripening as indicated by the appearance and proportions of half-Rutab and Rutab fruits during the remainder of this stage.

Figure 9-3 *Proportion of Bissr, half-Rutab and Rutab fruits at different times in bunches of cv Khalas pollinated with three different pollen types in 1996.*



At 150 d.a.p. less than 10 % of all fruits were in the half-Rutab and Rutab stages. In Khori pollinated bunches, even Khimri fruits (immature) were still present at that time. The percentage of all half-Rutab and Rutab fruits increased from between 15 and 32 % at 160 d.a.p. to between 40 and 50 % at 170 d.a.p.. Most of these percentages at 160 and 170 d.a.p. were due to Rutab fruits, while only between 5 to 12 % and 10 to17 %, respectively, were due to the proportion of half-Rutab fruits.

Table 9-5 PROPORTION OF HALF AND FULL RUTAB FRUITS IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

	half-Rutab (%)		*Rutab (%)*		*half-Rutab+Rutab (%)*	
Pollen type	*150 d.a.p.*		*160 d.a.p.*		*160 d.a.p.*	
Al Arudsabba	2.6	b	10	b	15	b
Bahlani	5.2	b	12	b	18	b
Khori	9.2	a	21	a	33	a

half-Rutab at 150 d.a.p. LSD @P< 0.05 = 3.3 %
Rutab at 160 d.a.p. LSD @P< 0.05 = 7.0 %
half + full Rutab at 160 d.a.p. LSD @P<0.05 = 12.0 %

While Table 9-4 shows that more Al Arudsabba pollinated fruits matured earlier, fruits pollinated by Khori ripened faster (Table 9-5). This resulted in more than twice the proportion of half-Rutab and Rutab fruits at 160 d.a.p. than in the bunches pollinated with the other two pollen types. Khori pollinated fruits ripened faster but at 170 d.a.p. all treatment means were again on par.

No data were available for 1995..

CV Khasab (200 d.a.p. to 245 d.a.p.):

No pollen effects were observed.

9.1.6. Yield

CV Khalas (150 d.a.p. to 170 d.a.p.):

Yield of Bissr fruits at 150 d.a.p. in 1996 was significantly ($P<0.05$) affected by pollen type as already reported in Section 8.1.8. with Al Arudsabba pollinated bunches bearing the highest yield of Bissr fruits. However, in the present stage, yields of half- and full Rutab fruits were not affected. In 1995 total yield at 170 d.a.p. was affected by pollen types (Table 9-6).

Table 9-6 TOTAL YIELD AT 170 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1995.

	Total bunch yield (g)	
Pollen type	*170 d.a.p.*	
Al Arudsabba	7002	ab
Bahlani	5615	b
Khori	10016	a

LSD @ P< 0.05 = 3040 g.

Total yield in Khori pollinated bunches was almost twice as high as in Bahlani pollinated ones. No conclusions can be however drawn about the nature of this pollen effect, as yield is a combination of different factors, i.e.: fruit number and fruit fresh weight. It is however of commercial importance.

CV Khasab (200 d.a.p. to 245 d.a.p.):

No pollen effects were observed in either year.

9.1.7. Appearance of fruits

CV Khalas (150 d.a.p. to 170 d.a.p.):

Plate 9-1 shows a representative sample of fruits of different stages of ripening in bunches of in cv Khalas at 160 d.a.p. in 1996. The purpose of this photograph was to assemble different stages in the proportion of their occurrence. It was not arranged to reflect the size differences between pollen treatments, although the larger size of Khori-pollinated fruit is evident. It was obvious that a relatively higher proportion of half and full Rutab fruits was present in Khori pollinated bunches (Section 9.1.5.) in comparison with Al Arudsabba and Bahlani pollinated ones. It was also observed that in Al Arudsabba and Bahlani pollinated bunches fruits were present, which were almost in the Tamr stage, i.e.: shrinkage and drying of fruits had begun, while in Khori pollinated ones only the first signs of shrinkage were visible. The pliability of fruits was coincident with this. At the same time the least ripe fruits, i.e.: Bissr fruits were more matured in Al Arudsabba pollinated bunches than in Khori pollinated ones as indicated by the more intense yellow colour. The above gave support to the thought put forward in Section 9.1.5, that Al Arudsabba pollinated bunches had matured earlier as indicated by the presence of fruits from fully mature to almost Tamr, while Khori pollinated bunches had matured later, but did ripen more uniformly and, therefore, on average ripened quicker. This uniformity makes Khori pollinated fruits also more amenable to bulk harvesting of ripe fruits, while Al Arudsabba pollinated ones would be of interest for consumers, who want fruits in different stages of ripeness.

Plate 9-2 shows that in Khori pollinated bunches even green Khimri stage fruits were present at 170 d.a.p. and also that some of these fruits had a distinct longitudinal line extending from the fruit base to near the equator, rarely present with the other pollen treatments. This was probably a left-over of the ridge between the indentations initially made by the other two carpels, which later sloughed of as a result of the dominance of the fertilized carpel.

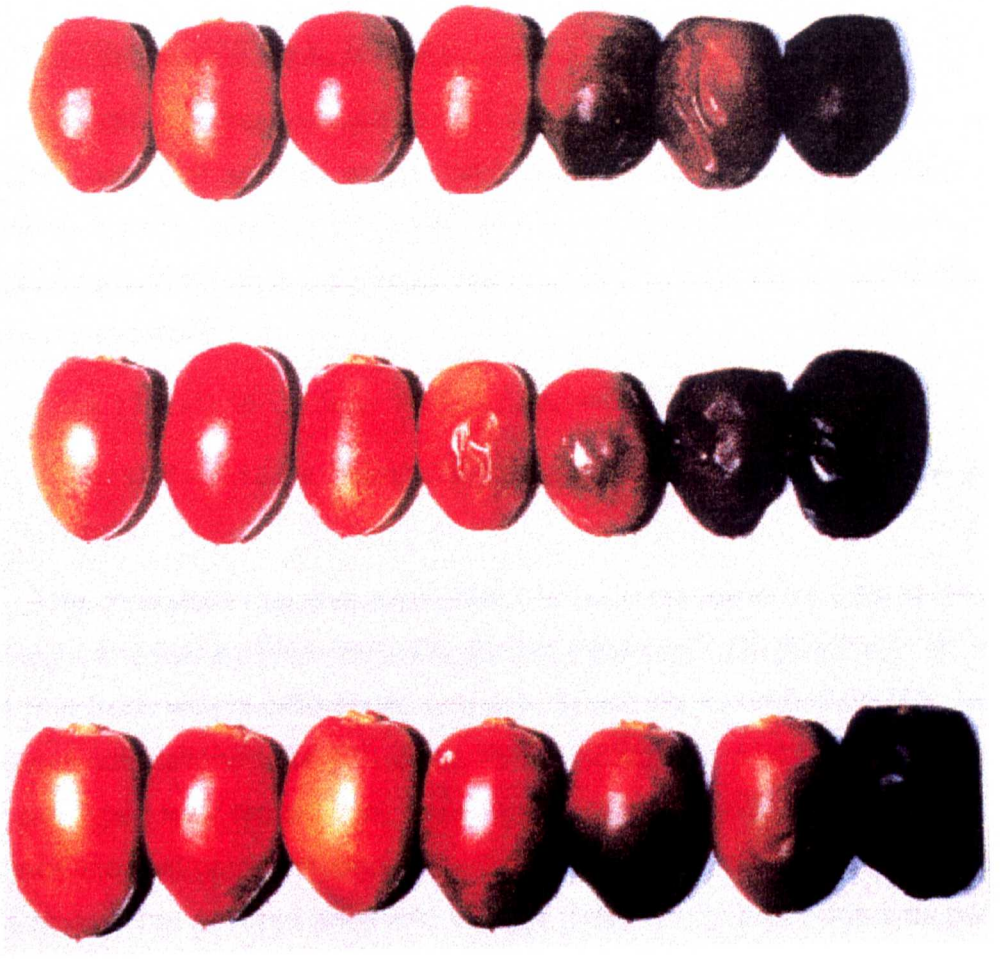
Plate 9-1 *Fruits of cv Khalas at 170 d.a.p .pollinated in 1996 with three different types of pollen in 1996. Top row: Al Arudsabba; middle row: Bahlani; bottom row: Khori.*

Plate 9-2 *Fruits of cv Khalas at 170 d.a.p. pollinated in 1996 with pollen type Khori. Khimri coloured fruits on the right side.*

CV Khasab (200 d.a.p. to 245 d.a.p.):

Plate 9-3 shows fruits of cv Khasab at 230 d.a.p. in 1996. The Khori pollinated fruits are mainly mature ones with only a few half-Rutab and full Rutab fruits, in which relatively little shrinkage had taken place in comparison with the shrinkage in the full Rutab fruits, which had been pollinated by Al Arudsabba and Bahlani. Although the proportion of Rutab fruits was approximately the same with all pollen types, it was apparent that Khori pollinated ones ripened the slowest. This supports the interpretation of correlations between thermal time and fruit fresh weight which will be presented in Section 9.2.2.. Al Arudsabba pollinated fruits are shorter.

Plate 9-3 *Fruits of cv Khasab at 230 d.a.p .pollinated in 1996 with three different types of pollen in 1996. Top row: Al Arudsabba; middle row: Bahlani; bottom row: Khori.*



9.2. Relationships between different variables

9.2.1. Fruits retained and fruit weight

CV Khalas (150 d.a.p. to 170 d.a.p.):

In 1996 fruit fresh weight at 160 d.a.p. (y) was significantly and negatively correlated with fruit set (%) at any time after 40 d.a.p. for the overall data and specifically for data blocked by pollen type Al Arudsabba. As a typical example, the relationships with the fruit set percentage at 140 d.a.p. (x) can be described by the regression equations

- $y = 17.3 - 0.16 \cdot x$, with $r^2 = 0.57$ and $P<0.01$ for all fruits and
- $y = 17.7 - 0.19 \cdot x$, with $r^2 = 0.88$ and $P<0.01$ for Al Arudsabba pollinated fruits.

The consistent negative correlations for all fruits taken together indicated that fruit weight and fruit set were inversely related. However, this relationship did not bring about fruit fresh weight differences between pollen blocks until after 170 d.a.p.. The consistent correlations until 150 d.a.p. for Al Arudsabba and their absence for the other two types was remarkable. Apparently, the weight of Al Arudsabba pollinated fruits was more strongly influenced by fruit set than the fruit weight of the other two pollen types. That Al Arudsabba and Bahlani differed in this respect, was particularly remarkable, as Bahlani pollinated fruits were on par with Al Arudsabba pollinated ones regarding fruit weight and set. This was probably a pollen effect in itself and possibly reflected differences in the causal mechanisms.

Correlations existed between fruit fresh weight and fruit set percentage at 160 d.a.p., but then they were found to be significant ($P<0.01$) for data blocked by pollen type Khori as well. In order to draw conclusions on which variable had affected the other, it was reasoned that the fresh weight of Khori pollinated fruits probably had a determining effects on fruit retention at 160 d.a.p., because:

- Khori had induced higher fruit weights already at 140 d.a.p. and the highest weight gain between 80 and 95 d.a.p., but no fruit set effects were found at those times.

- Now was the first time a Khori-specific correlation (negative) between fruit weight and fruit set appeared

The Khori block correlation was therefore likely to be caused by fruit weight affecting fruit set. The Al Arudsabba block correlations however probably directly reflected a pollen effect.

In 1995, fruit weight at 170 d.a.p. was also negatively correlated with fruit set percentage at any time after 50 d.a.p.. For example, at 140 d.a.p. an overall significant ($P<0.05$) negative correlation ($r = -0.6$) was observed. No correlations were observed when data were blocked by pollen type.

CV Khasab (200 d.a.p. to 245 d.a.p.):

In 1996 no correlations were found. In 1995 too many bunches had already lost fruits at this stage to provide reliable data for a correlation study.

9.2.2. Thermal time and fruit weight

The thermal time accumulated in bunches with an identical number of days after pollination "n-d.a.p." varied, because the day of pollination itself varied. This means that thermal time differences between bunches were solely due to the temperature factor if "n-d.a.p." was the same. The following experiment examined specific pollen influences on thermal time for fruit fresh weight accumulation.

CV Khalas (150 d.a.p. to 170 d.a.p.):

In 1996 Khori was found to induce accumulation of fruit fresh weight until 140 d.a.p. in less thermal time ($P<0.05$) than the other pollen types (Table 9-7).

Table 9-7 THERMAL TIME FOR FRUIT FRESH WEIGHT ACCUMULATION (°Cd/g) AT 150 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

	Thermal time per weight increment (°Cd/g)	
Pollen type	*150 d.a.p.*	
Al Arudsabba	114	a
Bahlani	108	a
Khori	95	b

LSD @ P< 0.05 = 12 °Cd/ g.

This confirms the pollen effects on fruit fresh weight reported in Chapters 8 and 9, in that fruits pollinated with Khori accumulated 1 g of fruit fresh weight for a thermal time increment about 10% lower than for the other two pollen types. However, this result could not be used for modeling, because there was no consistent correlation between thermal time and fruit fresh weight throughout growt and development, which was probably due to the phasic course of fruit development. Positive correlations were only found during the almost linear growth between mid Stage 2 (80 d.a.p.) and mid Stage 3 (110 d.a.p.).

In 1995, no such pollen effects (Table 9-7) were found probably due to the influence of differential fruit set such that particularly the high Khori-induced fruit set affected fresh fruit weight. This would have masked the effects. In addition, a slightly lower heat summation (3.7% at 170 d.a.p.) for the Al Arudsabba block limited a comparison between pollen blocks on a real time basis.

Thermal time units accumulated at 170 d.a.p. showed overall correlations with seed weight, flesh weight and fruit fresh weight in 1995, while in case of data blocked by pollen types, highly significant correlations were found for Al Arudsabba pollinated bunches (Table 9-8).

Table 9-8 COEFFICIENTS OF CORRELATIONS BETWEEN THERMAL TIME (X) AND WEIGHT (Y) OF FRUITS, SEEDS AND FRUIT FLESH AT 170 D.A.P. IN BUNCHES OF CV KHALAS POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1995.

			Correlations coefficients between x and y					
Pollen type	*Thermal time (°Cd) x*		*y = total fruit fresh weight*	*sig*	*y = seed fresh weight*	*sig*	*y = fruit flesh fresh weight*	*sig*
All	1851		-0.61	*	0.63	*	-0.63	*
Al Arudsabba	1803	b	-0.99	***	-	ns	-0.99	***
Bahlani	1872	a	-	ns	-	ns	-	ns
Khori	1879	a	-	ns	-	ns	-	*

Thermal time: LSD@P<0.05= 22.7 °Cd

The Al Arudsabba block had accumulated about 70 °Cd or 3.7% less than the other two blocks, which corresponded to the heat unit increment of 5 days in mid August 1995.

For all data taken together, seed weight was positively, while total fruit fresh and fruit flesh weight were negatively correlated. Positive correlations between these variables observed in the last stage (Section 8.2.3.) had become negative for the fruit flesh and the fruit as a whole, but had remained positive for seed weight. This indicated that mainly the temperature aspect of thermal time (time is the same, i.e.: 170 days) had a proportional effect on seed weight at this stage. However, it had an inverse effect on the fruit flesh, which was reflected by the fresh weight of the whole fruit and was probably due to loss of moisture during ripening. When data were blocked by pollen type, the Al Arudsabba block was clearly distinguished from the other two pollen blocks, showing highly significant ($P<0.001$), negative correlations between these variables. In the other two blocks, no correlations existed. The absence of correlations for the other two pollen types reflected that because Khori and Bahlani pollinated fruits ripened earlier (Section 9.1.5.), fruits in a bunch were in later stages of ripening, so diminishing and distinct moisture and fresh weight loss were no longer clearly related to thermal time. The seed was not affected by moisture loss. The relationship of thermal time (x) and flesh weight (y) could be described for the Al Arudsabba block by the regression equation:

$$\bullet\ y = 263 - 0.14 \bullet x, \qquad r^2 = 0.99 \text{ and } P<0.001$$

Fruits pollinated with this pollen type were still closer to their maximum fresh weight, from which initial moisture loss due to ripening was more clearly correlated to thermal time than for the other blocks. This supported the observations made in Section 9.1.2., i.e.: that Al Arudsabba matured and ripened later.

As was indicated in Section 9.1.2 fruit weight increments on a thermal time basis were looked at for cv Khalas in 1995, to determine whether the peculiar change of the response pattern to pollen treatments from A<K in Stages 1 and 2 to A>K in Stage 4 was due to fruit set influences or because of different thermal time. Figure 9.4. shows fruit fresh weight increments on a real and thermal time basis.

Figure 9-4: *Fresh weight (g) of cv Khalas fruits pollinated with three different pollen types in 1995 on the basis of real (A) and thermal (B) time.*

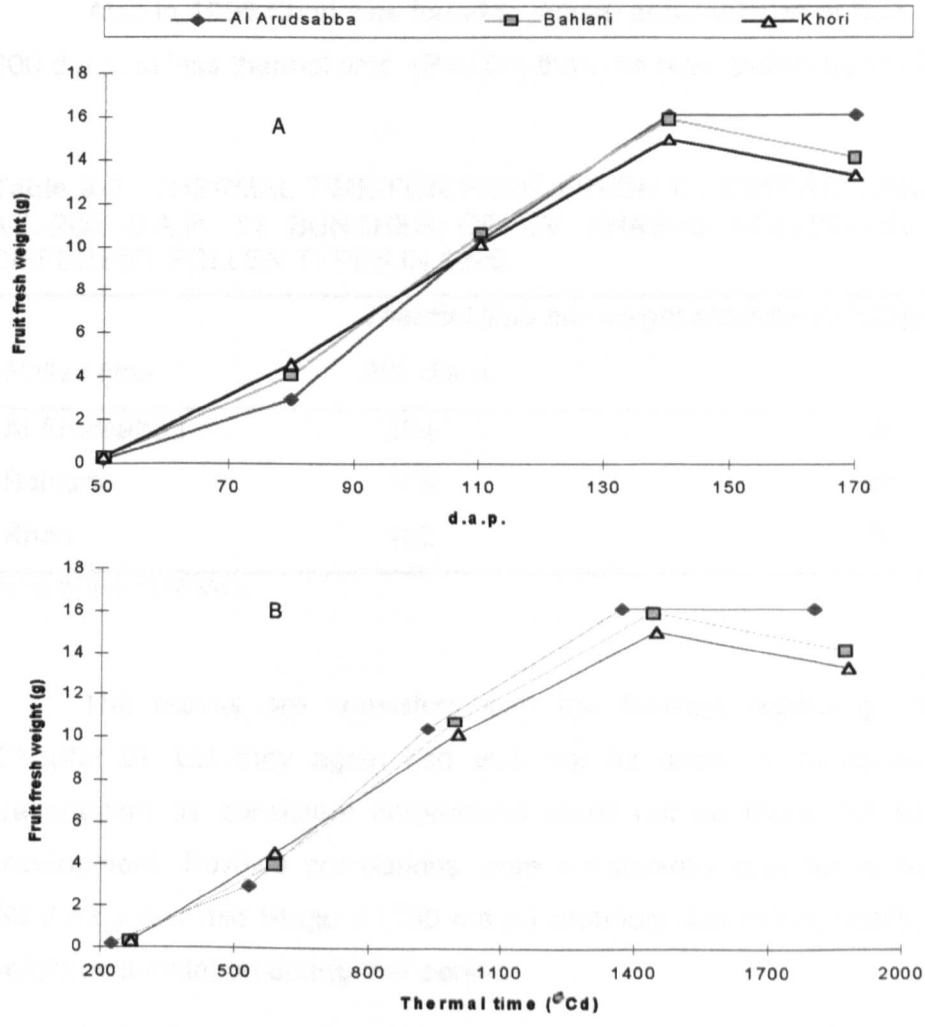


Figure 9-4 shows that the reversal of response pattern of fruit fresh weight to pollen treatments occurred between 80 and 110 d.a.p. (Figure 9-4A) or between

530 and 1000 °Cd (Figure 9-4B). As this phenomenon was observed in both cases, the earlier assumption that differential fruit set was responsible is validated. Figure 9-4 also supports field observations and the interpretation of earlier results in the present section that the Al Arudsabba block was at 170 d.a.p. not as advanced with regard to ripening as the other blocks.

In 1996, no pollen specific correlations between thermal time and other variables (weight, total sugars, colour) were found.

CV Khasab (200 d.a.p. to 245 d.a.p.):

Also in 1996 Khori was found to induce accumulation of fruit fresh weight until 200 d.a.p. in less thermal time ($P<0.05$) than the other pollen types (Table 9-9).

Table 9-9 THERMAL TIME FOR FRUIT FRESH WEIGHT ACCUMULATION (°Cd/g) AT 200 D.A.P. IN BUNCHES OF CV KHASAB POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

	Thermal time per weight increment (°Cd/g)	
Pollen type	*200 d.a.p.*	
Al Arudsabba	204	a
Bahlani	188	ab
Khori	182	b

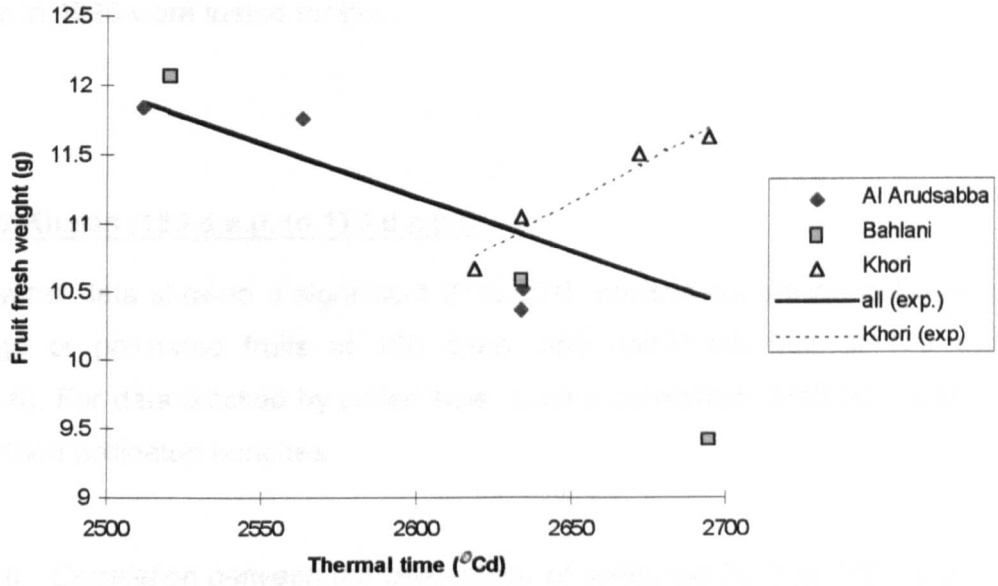
LSD @ P< 0.05 = 15.8 °Cd/ g.

The results are consistent with the findings regarding fruit fresh weight (Chapter 8), but they again can also not be used for modeling in their above presentation as consistent correlations could not be found for all stages of fruit development. Positive correlations were consistently only found between Stage 2 (50 d.a.p.) and mid Stage 3 (150 d.a.p.) probably due to the nearly linear fruit fresh weight accumulation during that period.

In 1996, an overall negative correlation ($r = -0.6$ at $P<0.05$), but a positive one ($r = 0.99$ at $P<0.05$) was found for data blocked by pollen type Khori (Figure 9-5). In

1995, too many bunches had lost fruit by this stage to provide reliable data for a correlation study.

Figure 9-5 *Correlations between thermal time and fruit fresh weight at 230 d.a.p. in bunches of cv Khasab pollinated with three different pollen types in 1996.*



The relationship between thermal time (x) and fruit weight (y) at 230 d.a.p. can be expressed by the regression equations

- $y = 31.3 - 0.008 \cdot x$, ($r^2 = 0.37$ at $P<0.05$, $n = 11$) for all data and
- $y = -21.9 + 0.012 \cdot x$, ($r^2 = 0.94$ at $P<0.05$, $n = 4$) for data blocked by pollen type Khori.

It is recalled that maturation occurred in the previous Stage starting with the appearance of the Khalal colour and ending with the fruit attaining maximum fruit fresh weight and its full Khalal colour. Ripening was subsequent and accompanied by loss of fresh fruit weight and the appearance of the half-Rutab, Rutab and eventually Tamr stages. The Bissr fruit is the border stage between maturation and ripening.

The overall negative correlation in this experiment indicated that fruit weight losses due to ripening were higher in fruit bunches for which more thermal time had been accumulated at 230 d.a.p.. Khori pollinated fruit probably ripened slower than the other two blocks as suggested by the above positive correlation for this pollen type. In other words, the correlation shown here reflected that the Khori block was still growing in terms of fresh weight with higher thermal time and that weight losses due to ripening had not occurred and so had not yet exerted high leverage on fruit weight.

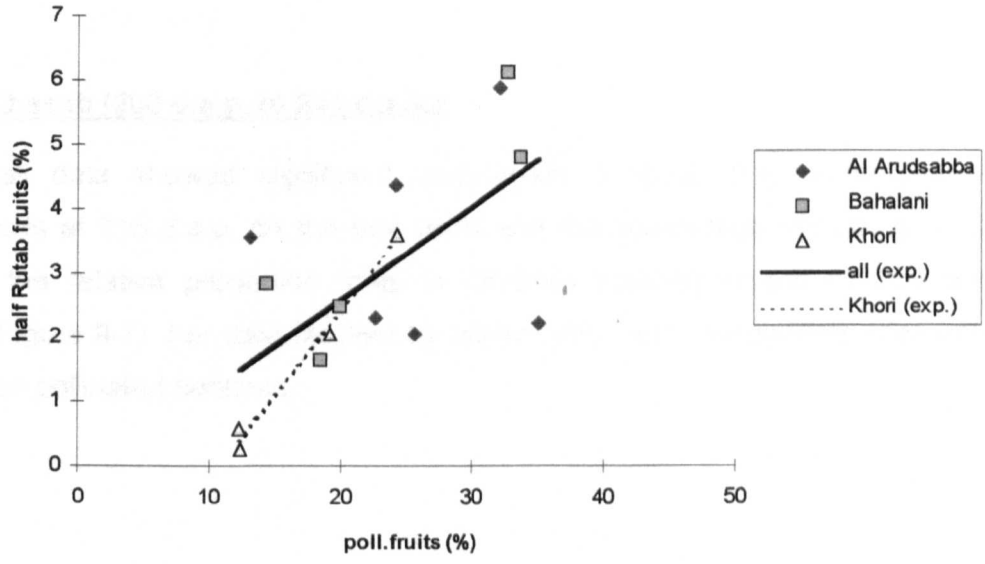
9.2.3. Fruits retained and ripeness

It was observed that Khori pollinated bunches exhibited distinct correlations between the percentage of pollinated fruits and fruits in different stages of ripening. Only fruits in 1996 were tested for this.

CV Khalas (150 d.a.p. to 170 d.a.p.):

Overall data showed a significant ($P<0.001$), positive correlation between the percentage of pollinated fruits at 160 d.a.p. and half-Rutab fruit at 170 d.a.p. (Figure 9-6). For data blocked by pollen type, such a correlation ($P<0.001$) was only found in Khori pollinated bunches.

Figure 9-6 *Correlation between the percentage of pollinated fruits at 160 d.a.p. and half-Rutab fruit at 170 d.a.p. in bunches of cv Khalas pollinated with three different pollen types in 1996.*



The relationship between the percentage of pollinated fruits at 160 d.a.p. and the percentage of half-Rutab fruits at 170 d.a.p. can be described by the regression equations:

- $y = -0.29 + 0.14 \cdot x$, ($r^2 = 0.44$ at $P<0.001$, $n = 15$) for all data and

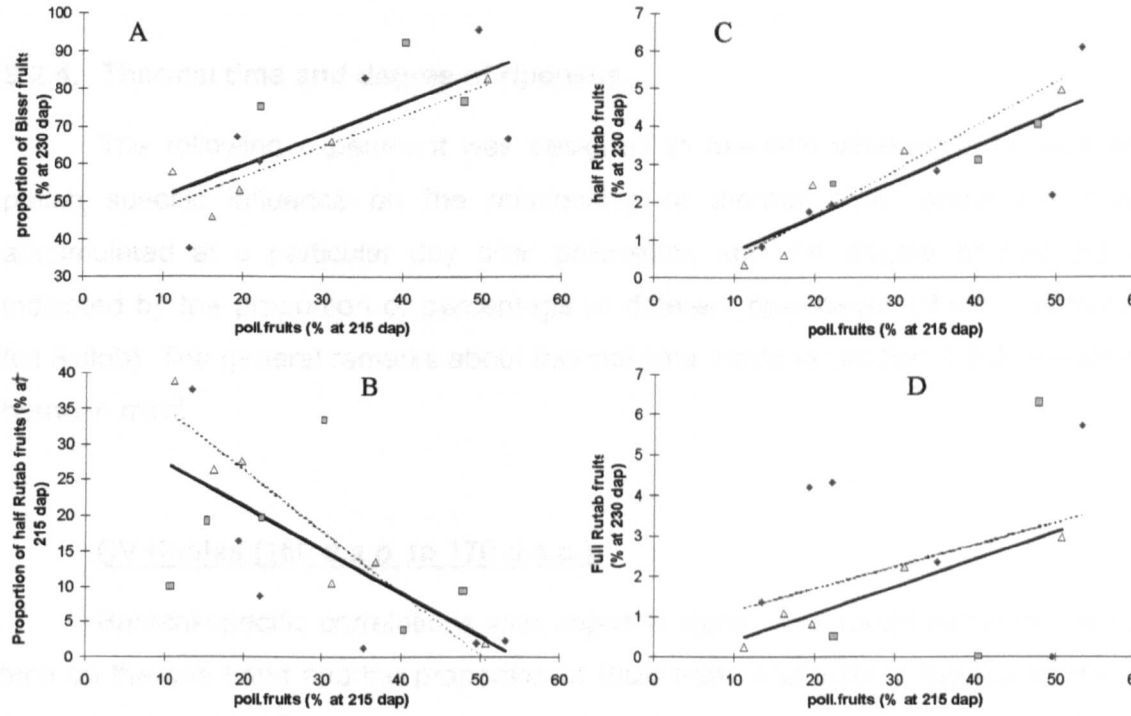
- $y = -2.84 + 0.26 \cdot x$, ($r^2 = 0.99$ at $P<0.001$, $n = 4$) for data blocked by pollen type Khori.

It was expected that the two variables would be strongly correlated for each pollen block, because their percentages both refer to the initial number of ovaries. However, only in Khori could such a correlation be observed. This suggested that Khori pollinated bunches were much more uniform than overall bunches, in that they contained the same proportion of half-Rutab fruits in relation to the percentage of pollinated fruits, as indicated by twice the slope for overall bunches. This was not the case with the other two pollen blocks. As fruit set with Khori was the lowest (Section 9.1.1.), it could be also that this distinct relationship was due to this generally lower level of fruit set. As mentioned in Section 9.2.1. this low level in itself may have been the result of a higher fruit fresh weight, which could have been a metaxenic effect.

CV Khasab (200 d.a.p. to 245 d.a.p.):

Overall data showed significant correlations between the percentage of pollinated fruits at 215 d.a.p. on the one hand and the percentage of half- and full Rutab and the relative proportion fruits in different ripening stages at 215 and 230 d.a.p. (Figure 9-7). For data blocked by pollen type, such correlations were only found in Khori pollinated bunches.

Figure 9-7 *Correlations between the percentage of pollinated fruits at 215 d.a.p. on the one hand and the proportion of Bissr fruits at 230 d.a.p. (A) and half-Rutab fruits at 215 d.a.p. (B) in a bunch and the percentage relative to initial number of ovaries of half-Rutab (C) and full Rutab fruits (D) at 230 d.a.p. on the other hand in bunches of cv Khasab pollinated with three different pollen types in 1996. (Observed values: Al Arudsabba ♦ , Bahlani ■ , Khori Δ ; expected values: all-thick line, Khori-thin line)*



Viewing all data, it was seen (Figure 9-7A) that bunches with a higher percentage of pollinated fruits (% of the total number of ovaries) contained a higher proportion (% of all fruits in the bunch at the time) of Bissr fruits than ones with a lower percentage. The opposite was the case for the relationship (Figure 9-7B) between the percentage of pollinated fruits and the proportion of half-Rutab fruits. This was to be expected, as the proportions of different ripening stages are complementary, adding up to 100 %. Notably, only in Khori could a clear linear relationship between these variables be identified, while the data for the other two pollen blocks were randomly dispersed. Moreover, the percentage of pollinated fruits on the one hand and the percentage (relative to initial number of ovaries) of half-Rutab fruits (Figure 9-7C) and full Rutab fruits (Figure 9-7D) are positively correlated for all data, but again specifically for the Khori block only. This suggested, that the percentage and proportions of ripening fruits were under the strong control of fruit set, particularly in Khori pollinated bunches. As fruit set was the same for all pollen types,

this pollen specific leverage of fruit set was considered a metaxenic pollen effect on ripening.

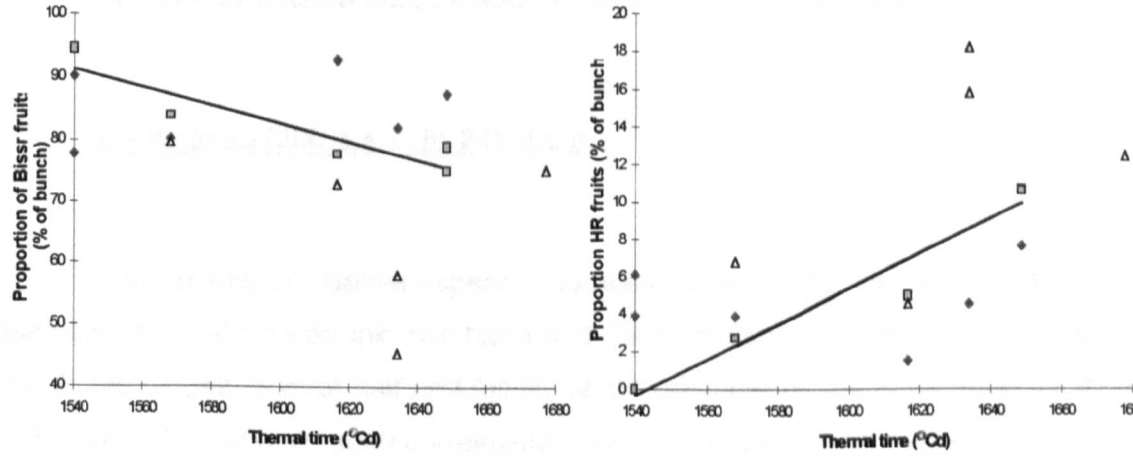
9.2.4. Thermal time and degree of ripeness

The following experiment was designed to examine whether there was any pollen specific influence on the relationship of thermal time, which had been accumulated at a particular day after pollination, and the degree of ripening as indicated by the proportion or percentage of different ripe stages (Bissr, half-Rutab, full Rutab). The general remarks about thermal time made in Section 9.2.2. should be borne in mind.

CV Khalas (150 d.a.p. to 170 d.a.p.):

Bahlani-specific correlations with opposite signs were found between thermal time on the one hand and the proportion of Bissr fruits and fruits in the Rutab stages (sum of half and full Rutab proportions) on the other hand as shown in Figure 9-8.

Figure 9-8 *Correlations between thermal time at 160 d.a.p. on the one hand and the proportion of Bissr fruits (A) and fruits in the Rutab stages (B) at 160 d.a.p. on the other hand in bunches of cv Khalas pollinated with three different pollen types in 1996. (Observed values: Al Arudsabba ♦ , Bahlani ■ , Khori Δ ; expected values: Bahlani-line)*



These correlations for the Bahlani block were negative (r= -0.91, P< 0.05 at n = 5) between thermal time at 160 d.a.p. and the proportion (%) of Bissr stage fruits at 160 d.a.p., but positive (r = 0.91, P<0.05 and n = 5) between thermal time at 160 d.a.p. and the proportion (%) of all Rutab stage fruits taken together at 160 d.a.p.. No such correlations existed for all data nor data blocked by any other pollen type. These Bahlani-specific relationships were closer examined by regression analysis and could be expressed by the equations:

- $y = 315 - 0.145 \cdot x$, ($r^2 = 0.83$ at P<0.05, n = 5) for the proportion (%) of Bissr stage fruits
- $y = -214 + 0.145 \cdot x$, ($r^2 = 0.83$ at P<0.05, n = 5) for the proportion (%) of fruits in the Rutab stages.

The opposite signs were to be expected, because the proportions of Bissr and Rutab fruits were complimentary, adding up to 100 %.

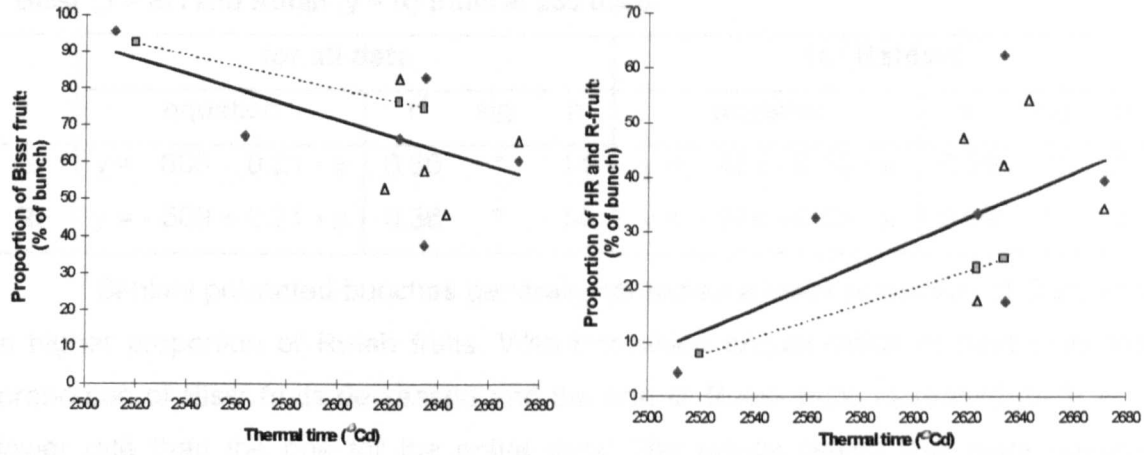
It appears that ripening in bunches pollinated with pollen type Bahlani is related to increasing thermal time, such that its Bissr proportion decreases at the same rate its Rutab proportion increase. The absence of such correlations in other pollen types, even for all data, suggests that in Bahlani pollinated bunches ripening is strongly related to accumulated heat units. As Bahlani was on par with Al Arudsabba with respect to fruit weight and set (Sections 9.1.1 and 9.1.2.), this particular effect of Bahlani on the relationship of thermal time and ripening in Bahlani was probably a specific pollen effect in itself, just as an Al Arudsabba specific pollen effect was found on the influence of fruit set on fresh weight (Section 9.2.1.). This relationship was however not reflected in faster ripening with Bahlani compared to Al Arudsabba.

In 1995 no suitable data for such an examination were available.

CV Khasab (200 d.a.p. to 245 d.a.p.):

Also in this cv, Bahlani-specific correlations with opposite signs were found between thermal time on the one hand and the proportion of Bissr fruits and fruits in the Rutab stages (sum of half and full Rutab proportions) on the other hand as shown in Figure 9-9. Moreover, such correlations were also observed for overall data.

Figure 9-9 *Correlations between thermal time at 230 d.a.p. on the one hand and the proportion of Bissr fruits (A) and fruits in the Rutab stages (B) at 230 d.a.p. on the other hand in bunches of cv Khasab pollinated with three different pollen types in 1996. (Observed values: Al Arudsabba ♦ , Bahlani ■ , Khori Δ ; expected values: all-thick line, Bahlani-thin line)*



These correlations for overall data and the Bahlani block between thermal time at 230 d.a.p. on the one hand and the proportion (%) of Bissr stage fruits at 230 d.a.p. and the proportion (%) of all Rutab stage fruits taken together at 230 d.a.p. on the other hand are shown in Table 9-10. No such correlations existed for data blocked by any other pollen type.

Table 9-10 CORRELATIONS BETWEEN THERMAL TIME AT 230 D.A.P. AND THE PROPORTION (%) OF BISSR FRUITS (Br) AND OF THE SUM OF THE PROPORTIONS OF HALF AND FULL RUTAB (Rt) FRUITS AT 230 D.A.P. IN BUNCHES OF CV KHASAB POLLINATE WITH THREE DIFFERENT POLLEN TYPES IN 1996.

	Correlation coefficients between thermal time at 230 d.a.p. and the proportion of Bissr (Br) and Rutab (Rt) fruits at 230 d.a.p.					
	for all data			*for Bahlani*		
Ripe stages	*r*	*sig.*	*n*	*r*	*sig.*	*n*
Br	- 0.60	*	14	- 0.99	**	3
Rt	0.60	*	14	0.99	**	3

These relationships were closer examined by regression analysis and could be expressed by the equations shown in Table 9-11.

Table 9-11 REGRESSION ANALYSIS OF THE RELATIONSHIP BETWEEN THERMAL TIME AT 230 D.A.P. (X) AND THE PROPORTION OF BISSR (Y = Br) AND RUTAB (Y = Rt) FRUITS AT 230 D.A.P. IN BUNCHES OF CV KHASAB POLLINATED WITH THREE DIFFERENT POLLEN TYPES IN 1996.

Regression equations between thermal time at 230 d.a.p. (x) and the proportion of Bissr (y = Br) and Rutab (y = R) fruits at 230 d.a.p.

	for all data				for Bahlani			
	equation	r^2	sig.	n	equation	r^2	sig.	n
Br	y = 608 - 0.21 • x	0.36	*	14	y = 471 - 0.15 • x	0.99	**	3
Rt	y = - 509 + 0.21 • x	0.36	*	14	y = - 374 +0.15 • x	0.99	**	3

Bahlani pollinated bunches generally contained a lower proportion of Bissr and a higher proportion of Rutab fruits. With increasing accumulation of heat units the proportion of Bissr fruits decreased and the one of Rutab fruits increased, both at a lower rate than the one for the entire data. The results reflect that more uniform ripening is under a comparatively stronger control by pollen type Bahlani than by the other types.

9.3. Summary and discussion

Effects on fruit set

Pollen treatments had significant effects on fruit set in cv Khalas in both years. In 1995, pollination with Khori again resulted in the highest fruit set (%), but in 1996 it was the highest with pollen type Al Arudsabba. The low fruit set in cv Khalas pollinated in 1996 with Khori was probably under the influence of the high coincident fruit weight.

Effects on fruit and seed weight

Pollen treatments had significant effects on fruit fresh weight in cv Khalas in both years. In 1996 Khori resulted in the highest fruit weight, while it was the highest with pollen type Al Arudsabba in 1995.

While in 1996 the same response pattern of fruit fresh weight to pollen type as in Stage 4 was observed in Stage 3 and in Stage 2, in 1995 such a continuous pattern did not exist. In 1995, Khori and Bahlani pollinated fruits were in Stage 1 (80 d.a.p.) also heavier than Al Arudsabba pollinated ones, but this pattern had reversed by

Stage 4. The reason was probably influence of fruit set and then earlier maturity and ripening in Bahlani and Khori pollinated fruits in 1995 as mentioned earlier (Section 8.1.4.). The pollen effects were on fresh fruit weight and not on dry weight, so that the effect was probably a reflection of water content.

Effects on fruit size

Pollen treatments had significant effects on fruit size and followed a pattern similar to fruit fresh weight (K>A,B in 1996, A>B,K in 1995).

Effects on total sugars

Pollen treatments had significant effects on the total sugar content of the pericarp in cv Khalas in 1995 and in cv Khasab 1996 with Al Arudsabba pollinated fruits containing the least. This probably indicated delayed ripening in these bunches.

Relationship between fruit retention and fruit-, seed weight

In cv Khalas in 1996, fruit weight at 160 d.a.p. were first inversely related to fruit set only at 140 d.a.p. for Al Arudsabba pollinated fruits, but when relating fruit weight to fruit set percentage at 160 d.a.p. a significant ($P<0.01$) correlation for data blocked by pollen type Khori was found as well. It was reasoned that the fresh weight of Khori pollinated fruits was the probable cause for differences in fruit retention at 160 d.a.p..

Effects on harvested products

In cv Khalas in 1996, more Al Arudsabba pollinated fruits matured earlier, but fruits pollinated by Khori ripened faster than in the bunches pollinated with the other two pollen types. The changes taking place are complex and include metaxenic effects on fruit fresh weight, which are influenced by ripening, fruit drop and damage of ripe fruits.

Effects on yield

In cv Khalas in 1995, total yield in Khori pollinated bunches was almost twice as high as in Bahlani pollinated ones.

Relationship between thermal time and fruit weight

1. In 1996 Khori pollinated bunches of both cvs had in less thermal time accumulated the same fresh weight in mature fruits as those pollinated by the other pollen types.
2. In cv Khalas in 1995, a distinct positive correlation between thermal time and fruit/flesh weight was found for treatment with pollen type Al Arudsabba. The absence of correlations for the other two pollen types reflected that Khori and Bahlani pollinated bunch had matured earlier and were at different and more advanced stages of ripening.
3. Given an overall negative correlation of thermal time and fruit fresh weight at 230 d.a.p. in cv Khasab in 1996, a positive correlation for pollen type Khori suggested that Khori pollinated fruits ripened slower than fruits of the other two blocks.
4. In a comparison of female cvs Khori delayed maturity in both (except cv Khalas in 1995), advanced ripening in cv Khalas, but delayed it in cv Khasab.

Relationship between fruit retention and ripeness

In cv Khalas in 1996, only with Khori was a specific correlation between the percentage of pollinated fruits at 160 d.a.p. and half-Rutab fruit at 170 d.a.p. was observed, suggesting that Khori pollinated bunches ripened much more uniformly.

Relationship between thermal time and ripeness

In both female cvs ripening was stronger controlled by pollen type Bahlani than by other pollen types.

10. General discussion

The aim of this study was to test claims of pollen effects on fruit development, to quantify the effects, to suggest mechanisms and to assess their commercial applicability. The hypothesis was that the nature of the pollen used in the Sultanate Oman to fertilize date palm flowers would affect the processes of fruit growth and development. Early effects would depend on substances contributed to the fruit [1] or ovule prior to, and during fertilisation, whilst later effects would be the consequence of the genetic contribution by the pollen. Interactions with maternal type were expected.

The present study has shown that Khori was most attractive in bringing about relatively stable yields and large, heavy and sweet fruits. It was, however, limited due to the late maturity of its fruits, but in many commercial situations its faster ripening can be put to good use. Al Arudsabba produced a slightly higher cumulative yield of similar yield stability, but was limited due to its effect of inducing fruits of poor quality in regard to fruit size, fresh weight and a low total sugar content. Bahlani had clear advantages, in that it induced sweet fruits, but produced unstable yields of relatively low weight and small fruits.

Pollen effects on fruit growth and development in the Omani date palm cvs Khalas and Khasab have been tested and described in the previous Chapters for each distinct phase of growth and development and for each variety and year of study. This discussion will now focus on each variable during the entire course of fruit growth and development. It will suggest mechanisms for the pollen effects using both the results from the present study and the findings of other research workers. For each variable, cvs and the years of the study will be compared. From this, a test of the hypothesis as presented in the introduction (Chapter 1) will be possible. More weight has been attached to the results obtained in 1996 than to those of 1995, because experiments then were better designed as a result of experiences gained during the 1995 study year.

The primary question was: did pollen types differ in their effects on fruit growth and development and to what extent, and in which particular aspects did they differ? Following on from this, questions arose of whether the mechanisms of their effects

[1] this contribution may have been during pollen tube growth to the stigma and ovarian tissues other than the ovule.

differed and whether the xenic or metaxenic potential of a pollen type was identifiable by physical or chemical analysis. The term "Metaxenia" is used to denote the direct effect of pollen on the parts of the seed and fruit lying outside the embryo and endosperm, while "Xenia" denotes its influence on the endosperm of the seed (Swingle, 1928) This latter question was not rigorously tested and, as regards fruit growth responses, no great significance is attached to it .

In any study on pollen effects, a key question must be whether effects on fruit development were indirect and merely a consequence of differential fruit set or whether they acted independently of fruit set and were directly attributable to pollen. Osman et.al. (1974) examined the effect of pollen type in Date Palms and showed large metaxenic effects on the size and shape of the pericarp and seed, on date of ripening and on the uniformity of each character between replicate fruits. In that study, however, palms with abnormal fruit set were excluded from the results, thereby denying any examination of the influence of fruit set on the pollen effects. In the present study, an assessment of this possible influence was deemed necessary as it is relevant not only to an understanding of how the pollen exerts its effects, but also to commercial date fruit production. Nixon's study (1928b) showed pollen to affect size of both fruit and seed and to change the time of ripening in cv Deglet Noor. This led him to suggest the use of pollen as an aide to cultural practices in producing high-grade standardized fruit. He also reported differences in fruit set for different pollen types in different palms, but did not closely examine their influence on variables measured.

Pollen was shown in the present study to affect fresh weight and size of fruits independently of fruit set differences up to a point at which the leverage of these differences became too strong. This independence existed despite an inverse relationship observed between these variables and fruit set. This was shown under conditions of equal fruit set for different pollen treatments and by interactions of growth regulator treatments with pollen type. The influence of fruit set on fruit fresh weight highlighted the need to factor in fruit set differences when discussing pollen effects.

Fruit set commonly influences fruit weight or size. Luckwill (1953) observed that individual apple fruit weight at harvest increased with decreasing fruit set. Furr (1961) observed a similar relationship between crop load and fruit size in Deglet Noor

date palms. In the present study, the same pollen type caused different fruit set in different years and varieties (Chapters 5,6,7 and 9). PGR treatments inducing a decrease in fruit set also caused an increase in fruit fresh weight. Inverse relationships between fruit fresh weight and fruit set were apparent during all Stages of fruit development following Stage 1 (Chapters 7,8 and 9)., but only in one case (cv Khalas in 1995) was it strong enough to alter pollen effects on fruit fresh weight late in Stage 4. This late influence of fruit set on fruit weight was in spite of these fruit set differences already existing in Stage 1. Typically in all varieties and years, Khori produced heavier and larger fruits than Al Arudsabba and the initial response pattern to pollen treatment continued throughout, in the absence of differential fruit set. It can be concluded that at some time between late Stage 2 and late Stage 4 the influence of differential fruit set was the basic mechanism which reversed the response pattern of fruit fresh weight to pollen type in Khalas in 1995, such that Al Arudsabba pollinated fruits were heavier than Khori pollinated ones.

Differential fruit set influenced pollen effects to some extent through intrabunch competition for resources. The influence of fruit set on characteristics of fruits was clearly demonstrated in earlier research involving thinning trials in the date palm (Nixon, 1956) and is also known in other fruit trees attributable to resource allocation (Wright, 1989; Janick, 1931). The leverage of differential fruit set on the pattern of pollen effects on fresh weight became clear in cv Khalas in 1995. Here, from stage 1 onwards, fruiting was characterized by the comparatively higher set in bunches pollinated with Khori. Therefore, competition for resources between the fruits in these bunches was probably so much more in comparison to other bunches during Stages 2 and 3, that the expected superior effect of Khori on fresh weight was compensated by Stage 4. However, as will be discussed later, this influence can be also exerted in the other direction in that fruit weight affects fruit retention, illustrating the complex interaction between these variables. In 1995 bunches in cv Khalas emerged closer to each other in time, which probably increased competition amongst bunches (Chapter 5) when compared to 1996. This competition has added to the complexity of assessing the influence of fruit set on fresh weight in 1995.

In a commercial orchard, pollen types which cause variable, and therefore unreliable fruit set, could not be recommended for use. Khori would have been such a type were it not for its distinct advantages with regard to maturity, ripening and fruit weight made it otherwise very desirable. The effect of pollen Al Arudsabba on fruit

fresh weight was more sensitive to fruit set differences than in the other two types. Fortunately, from a producer's point of view, this pollen type induced a relatively consistent fruit set in the different years, so that its overall effect on yield, though not on fruit fresh weight and size, was commercially beneficial. Further studies could examine whether this sensitivity to fruit set can be utilized to produce larger fruits as a result of thinning. Recent experiments, not reported in this study, indicate that this is indeed the case for Al Arudsabba, but not for Khori.

Exogenous, applied hormones were shown here to influence fruit set depending on pollen type and it was likely therefore that biochemical constituents of pollen, probably hormones, were responsible, in part at least, for differential fruit set in bunches treated with different pollen types. No previous work has been done on the interaction of pollen and plant growth regulators treatments in date palms. The present study showed that in cv Khalas, NAA treatment could reduce the percentage of unpollinated fruits in bunches only for pollen Khori, but not Al Arudsabba. This suggested that differences in endogenous plant growth regulators between pollen blocks existed and were altered by external hormone applications. In the case of pollen Khori, but not Al Arudsabba, this caused a fruit set response. This supports one of the mechanisms proposed for direct pollen effects, i.e.: that biochemical constituents are contributed or their synthesis stimulated by pollen type (Swingle, 1928; Denney, 1994). It does not, however, clarify whether the external application acted complimentary to internal biochemical constituents which differed between pollen blocks or whether it brought about supra optimal levels. Both scenarios have been reported. Varma (1979) suggested such differential effects in Cotton, in that retention/abscission of bolls was dependent on the balance of endogenous auxin and ascorbic acid. In Mango, deficiency in endogenous cytokinins, gibberellins and auxins resulted in fruit drop but this could be overcome by applying sprays of exogenous growth regulators at fruit set (Sant Ram, 1992). Looney (1984) noted that supra-optimal levels of GA may be responsible for fruit drop in grapes.

Positive correlations between fruit set and activity of growth promoters other than auxin during the first period of growth till late Stage 3 (Reuveni, 1986) and observations that application of auxins cause fruit thinning, are large consistent with our results in 1996 with cv Khasab. However, application of NAA (6 d.a.p.) resulted in opposite effects in the other cv in the same year, indicating biochemical or physiological differences between the cvs. NAA can reduce fruit drop in other crops

as was shown in Litchi (Joubert, 1986). It is possible that the applications, probably supra-optimal in cv Khasab, but optimal in cv Khalas, influenced the balance of endogenous hormones (Varma, 1979). GA applications to cv Khasab in 1996, increased fruit set compared to control, due possibly to extended embryo longevity, as reported by Browning (1989) for Peaches. In pear, where fruit retention and growth is promoted by GA (Gil, 1972), the GA might have conferred on the zygote and entire ovary the ability to develop autonomously in substituting for deficiencies from pollination. Such substitutive effects were also apparent in tissue culture studies conducted on *Nicotiana* by Siddiqi (1964). The complexities of the role of hormones in the set of fruits are not clearly understood (Browning, 1989) and the present study cannot present anything but different possible explanations for their role in fruit set in the Date Palm. The hormonal aspect of fruit set merits further research

Khori pollen appeared most effective in fertilization of cv Khalas. This was probably attributable both to its greater vigour of pollen tube growth and to it contributing substances to the ovule which increased the fresh weight and size of fruits. The better fertilisation potential for Khori may be reflected in its larger pollen diameter. Larger pollen indicates a lower level of incompatibility in Nicotiana (Pandey, 1971). Khori pollen also displayed very uniform pollen tube lengths within 24 hours after germination. These features indicate higher vigour, which could have overcome incompatibility reactions in the style to a greater extent than less vigorous types. In cv Khasab, incompatibility may have been more pronounced, so that it was not as well overcome by pollen type Khori in comparison to cv Khalas. Rosen's findings (1971) imply such differential incompatibility reactions in that in pollen with sufficient reserves, the tube is able to switch during growth from autotrophic to heterotrophic growth thereby overcoming stylar (not stigmatic) incompatibility. A further intrinsic peculiarity of pollen type Khori may be its biochemical composition, which set it apart from the other two pollen types (Chapter 4). Assay of pollen extracts using the lettuce hypocotyl test suggested that Khori pollen had a higher GA content than Al Arudsabba. It is likely that these compositional differences affected pollen germination (Stanley, 1974) and pollen tube growth. This is consistent with the findings of Pharis and King (1985) that such pollen hormones are involved in pollen growth, although they considered this as their only role. This indicated a very early pollen effect occurring within a few hours after pollination. The results on PGR effects on unfertilized ovaries in the present study (Section 7.1.1) raised the possibility that

pollen effects had occurred in the absence of syngamy suggesting that they were physiological and non-hereditary. This is consistent with the hypothesis that early pollen effects on fruit set are due to specific events during pollen tube growth, precipitated by the pollen type, but dependent on the female. No genetic interaction between male and female types would have occurred at this stage, so that this mechanism can be safely excluded as having contributed to the early effect on fruit set. This source of variability in pollen treatments provided an opportunity to relate pollen effects on, for example, fruit weight with fruit set.

The possibility that the observed differences in fruit set in cv Khalas could have been due to viability of pollen in 1995 was considered unlikely. Equal fruit set for all pollen types in the other cv, Khasab, in 1995 indicated that differences in viability were not responsible for differential fruits set in cv Khalas in the same year. This was also in agreement with visual assessment of pollen viability. Viability appears not to have been different between years. Laboratory results in 1996 involving *in vitro* germination tests (Furr and Ream, 1968) were also consistent with visual assessment. Also the excess of pollen applied would have largely compensated any influence of viability on fruit set which was an observation also made by Ream and Furr (1969). This supports the earlier conclusion that fruit set differences were due to female variety and, within a variety, to pollen. Furthermore, the effects could have been dependent on temperature, but again, these would have been independent of viability.

Fruit set differences may themselves be the result of pollen x temperature interactions (Stoler et al., 1966). In the present study there was some evidence that when temperatures differed at the time of pollination with the same pollen types, fruit set varied (Chapter 4). This was consistent with the *in vitro* findings of Furr and Ream (1968), who observed that the time course of pollen germination was dependent on temperature. They reported fast pollen germination at similar temperatures to those used in the present study. The particular responsiveness of fruit set with pollen Khori in cv Khalas 1995 might have been due to some critical temperature having been exceeded, with temperature dependent pollen germination and fruit set responses then occurring. However, the difference in mean temperatures for pollen blocks were relatively small, so that the high fruit set for Khori could have been due to intrinsic characteristics of this pollen type, which are discussed in the following paragraph. The absence of a similar temperature-fruit set response in cv Khasab, possibly indicates male-female incompatibilities.

Variability between female cultivars and between the two years of the study, was expected considering reports from elsewhere (Reuveni, 1986). It was reduced by basing the experiments on the physiological Stages of fruit growth and development rather than chronological time, and by examination of some results on the basis of thermal time. This basis was also adopted for comparison of some results between years. The mean date of pollination in 1996 was more than a week earlier than in 1995, which had a bearing on thermal time accumulated over chronologically equal periods. Thermal time accumulated in 1996 was 1,513 °Cd as compared to 1,604 °Cd in 1995, in each case counting thermal time for 150 days following each year's mean pollination date.

Did the different pollen types cause differences in fruit fresh weight ? Commercially, this is a vitally important question. Khori pollen had a marked promotive effect on fruit fresh weight. This was the case in all cvs, years and stages with just one exception, Stage 1, when the influence of differential fruit set was probably too strong. The exception will be discussed separately later.

By nature, the three pollen types were different in their physical, biochemical and physiological characteristics, which are likely to be due to the genetic differences between male cultivars. In addition, their chemical composition differed, with Khori pollen grains containing relatively more of most minerals tested and a particularly high copper content. While general mineral composition may reflect habitat differences (Heslop-Harrison, 1971) the interpretation for the copper content differs. It was likely that Khori plants were genetically predisposed to take up relatively higher amounts of copper given the adverse calcareous soil conditions in their habitat, which resulted also in a high Calcium content. Pollen grains from Bahlani Palms, in contrast, contained very little copper under similar conditions. It has been reported (Stanley, 1974) that the parent plants capacity to accumulate salts in the pollen is related to the species. These differences could have affected the vigour and uniformity of pollen tube growth and, in the case of pollen type Khori, were possibly responsible for an earlier and, possibly higher, fruit set. This would be in line with the specific roles ascribed by Stanley (1974) to different plant growth regulators in pollen, in particular critical levels of GA, which control pollen germination and pollen tube growth and elongation (Looney, 1984). He noted that other growth substances diffusing from the pollen may stimulate the maturation or receptivity of the egg cell. These observations support the hypothesis that contributions made by the pollen to the entire ovary or

ovule in the earliest stages of development affect fertilization and fruit set and thereby set the stage for the consistent effects on fruit fresh weight after Stage 1.

Initial fruit growth and development responses to pollen treatments differed from those occurring later and, as regards fruit fresh weight, were not consistent between years and cvs. In cv Khalas, pollination with Khori resulted in the lightest fruits in 1996, but the heaviest, on par with Bahlani, in 1995. In cv Khasab, early fruit weight gain was lower with Khori and Al Arudsabba than with Bahlani. This emphasizes the need to consider effects carefully in relation to year and female parent.

Intrinsic characteristics of the pollen type were undoubtedly important in mediating early effects on the fruit . Early in Stage 1, a dormant zygote was present and at the end of the stage the proembryo was growing in the presence of a still syncitial endosperm (Chapter 4). These morphogenetic results were consistent with the findings of Reuveni (1986) and Long (1943) and suggested that the early effects in cv Khasab in Stage 1 were unlikely to be the result of genetic recombination because no substantial syngamous tissue, except the zygote, was present at that time. Looking at the biochemical composition of ovaries one day after pollination with different male types, similarity between Al Arudsabba and Khori pollinated was evident despite the grains of these pollen types having markedly different biochemical profiles. The difference between the two biochemical analyses (of pollen grains and then ovaries one day after pollination) largely precludes the possibility that the early growth response was directly due to the mere addition of substances contributed by the pollen grains. Although it has been suggested (Strauss and Arditti, 1982) that pollen-borne auxin can be translocated to orchid ovaries, it was considered unlikely in the present study that mere addition of growth regulators could have caused long term pollen effects. Only a few pollen grains land and adhere to the stigma, probably contributing insignificant substances, insufficient to explain the substantial growth differences observed. This interpretation is consistent with the findings of Pharis and King (1985). It is however possible that substances formed following an interaction between pollen grain and stigma/style, such as is commonly seen in incompatibility reactions (Rosen, 1971), were the cause of the effects. O'Neill (1997) demonstrated in orchids that pollination itself, rather than fertilization, triggered the initial stages of ovary development.

Another possible explanation for this growth response, and for the enhanced early fruit growth effect induced by pollen Bahlani seen consistently in all cvs and years, may lie in Bahlani's early, rapid tube growth rate. Bahlani pollen tubes could have reached the ovaries relatively earlier than those of Al Arudsabba. This would imply that biochemical pathways triggered by pollination events occurred earlier in the case of Bahlani when compared to the other two types. This would be consistent with the wider range of peaks eluted in the HPLC analysis of ovules pollinated one day earlier with Bahlani and expected if the biochemical processes triggered by pollination (Browning, 1989) were more advanced. Khori pollen germinated as rapidly as Bahlani but did not induce such beneficial fruit growth responses. This difference may relate to the different HPLC profiles for fruits pollinated by the two different males. The HPLC analyses were only preliminary and would merit further investigation.

It appeared likely that pollen-borne substances mediated effects on fruit fresh weight from late Stage 1 onwards, by stimulating the activity of growth promoting substances or inactivating inhibiting substances in the fruit, rather than by merely adding substances directly from the pollen. This would be in line with roles ascribed to pollen by Stanley (1974). The effects occurring in cv Khalas from late Stage 1 onwards in 1996 were examined more closely by looking at the biochemical composition of ovaries 14 days after pollination with different male types. Pollen types were similar regarding compositions of their variously pollinated ovaries two weeks later and fruit fresh weight responses. This was consistent with effects due to Al Arudsabba and Bahlani being on par. As one day after pollination, biochemical analysis showed Al Arudsabba and Khori to be on par, this suggests that their similar responses could be due to substances introduced by the pollen. They would, however, only in the longer term induce specific metabolic changes. Such a role was ascribed to plant growth regulators by Lee (1997), who postulated that IAA exported from seeds to the mesocarp of melon, stimulated cell wall-bound and soluble invertase activities, thereby strengthening its sink activity during fruit development. No clear interpretation emerges of whether and which of these pollen effects are directly or indirectly due to a genetic interaction or whether they are due to mere non-genetic biochemical interaction.

It may be recalled that early (Stage 1) effects on fruit fresh weight were inconsistent for Al Arudsabba and Khori, while pollination with Bahlani consistently caused the highest weight. In Stage 2, pollination with Khori consistently gave the

heaviest fruits in both female cvs, with Bahlani generally being on par when pollinating cv Khasab, but not cv Khalas. A question arising here was, what brought about the differences in pollen effects before and after the transition from Stage 1 to Stage 2. Given that no seed measurements were taken until early Stage 2 when endosperm cellularization had started, it was assumed that no pollen effects on seed fresh weight existed before, so that the early effects on fruit fresh weight in Stage 1 were probably due to fresh weight differences in tissues lying outside the ovule. These would be the classically defined metaxenic effects (Swingle, 1928), as the ovule would contain late in Stage 1 the developing embryo and syncitial endosperm undergoing cellularization. Development of the embryo precedes endosperm development, as demonstrated in Chapter 4 and reported by Reuveni (1986). Morphogenesis of embryo, endosperm and extra-ovular tissues takes place, partially in sequence and in part synchronously. This situation makes resource allocation between these sinks likely, as suggested by Pharis and King (1985) in that endosperm hormones, in addition to supplying the heterotrophic embryo, also serve to slow embryogenesis until competition from fruit growth is reduced, upon which embryo growth resumes. Stanis and Chesonis (1988) observed *in vitro* that the tissues surrounding the embryo inhibited its development. Early pollen effects would be modified by such differential growth and longer term effects would only appear once the tissues and organs of the seed have developed. This was evident in the present study in that the long term pollen effect became largely consistent after mid-Stage 2, when fruit growth would be mainly by cell expansion which is affected by the kind of seed developed, as reported in Date Palm by (Reuveni 1984; Schroeder, 1958).

Comparison of pollen effects on fruit and seed fresh weight between the two female varieties in Stage 3 showed long term effects to be genetic, in that clear male x female interactions were evident. This was consistent with the findings of Al-Ghamdi (1984) on male x female interactions in Date Palms, who went on to describe them as metaxenic effects, although here we consider them more likely to be secondary effects possibly originating from xenic effects. Another typical example was described by Crane and Iwakiri (1980) for Pistachio where the interaction of pollen type and female type induced long term effects which originated from xenia. Bahlani resulted in the highest fruit and seed fresh weight, on par with Khori, only in cv Khasab. Khori alone had this effect in cv Khalas (Chapter 7). Khori consistently resulted in the highest fruit or seed weight, apart from with cv Khalas in 1995, which was probably

due to the already discussed influence of differential fruit set. However, here also Khori induced the highest fruit and seed weight in mid Stage 2, which was consistent with the results in other cvs and years. Pollen effects occurred on seed fresh weight well before fruit fresh weight. However, no seed weight differences were observed at the time fruit weight differences occurred. It therefore appears that these pollen effects are primarily xenic, which in turn influenced the fresh weight of the entire fruit.

The pericarp fresh weight responses were largely the same as those of the entire fresh fruit. The shift from effects exclusively on seed fresh weight in mid Stage 2, to effects exclusively on pericarp weight at the end of this Stage, suggests that a relocation of resources from seed to the pericarp had taken place. The pollen effects on the fresh weight of the seed coincided in both female cvs with the time when it stopped growing. The same coincidence existed for fruit fresh weight. Considering together the male-female interaction with regard to Bahlani and the above xenic effect, a genetic mechanism acting primarily on the seed appears possible. However, no rigorous testing of this possibility was undertaken. The subsequent, and probably consequential, pollen effects on the pericarp highlight the limitation of the definition of 'Metaxenia'. If the fruit weight differences had been seen alone, a metaxenic effect would have been concluded. Here, however, the effect largely turns out to be the consequence of 'Xenia' with some influence being exerted stage of maturity and ripeness of the fruits and the associated differences in moisture loss. This supports the view put forward by Denney (1984) that xenia includes metaxenia.

Pollen effects on fresh weight in Stage 2 were probably mediated through the action of endogenous plant growth regulators. This is a valid assumption in view of earlier research which showed that pollination increased hormones in ovaries (Browning, 1989) and because of PGR x pollen type interactions observed in the present study (Chapter 7). Biochemical differences were found between fruits pollinated with different pollen types. Applications of growth substances such as GA3 and HFCA exerted different effects on fruit fresh weight according to the pollen used to set the fruit. As the fruits alone were treated, it is unlikely that competing growth had been induced elsewhere. It is possible that the applications resulted in supra-optimal endogenous levels in some cultivars (Looney, 1986), thereby inhibiting growth, while in others, suboptimal endogenous levels may have been brought to near optimal levels by the same treatment. For example, endogenous GA-levels may be *a priori* higher in Khori than in Al Arudsabba and this could account for the superior

performance of Khori-pollinated fruits with regard to weight in the pollen experiments. It must be borne in mind that observations on the entire fruit do not reflect the complex changes in the separate tissues, a concern also raised in other research on hormone physiology (Browning, 1989).

The relationships between fruit fresh weight and fruit set in Stages 1, 3 and 4 showed some dependency on pollen type. Fruit fresh weight and fruit set in Stage 3 were consistently and negatively correlated only in bunches pollinated with Al Arudsabba. In the case of the other two pollen types, some compensation mechanism was presumably at work which prevented this. It is suggested for Khori-pollinated fruits of the cv Khalas that high fruit weight reduced fruit retention.. Generally and irrespective of pollen type, a similar influence has been shown for cv Khasab (Chapter 5) in that high fruit set and rates of abscission on the one hand were related to low fruit fresh weight and fresh weight gain on the other hand. This is consistent with research on other crops (Lakso, 1989) showing that fruit abscission occurred after a critical reduction in fruit growth rate.. The absence in cv Khasab of the pollen-specific correlations found in cv Khalas possibly indicates genetic causes arising from the male x female interaction, but could be also related to the climatically distinct periods to which fruits were exposed in Stage 4. Reuveni (1986) also observed a susceptibility of the developing fruit, particularly maturing fruits to weather and water conditions.

To eliminate differences due to climatically distinct periods of equal real time (d.a.p.), pollen effects were examined on a thermal time basis. All observations on pollen blocks within a year and cv were at equal real and thermal time except for substantial differences in Stage 1 in cv Khalas in 1995. In Stage 3 Khori pollen was then found to induce fruit fresh weight increase in less thermal time than the other types. This was the case for physiologically mature fruits in both female cvs. It is recalled that in cv Khalas, but not cv Khasab, maturity of this large Khori-pollinated fruits was relatively late. Considering that the time to maturation depended in the date palm on cultivar (Pereau-Leroy, 1958), it appears that Khori-pollinated fruits behave like an own 'cultivar', which would be consistent with expectations that pollen effects are hereditary in nature at this stage. This result could not be used for modelling because there was no consistent correlation between thermal time and fruit fresh weight, but it indicated that Khori pollinated bunches had overall accumulated comparatively more fresh weight for a given total thermal time accumulation.

The absence of clear correlations suggested that other mechanisms were at work, probably differential fruit set and extreme weather conditions, to which individual bunches were exposed at different chronological but equal thermal time. This would be consistent with findings by Reuveni (1986) that fruit set and extreme weather influenced fruit development.

Largely consistent positive correlations between fruit or seed fresh weight and thermal time for Bahlani pollinated fruits between Stage 1 and early Stage 3 represented another pollen effect. As thermal time reflects both time and temperature conditions, it can be reasoned that Bahlani pollinated fruits are more responsive to, and possibly dependent on them, than the other two pollen types. Thereafter correlations became less consistent, probably due to the influence of climatic conditions and ripening changes causing loss of fresh weight. Pollen effects on correlations between thermal time and fruit set on the one hand, and weight on the other, were found in Stage 4, but have to be interpreted in the light of maturity and ripening changes. They will be discussed later.

Khori generally induced the highest fruit fresh weight and was therefore a commercially exploitable pollen type. Large fruited dates of good quality have always been in demand as evidenced by preference for such cvs in the Sultanate Oman (Macki, 1992), the Gulf States and of cvs Deglet Noor and later Medjool as prime quality dates in the US (Nixon, 1966). Bahlani is similar, but limited in productive applications to the female cv Khasab. The particular superiority of Khori was apparent from the results of three out of the four sets of experiments involving both cvs in two years. High fruit fresh weight is a desirable quality aspect of Bissr fruits, i.e.: consumable fruits, which are physiologically mature and just starting to ripen (Macki, 1992). Ripening involves moisture and fresh weight losses (Reuveni, 1986). In cv Khalas, these changes did not affect Khori's superiority over the other two pollen types with regard to fruit fresh weight even after the Bissr Stage. They were however probably responsible for obliterating Khori's advantage in cv Khasab, where no pollen effects existed after the Bissr stage. The comparison between cvs suggests that the pollen effects in cv Khasab during ripening were largely equalized as a result of moisture losses, which were disproportional to fruit fresh weight, while this was not the case for cv Khalas. If it had been proportional then pollen effects on fresh weight would probably have still been detected. In contract in cv Khalas, the fresh weight

differences between pollen treatments persisted. In line with earlier published work (Reuveni, 1986) a reason for this different behaviour in Stage 4 may lie indirectly in the distinctly different climatic conditions during maturity and ripening of these two cvs. In cv Khalas, Stage 4 took place during the hot and windy months of July and August (mean 34.5 ° C) and in cv Khasab during the markedly cooler and much calmer months of September and October (mean 28.6 ° C).

Dimensions of fruit and seed were affected by pollen type, confirming earlier observations (Swingle, 1928). Effects in Stage 1 were inconsistent for pollen type Al Arudsabba and Khori, while Bahlani consistently induced the widest fruits. In Stages 2 and 3, Khori consistently induced the largest fruits in terms of length, width or volume. These effects were independent of female cv and year. In contrast, Bahlani had an effect dependent on female cv, in that it was on par with Khori in cv Khasab, but not in cv Khalas. These findings largely coincide with the observations of local growers in the Sultanate Oman. In Stage 4 the only consistent pollen effect was Bahlani's which induced the smallest fruits in cv Khalas. These results are consistent with our previous observations on fruit and seed fresh weight.

Fruit dimensions were influenced by differential fruit set. Bunches which set most fruits with pollen Khori in cv Khalas, contained smaller fruits in the mature stages, despite these same fruits having been the biggest until Stage 2. This effect had been also reported from thinning experiments in date palms (Nixon, 1956). As was argued in case of fresh weight, intrabunch competition for resources probably brought about these changes. Looking at data for 1996, Khori produced the largest fruits and it was expected that the same would have also occurred in 1995. It did not, possibly because fruit set differences occurring then between pollen blocks and a competition effect coming into play .

The mechanisms by which pollen types bring about differential fruit size may differ depending on whether effects occur in the early or late stages. As the effects are similar to those on fresh weight it is reasonable to assume similar mechanisms, in that substances induced by pollen type are responsible for early and genetic mechanisms responsible for late effects. In particular, the late effect of Bahlani is dependent on the female cv indicating that it is indeed under the influence of male x female interactions. The suggested early mechanisms are in line with Swingle's (1928) postulated action of growth substances being responsible. Schroeder and Nixon (1958) suggested that different pollen types affect fruit size in

the later stages of development by increasing the cell number through cell division in the early stages of development. The findings of the present study did not support this suggestion as they did not reveal any early response pattern of early effects (Stages 1 and 2) which would have persisted in its initial form until physiological maturity.

Fruit dimensions are a primary quality aspect in commercial date production. Khori has the distinct advantage of producing the largest Bissr fruits in both female cvs, while Bahlani could be used for this purpose only in the female cv Khasab. Less desirable was that effects on the size of fruits coincided with those on the seeds. Search for a ideal pollen type inducing large fruit and small seed size merits further research. Mature fruits, in particular of the cv Khasab, can be regulated by pollen type to produce seeds of different size.

Pollen type affected maturity and ripening of fruits. Pollen effects depended on the female type and influenced both time to maturity and the time taken for fruits to progress through the ripe stages from Bissr to Rutab. Maturity is taken in this study as the culmination of positive fruit growth in terms of fresh weight. It is coincident with the attainment of its full Khalal colour and is near to its maximum fresh weight. The term ripening is used to denote the period during which fruits lose fresh weight, soften and darken. These changes are senescent and would eventually culminate in fruit drop unless fruits are first harvested.

Pollen type is reported to affect maturity and ripening of fruits in many tree, including dates (Nixon, 1928b). In the present study, pollen type appeared to affect physiological maturity (percentage of mature fruits as indicated by their colour) only in cv Khalas. The absence of effects on maturity in the later cv, Khasab, may be the result of male x female interaction, although according to Nixon it had been expected that late cvs like Khasab would have been affected. Al Arudsabba and Bahlani induced earlier maturity compared to pollen type Khori (second half of Stage 3) in 1996, but at the end of Stage 3 no differences existed. However, the rate of ripening was not congruent with the observations on differential maturity, in that Khori appeared to induce faster ripening in the cv Khalas than the other two pollen types as was seen by mid Stage 4. Correlations between fruit fresh weight and maturity (Section 8.2.2.) suggest a reason for the late maturity of Khori pollinated fruits. The correlations were negative and existed only for Khori, indicating that these fruits became heavier while maturing later. They continued to grow and maturity set in later, while fruits pollinated with the other types had almost stopped growing. This

explanation was also supported by the larger fresh weight gain observed in Khori pollinated fruits over the respective period in Stage 3 than those pollinated by the other types. Although it is not possible to draw firm conclusions from these observations about which variable influenced the other, it can be assumed that endogenous substances such as hormones or enzymes, which would affect maturity and subsequent ripening, acted differently in Khori pollinated bunches than in the other two types. Candidates for such hormones are GA as a maturation inhibitor in dates (Abou Aziz, 1983) and ABA as a promoter, while invertase is an enzyme involved in ripening as reported in date cvs maturing where it was present at substantially different levels (Kanner, 1978). It was apparent that whilst Al Arudsabba and Bahlani advanced maturity, Khori induced faster ripening thereafter.

In 1995, pollen type Al Arudsabba induced later maturity in comparison to the other two types in fruits of the cv Khalas. This pollen effect was revealed by the results of correlations between thermal time and fresh weight in Stage 4 in that Al Arudsabba pollinated fruits lost moisture with increasing thermal time, while fruits pollinated with the other two pollen types did not show this linearity at equal chronological time. Although real time was equal, these observations were made at different thermal times, so that the influence of temperature as one of the two components of heat summation remains to explain the differential fresh weight loss. It may be speculated that fruits in different pollen blocks contained distinctly different compliments of biochemical constituents, which react to temperature causing distinct changes in the fruit. Invertase influences the water activity in fruits (Kanner, 1978) and varied much between cvs. This linearity for the Al Arudsabba block suggested that fruits of this type had undergone less advanced ripening and were still closer to their preceding maximum fresh weight, so that moisture loss from them was still more clearly related to thermal time, especially temperature, than in the case of fruits pollinated with the other two pollen types. This suggested that, unlike in 1996, Al Arudsabba pollinated fruits matured later in 1995. This had been expected considering that sometime between Stages 2 and 4, Al Arudsabba went from producing the lightest to inducing the heaviest fruit, which had been attributed to differential fruit set in the earlier discussion. Assuming that differential fruit set had a similar effect on the response pattern of maturity to pollen treatment as it had in case of fresh weight, then the low set of Al Arudsabba-pollinated fruits in 1995 could have brought about heavier fruits and in turn later maturity.

Pollen effects on maturity and ripening depended on the female cv, which highlighted the influence of male x female interactions. Regression analysis of thermal time on fruit weight in Stage 4 (Section 9.2.2.) in the second female type (cv Khasab) provided further evidence that Khori pollinated fruits matured later and ripened slower respective to the other two pollen types. This response to Khori is consistent with its effect of causing late maturity in the other female cv, but then faster ripening. Notably, this effect is parallel to Khori's effect of causing the heaviest fruits in both female cvs. However, such parallel effects could not be found for pollen type Bahlani, which instead caused in one female lighter and in the other heavier fruits, but induced the same early maturity in both. This not only suggests genetic interactions, but also that fresh weight and maturity as indicated by colour are mediated by different mechanisms which are under the influence of both the male and female types.

Pollen type consistently defined the extent of the relationship between fruit set and ripeness. Although an expected overall direct linear relationship between fruit set and the percentage of ripening fruits in bunches in late Stage 4 was observed, it could be defined clearly only for fruits pollinated by Khori. This means that bunches which were pollinated with this type contained a higher proportion of ripe fruits (expressed as percentage of fruits as a percentage of the initial number of ovaries) if they contained more fertilized fruits. It appeared therefore that ripening in Khori pollinated bunches was in some manner regulated by fruit set and that this regulation was a pollen effect in itself.

Ripening was more uniform and therefore predictable with pollen type Bahlani than with the other types. Given equal chronological time, Bahlani pollinated bunches contained between 5 and 20 % ripe fruits depending on thermal time, while the respective proportion of those pollinated with other types varied much more widely. This was revealed by correlations between thermal time and the above proportion (Section 9.2.4.). As real time was equal for all bunches, the temperature regime appears to regulate ripening particularly in Bahlani pollinated bunches.

Pollen effects are likely to be mediated through changes in endogenous hormones, with auxins and GA probably having key roles. The discussion of physiological and biochemical characteristics of the pollen types has highlighted distinct differences. Although no causal relationship between these characteristics and the subsequent effects induced by the pollen types has been established, Khori performed better in many respects than other pollen types and was also distinct in

having the largest pollen grains and the most uniform *in vitro* pollen tube growth. However, it went beyond the scope of this study to examine this relationship rigorously.

Pollen types Al Arudsabba and Bahlani are of commercial interest because they advanced maturity, which is useful for the production of Bissr fruits (Macki, 1992). For growers producing Rutab fruits in bulk, Khori has potential because it induced faster ripening although after a later onset of maturity. Bahlani induced the most uniform ripening. It must however be kept in mind that commercial considerations depend on market requirements, which may call for either bulk harvesting of one of the products, i.e: Bissr or Rutab fruits, or for an extended sequential production and harvesting of these products. In the first case Khori would be the right pollen selection, while for the second one the other types, particularly Bahlani with its more uniform ripening effect would be preferable.

Pollen had an effect on the sucrose and total sugar content of fruits. Al Arudsabba induced the lowest sucrose content in mature Khalas fruits in 1995. This result could be interpreted in view of the previous results, so that it either reflected the delayed maturity in Al Arudsabba pollinated bunches in that the sucrose content was still accumulating or that Al Arudsabba directly induced a lower sucrose content. Generally, sucrose content increases towards maturity, but thereafter reduces as sucrose catalyses into glucose and fructose, resulting in a decrease of sucrose content with advancing ripeness (Reuveni, 1986). The consistency of Al Arudsabba's effect in reducing total sugar content was apparent also in ripe fruits (late Stage 4) in the same year and in ripe fruits (mid stage 4) of cv Khasab in the next year. Considering that Al Arudsabba delayed maturity in the first case, but advanced it in the second case, it may be that the regulation of sugar content by pollen type was direct and independent of year and female cv. However, this effect was not found in both years in both female cvs. It is suggested that Al Arudsabba induces *per se* a lower sugar content. It would do this more directly than indirectly as a result of ripening changes. Total sugar content is therefore a poor indicator of maturity and ripeness. Other important aspects of fruit quality like tannin and acid contents were not affected by pollen type.

The mechanisms mediating pollen effects on total sugar content can be only speculated upon. They appear to act separately from the general ripening changes and there is no evidence that they are due to male x female interaction, although this

possibility is not precluded. A possible role for the enzyme invertase is discussed earlier (Kanner, 1978). The changes are too far removed in time from pollination to attribute them with confidence to this process. The questions arising here highlight the need for further research into this point.

From a commercial point of view, decisions on pollen type will be often guided by minimizing adverse effects. It would be therefore wise to select Khori and Bahlani, in preference to Al Arudsabba, to exploit their possible potential for inducing higher sugar content, unless other production requirements influence such a decision. In commercial assessments, Bahlani is frequently on par with Al Arudsabba, so that it would be sensible to give Bahlani preference over Al Arudsabba.

Pollen type affected uniformity of fruit and seed size in the cv Khalas, but not in cv Khasab. Earlier researchers have described effects on fruit and seed size as well as on the uniformity of these variables in dates (Osman, 1974). In the present study Bahlani consistently induced the most uniform size of fruits and seeds at maturity. This result is consistent with the predictable performance of this pollen type as already discussed. Although the other two types had inconsistent effects depending on the year, it appears that Al Arudsabba is similar to Bahlani, at least for 1996. It can be speculated with some degree of confidence that this would have been the case in 1995 as well, were it not for the influence of differential fruit set in that year. That difference caused changes in the response pattern of many fruit variables to pollen types between Stages 2 and 3. The difference between female cvs in pollen effects on fruit-, seed size and on the dispersion of measurements suggests genetic control, which would be in line with Osman's observations(1974). He attributed the dispersion effect to different levels of pollen heterozygosity.

Pollen type also affected the uniformity of maturity, but this effect depended on the female cv, indicating a genetic mechanism. Maturity was the most uniform with pollen type Bahlani in cv Khalas and with Khori in the cv Khasab. Bahlani pollinated bunches were intermediate in this regard. This could reflect different levels of heterozygosity between the male parents in that pollen from heterozygous plants would have particular genes present in both allelic forms (Redei, 1986), which would then result in genetic differences between pollen grains from the same parent. This is in line with findings of Osman (1974) that a significant part of the spread of time of ripening on a given date bunch are related to the pollen type's level of heterozygosity. Uniformity of Bissr fruit production can be to some extent regulated by selecting a

suitable pollen type, i.e.: Bahlani for cv Khalas and Khori or Bahlani for use with cv Khasab. In a harvesting period extending over several weeks the production of Bissr fruits is less risky than the production of Rutab fruits. This is because, if the harvest of Bissr fruits is delayed, it will still be possible to utilize these fruits when they enter the Rutab stages. However, delayed Rutab harvest bears the risk of fruit drop, spoilage and commercial loss. As already discussed, Khori pollination results in a shorter period for Rutab production, which in itself is a beneficial aspect of uniform production. Ample opportunity exists therefore to adopt a pollen regime suitable for various conditions of market demand.

Pollen effects on bunch yield in cv Khalas proved to be inconsistent, with a clear dependency on fruit set. In cv Khasab no effects were detected. As different stages of fruit are harvested from date palms, it is necessary to assess the potential total yield by using the numbers and fresh weights of physiologically mature fruits. High fruit set increased the number of fruits to a large extent and decreased fruit fresh weight to a lesser extent. Both are factors used in calculating yield . Fruit number had a stronger leverage on yield than fruit fresh weight. It must be borne in mind that the concept of yield assesses the entire bunch directly. This is a system on a higher level of complexity than the single fruit, which so far has been the principal subject of this discussion. Yield derives from combining variables on lower levels of complexity, which are probably affecting each other, e.g.: fruit number and fruit set as characteristics of the bunch on the one hand and fruit fresh weight as a characteristic of the single fruit on the other. Yield calculation also used the means of fruit numbers as multiplicators, which cannot be confirmed to be statistically different, but which have a large leverage. It was evident in this study that the effect of pollen type on fruit fresh weight was independent of the effect of fruit numbers. It is necessary to view yield with caution when assessing pollen effects and to look at cumulative yields over several years of production.

Cumulative total yields over two years proved to be similar for all pollen types with Al Arudsabba and Khori proving to be the most reliable, in that they produced the least difference between annual yields. Bahlani was in this regard the least reliable. Bissr yield was not consistently and directly regulated by pollen type. This was, firstly, because these effects were governed by the same conditions of fruit set as discussed for total yield and, secondly, because they were not direct in that they reflected pollen effects on time of maturity. As already discussed, Khori pollinated bunches matured

later, but then ripened faster, so that they passed through the Bissr stage faster. However, total yield is a suitable measure of Bissr yield, because every fruit passes through all stages of maturity and ripening. The results on Bissr yield reveal however, the limitations of using Khori for Bissr production, in that this product is only available for a short time and is bound to ripen quickly into Rutab fruits. Nevertheless, for many consumers this is a desirable feature.

Visual assessment of fruits was consistent with the previously discussed pollen effects on maturity, ripening and uniformity.

Commercially, each pollen type had its distinct merits as described in the beginning of this discussion. The characteristics attributed to these pollen types by growers in the interior of the Sultanate Oman (Anon., 1996) coincide with our present findings on Khori and Bahlani, but differ in case of Al Arudsabba. The reason for this difference are most likely due to climatic influences. The limitations of the locality for this study, the Northern Batinah region, must be borne in mind in that here climatic conditions are significantly different from the interior regions, which is the traditional area for the production of prime quality dates (Macki, 1992. It is therefore necessary to view the evaluation of the regulatory effects of pollen as limited to the locality of the present study.

It appears that Khori is the most promising of the tested pollen types and perhaps local production of male inflorescences from this type should be adopted. As a matter of fact, male Khori plants have been planted in the area of this study and it is hoped that they can produce the same benefits as the Khori from inflorescences were brought in from the interior areas of the Sultanate Oman. As the important effects, i.e.: the late effects on quality and yield, are thought to be genetic, a certain degree of confidence exists that the change of locality does not adversely affect Khori's potential.

Results from this study are largely consistent with Swingle's hypothesis in that early pollen effects appeared to be due to mechanisms induced by substances contributed by the pollen type or its physiological characteristics. Later effects were probably due to genetic interactions, which different schools of thought have predicted (Denney, 1992; Reiger 1976; Osman, 1974). However, this study went on to show that pollen effects, especially those commonly termed Metaxenia, are the result of complex interactions of different variables. Earlier studies have not sufficiently

considered the major influence which differential fruit set will exert on the expression of pollen effects. The present study has done this and has attempted to explained it. At the same time, a comprehensive assessment has been made of other aspects of date production, such as quality and yield, and their responses to pollen type and fruit set. Another new approach taken in this study was the detailed evaluation of changes occurring during the entire growth and development of fruits on the basis of real and thermal time. This revealed that early pollen effects differ clearly from later ones and led to a distinction between the possible mechanisms underlying those effects. A further new point made was the commercial assessment of each pollen type and recommendations as to their applicability to practical horticulture in the region.

FURTHER RESEARCH:

Further studies should concentrate on the following:

- a screening of the physiological characteristics of further pollen types and their effect on the quality and yield of fruits pollinated by them. This is presently being done in the Sultanate of Oman.

- studies examining the relationship between the above.

- an assessment of fruit set effects on the expression of pollen effects. A trial is presently in progress in which different pollen type are combined with different levels of fruit thinning.

- a biochemical assessment of the pollen types and their fruits, trying to modify certain biochemical components to then identify their function in mediating pollen effects.

- a rigorous examination of source-sink relationships in date palm and the influence pollen treatments have on them, including the mechanisms by which pollen type influences sugar content.

- an examination of the histological and physiological changes taking place in the tissues of fruits treated with different pollen types. This may reveal whether effects are reflected in such key factors as cell number, volume and cell wall permeability.

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Appendices

Appendix 1 : Climatic data - 1995 and 1996 (Sohar, Sultanate Oman)

1995: Metereological observations

January

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	38	80	59.0	10.0	25.0	17.5
2	34	81	57.5	10.0	27.0	18.5
3	36	70	53.0	11.0	25.0	18.0
4	38	79	58.5	12.0	25.0	18.5
5	45	80	62.5	14.0	25.0	19.5
6	38	78	58.0	11.0	25.0	18.0
7	26	76	51.0	11.0	25.0	18.0
8	54	80	67.0	12.0	25.0	18.5
9	42	82	62.0	11.0	25.0	18.0
10	48	80	64.0	12.0	24.0	18.0
11	36	80	58.0	12.0	24.0	18.0
12	50	80	65.0	12.0	24.0	18.0
13	51	80	65.5	12.0	26.0	19.0
14	36	79	57.5	13.0	28.0	20.5
15	20	80	50.0	13.0	27.0	20.0
16	41	80	60.5	12.0	27.0	19.5
17	44	80	62.0	12.0	26.0	19.0
18	34	80	57.0	12.0	27.0	19.5
19	56	80	68.0	13.0	27.0	20.0
20	34	79	56.5	13.0	28.0	20.5
21	44	80	62.0	13.0	29.0	21.0
22	25	80	52.5	13.0	29.0	21.0
23	38	80	59.0	12.0	29.0	20.5
24	38	80	59.0	12.0	28.0	20.0
25	25	80	52.5	12.0	27.0	19.5
26	40	80	60.0	13.0	27.0	20.0
27	30	70	50.0	14.0	27.0	20.5
28	38	78	58.0	11.0	27.0	19.0
29	46	80	63.0	11.0	27.0	19.0
30	52	80	66.0	11.0	27.0	19.0
31	56	80	68.0	12.0	27.0	19.5

February

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	54	80	67.0	13.0	28.0	20.5
2	58	80	69.0	12.0	27.0	19.5
3	22	79	50.5	11.0	30.0	20.5
4	26	80	53.0	12.0	29.0	20.5
5	14	80	47.0	14.0	29.0	21.5
6	64	80	72.0	15.0	29.0	22.0
7	65	79	72.0	19.0	29.0	24.0
8	61	80	70.5	17.0	28.0	22.5
9	60	78	69.0	18.0	29.0	23.5
10	49	79	64.0	17.0	26.0	21.5
11	22	77	49.5	11.0	25.0	18.0
12	22	76	49.0	10.0	28.0	19.0
13	24	79	51.5	11.0	26.0	18.5
14	38	79	58.5	12.0	27.0	19.5
15	46	80	63.0	11.0	27.0	19.0
16	44	80	62.0	12.0	28.0	20.0
17	24	80	52.0	12.0	31.0	21.5
18	17	81	49.0	12.0	31.0	21.5
19	40	80	60.0	14.0	26.0	20.0
20	43	81	62.0	16.0	28.0	22.0
21	50	80	65.0	13.0	22.0	17.5
22	40	80	60.0	10.0	28.0	19.0
23	48	80	64.0	11.0	28.0	19.5
24	54	79	66.5	15.0	28.0	21.5
25	37	79	58.0	14.0	26.0	20.0
26	28	74	51.0	12.0	27.0	19.5
27	46	80	63.0	13.0	27.0	20.0
28	50	80	65.0	16.0	29.0	22.5

March

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	48	80	64.0	14.0	27.0	20.5
2	42	80	61.0	13.0	28.0	20.5
3	44	78	61.0	13.0	28.0	20.5
4	53	81	67.0	12.0	23.0	17.5
5	50	80	65.0	10.0	27.0	18.5
6	7	76	41.5	11.0	30.0	20.5
7	18	80	49.0	13.0	29.0	21.0
8	42	80	61.0	13.0	27.0	20.0
9	53	79	66.0	13.0	29.0	21.0
10	52	80	66.0	14.0	29.0	21.5
11	46	79	62.5	14.0	29.0	21.5
12	55	80	67.5	16.0	28.0	22.0
13	58	80	69.0	17.0	22.0	19.5
14	50	80	65.0	15.0	23.0	19.0
15	35	80	57.5	15.0	32.0	23.5
16	47	80	63.5	13.0	28.0	20.5
17	42	80	61.0	15.0	28.0	21.5
18	53	79	66.0	15.0	28.0	21.5
19	62	79	70.5	18.0	29.0	23.5
20	66	78	72.0	19.0	29.0	24.0
21	66	79	72.5	19.0	28.0	23.5
22	60	79	69.5	18.0	29.0	23.5
23	52	79	65.5	20.0	28.0	24.0
24	60	79	69.5	18.0	28.0	23.0
25	39	79	59.0	16.0	30.0	23.0
26	34	80	57.0	16.0	31.0	23.5
27	20	80	50.0	17.0	37.0	27.0
28	8	44	26.0	20.0	35.0	27.5
29	42	78	60.0	16.0	35.0	25.5
30	31	80	55.5	15.0	30.0	22.5
31	16	80	48.0	16.0	33.0	24.5

April

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	14	80	47.0	14.0	31.0	22.5
2	29	79	54.0	15.0	32.0	23.5
3	15	80	47.5	15.0	31.0	23.0
4	30	80	55.0	16.0	33.0	24.5
5	10	74	42.0	16.0	35.0	25.5
6	16	71	43.5	16.0	37.0	26.5
7	0	71	35.5	16.0	38.0	27.0
8	10	73	41.5	15.0	35.0	25.0
9	30	74	52.0	12.0	30.0	21.0
10	22	80	51.0	12.0	32.0	22.0
11	38	80	59.0	17.0	34.0	25.5
12	38	80	59.0	18.0	31.0	24.5
13	54	79	66.5	18.0	30.0	24.0
14	9	78	43.5	18.0	39.0	28.5
15	2	70	36.0	19.0	36.0	27.5
16	16	66	41.0	20.0	38.0	29.0
17	11	58	34.5	20.0	40.0	30.0
18	4	69	36.5	15.0	37.0	26.0
19	28	79	53.5	16.0	32.0	24.0
20	52	78	65.0	20.0	32.0	26.0
21	61	78	69.5	21.0	32.0	26.5
22	44	78	61.0	21.0	33.0	27.0
23	24	76	50.0	20.0	37.0	28.5
24	1	76	38.5	21.0	39.0	30.0
25	31	78	54.5	20.0	38.0	29.0
26	40	78	59.0	17.0	33.0	25.0
27	20	79	49.5	18.0	32.0	25.0
28	26	72	49.0	18.0	33.0	25.5
29	18	78	48.0	18.0	35.0	26.5
30	18	77	47.5	18.0	35.0	26.5

Abbreviations:

Rhmin	minimum relative humidity (%)
Rhmax	maximum relative humidity (%)
Rhave.	mean relative humidity (%)
Tmin	minimum temperature (degrees Centigrade)
Tmax	maximum temperature (degrees Centigrade)
Tave.	mean temperature (degree Centigrade)

May

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	16	78	47.0	18.0	37.0	27.5
2	12	79	45.5	18.0	37.0	27.5
3	16	78	47.0	18.0	37.0	27.5
4	16	68	42.0	18.0	39.0	28.5
5	12	70	41.0	20.0	39.0	29.5
6	11	68	39.5	20.0	40.0	30.0
7	37	71	54.0	19.0	38.0	28.5
8	9	80	44.5	21.0	41.0	31.0
9	15	69	42.0	20.0	39.0	29.5
10	6	42	24.0	21.0	43.0	32.0
11	10	70	40.0	20.0	40.0	30.0
12	14	50	32.0	21.0	40.0	30.5
13	18	75	46.5	21.0	37.0	29.0
14	9	55	32.0	22.0	40.0	31.0
15	0	48	24.0	24.0	44.0	34.0
16	2	41	21.5	19.0	43.0	31.0
17	14	68	41.0	20.0	42.0	31.0
18	40	79	59.5	20.0	38.0	29.0
19	20	73	46.5	20.0	38.0	29.0
20	6	78	42.0	20.0	40.0	30.0
21	33	81	57.0	21.0	39.0	30.0
22	11	78	44.5	21.0	39.0	30.0
23	3	79	41.0	22.0	40.0	31.0
24	20	79	49.5	23.5	43.0	33.3
25	51	76	63.5	25.0	34.5	29.8
26	38	76	57.0	23.5	37.0	30.3
27	43	76	59.5	20.5	35.5	28.0
28	25	77	51.0	22.0	37.0	29.5
29	22	73	47.5	21.5	41.0	31.3
30	24	80	52.0	24.0	40.0	32.0
31	34	78	56.0	25.0	43.0	34.0

June

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	10	77	43.5	23.0	40.0	31.5
2	10	71	40.5	21.0	41.0	31.0
3	19	68	43.5	22.5	41.0	31.8
4	34	75	54.5	25.0	41.0	33.0
5	24	77	50.5	24.0	41.0	32.5
6	14	60	37.0	22.0	42.0	32.0
7	0	73	36.5	21.5	41.0	31.3
8	16	78	47.0	21.0	41.0	31.0
9	16	79	47.5	23.0	41.0	32.0
10	13	74	43.5	25.0	41.0	33.0
11	0	76	38.0	24.0	45.0	34.5
12	0	60	30.0	24.0	45.0	34.5
13	36	79	57.5	23.0	46.0	34.5
14	16	79	47.5	24.0	42.0	33.0
15	60	79	69.5	25.0	37.0	31.0
16	60	78	69.0	27.0	35.0	31.0
17	61	78	69.5	28.0	36.0	32.0
18	24	76	50.0	23.0	36.0	29.5
19	22	77	49.5	24.0	36.0	30.0
20	38	79	58.5	26.0	39.0	32.5
21	24	78	51.0	27.0	40.0	33.5
22	26	77	51.5	27.0	41.0	34.0
23	40	74	57.0	27.0	38.0	32.5
24	1	75	38.0	26.0	45.0	35.5
25	33	78	55.5	23.0	37.0	30.0
26	33	80	56.5	25.0	37.0	31.0
27	63	78	70.5	26.0	37.0	31.5
28	50	79	64.5	25.0	37.0	31.0
29	36	78	57.0	23.0	38.0	30.5
30	19	77	48.0	23.0	40.0	31.5

July

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	17	74	45.5	24.0	42.0	33.0
2	8	73	40.5	25.0	41.0	33.0
3	0	72	36.0	25.0	41.0	33.0
4	48	76	62.0	25.0	37.0	31.0
5	26	70	48.0	27.0	41.0	34.0
6	2	76	39.0	27.0	45.0	36.0
7	23	79	51.0	29.0	41.0	35.0
8	62	78	70.0	29.0	37.0	33.0
9	54	76	65.0	29.0	37.0	33.0
10	64	78	71.0	29.0	37.0	33.0
11	60	78	69.0	30.0	37.0	33.5
12	22	80	51.0	29.0	41.0	35.0
13	63	78	70.5	29.0	36.0	32.5
14	60	78	69.0	30.0	36.0	33.0
15	64	78	71.0	30.0	36.0	33.0
16	61	78	69.5	29.0	36.0	32.5
17	63	79	71.0	29.0	36.0	32.5
18	61	78	69.5	28.0	36.0	32.0
19	52	78	65.0	28.0	37.0	32.5
20	36	78	57.0	30.0	38.0	34.0
21	66	78	72.0	30.0	35.0	32.5
22	48	79	63.5	26.0	35.0	30.5
23	54	79	66.5	25.0	35.0	30.0
24	65	78	71.5	26.0	35.0	30.5
25	61	78	69.5	26.0	33.0	29.5
26	61	78	69.5	27.0	34.0	30.5
27	60	78	69.0	28.0	35.0	31.5
28	53	78	65.5	26.0	35.0	30.5
29	52	78	65.0	27.0	36.0	31.5
30	49	78	63.5	27.0	38.0	32.5
31	61	78	69.5	28.0	38.0	33.0

August

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	49	80	64.5	30.0	36.0	33.0
2	66	78	72.0	30.0	36.0	33.0
3	51	78	64.5	29.0	37.0	33.0
4	49	80	64.5	29.0	39.0	34.0
5	43	78	60.5	31.0	39.0	35.0
6	35	78	56.5	29.0	37.0	33.0
7	15	78	46.5	28.0	40.0	34.0
8	34	80	57.0	29.0	40.0	34.5
9	45	79	62.0	29.0	38.0	33.5
10	63	78	70.5	29.0	36.0	32.5
11	61	79	70.0	29.0	36.0	32.5
12	61	79	70.0	28.0	35.0	31.5
13	60	78	69.0	28.0	36.0	32.0
14	14	78	46.0	27.0	43.0	35.0
15	32	80	56.0	26.0	42.0	34.0
16	35	79	57.0	29.0	37.0	33.0
17	64	78	71.0	29.0	35.0	32.0
18	66	78	72.0	29.0	35.0	32.0
19	63	79	71.0	28.0	34.0	31.0
20	66	78	72.0	29.0	35.0	32.0
21	58	78	68.0	29.0	36.0	32.5
22	62	79	70.5	29.0	36.0	32.5
23	65	77	71.0	28.0	34.0	31.0
24	60	79	69.5	28.0	32.0	30.0
25	65	78	71.5	28.0	34.0	31.0
26	64	78	71.0	28.0	35.0	31.5
27	65	78	71.5	28.0	35.0	31.5
28	62	78	70.0	29.0	35.0	32.0
29	63	80	71.5	28.0	35.0	31.5
30	56	78	67.0	28.0	36.0	32.0
31	62	78	70.0	28.0	35.0	31.5

September

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	58	78	68.0	27.0	34.0	30.5
2	60	79	69.5	26.0	35.0	30.5
3	50	79	64.5	26.0	36.0	31.0
4	28	78	53.0	21.0	40.0	30.5
5	34	80	57.0	21.0	42.0	31.5
6	12	80	46.0	21.0	42.0	31.5
7	28	82	55.0	22.0	40.0	31.0
8	62	80	71.0	21.0	37.0	29.0
9	60	80	70.0	26.0	36.0	31.0
10	62	80	71.0	26.0	35.0	30.5
11	63	80	71.5	25.0	35.0	30.0
12	61	80	70.5	26.0	35.0	30.5
13	60	80	70.0	25.0	35.0	30.0
14	59	80	69.5	25.0	35.0	30.0
15	36	80	58.0	24.0	39.0	31.5
16	34	80	57.0	25.0	40.0	32.5
17	32	80	56.0	26.0	40.0	33.0
18	52	80	66.0	27.0	35.0	31.0
19	64	80	72.0	25.0	34.0	29.5
20	65	80	72.5	25.0	34.0	29.5
21	59	80	69.5	23.0	36.0	29.5
22	30	76	53.0	22.0	39.0	30.5
23	42	80	61.0	22.0	41.0	31.5
24	66	80	73.0	24.0	35.0	29.5
25	54	81	67.5	23.0	35.0	29.0
26	46	81	63.5	23.0	38.0	30.5
27	20	80	50.0	22.0	39.0	30.5
28	59	80	69.5	22.0	39.0	30.5
29	57	80	68.5	23.0	36.0	29.5
30	52	80	66.0	23.0	35.0	29.0

October

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	60	77	68.5	23.0	35.0	29.0
2	38	80	59.0	23.0	37.0	30.0
3	34	80	57.0	21.0	38.0	29.5
4	62	80	71.0	21.0	37.0	29.0
5	36	76	56.0	21.0	38.0	29.5
6	30	80	55.0	22.0	37.0	29.5
7	22	78	50.0	23.0	37.0	30.0
8	52	78	65.0	24.0	36.0	30.0
9	57	78	67.5	24.0	35.0	29.5
10	58	79	68.5	22.0	35.0	28.5
11	20	79	49.5	21.0	39.0	30.0
12	28	78	53.0	21.0	37.0	29.0
13	33	79	56.0	21.0	36.0	28.5
14	54	78	66.0	20.0	34.0	27.0
15	30	79	54.5	20.0	37.0	28.5
16	24	79	51.5	19.0	35.0	27.0
17	22	78	50.0	20.0	35.0	27.5
18	53	78	65.5	21.0	33.0	27.0
19	61	78	69.5	23.0	33.0	28.0
20	48	79	63.5	22.0	35.0	28.5
21	57	80	68.5	20.0	33.0	26.5
22	54	79	66.5	21.0	33.0	27.0
23	60	79	69.5	22.0	32.0	27.0
24	60	80	70.0	23.0	32.0	27.5
25	60	80	70.0	22.0	32.0	27.0
26	48	80	64.0	20.0	32.0	26.0
27	33	80	56.5	19.0	33.0	26.0
28	35	80	57.5	19.0	32.0	25.5
29	22	81	51.5	16.0	32.0	24.0
30	14	78	46.0	13.0	32.0	22.5
31	25	78	51.5	12.0	32.0	22.0

November

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	20	80	50.0	12	32	22.0
2	26	82	54.0	13	31	22.0
3	40	80	60.0	14	31	22.5
4	26	80	53.0	13	32	22.5
5	26	80	53.0	14	33	23.5
6	33	80	56.5	15	33	24.0
7	32	80	56.0	19	31	25.0
8	58	80	69.0	21	30	25.5
9	60	79	69.5	19	29	24.0
10	60	79	69.5	16	29	22.5
11	11	79	45.0	15	32	23.5
12	22	80	51.0	16	31	23.5
13	47	80	63.5	16	30	23.0
14	48	80	64.0	16	30	23.0
15	58	80	69.0	17	28	22.5
16	31	79	55.0	14	29	21.5
17	38	80	59.0	15	28	21.5
18	35	80	57.5	14	28	21.0
19	49	80	64.5	14	28	21.0
20	38	80	59.0	14	27	20.5
21	41	80	60.5	15	27	21.0
22	44	80	62.0	15	28	21.5
23	47	80	63.5	14	28	21.0
24	52	80	66.0	16	27	21.5
25	46	80	63.0	14	27	20.5
26	32	80	56.0	15	28	21.5
27	19	68	43.5	15	29	22.0
28	36	79	57.5	14	25	19.5
29	38	80	59.0	14	25	19.5
30	44	80	62.0	14	25	19.5

December

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	46	82	64.0	13.0	25.0	19.0
2	38	82	60.0	14.0	25.0	19.5
3	40	83	61.5	15.0	26.0	20.5
4	37	81	59.0	15.0	28.0	21.5
5	44	81	62.5	16.0	28.0	22.0
6	68	80	74.0	16.0	26.0	21.0
7	60	80	70.0	17.0	26.0	21.5
8	47	79	63.0	18.0	28.0	23.0
9	58	80	69.0	18.0	26.0	22.0
10	64	80	72.0	18.0	25.0	21.5
11	64	80	72.0	19.0	25.0	22.0
12	64	80	72.0	18.0	24.0	21.0
13	60	80	70.0	18.0	25.0	21.5
14	56	80	68.0	19.0	26.0	22.5
15	58	80	69.0	15.0	25.0	20.0
16	44	80	62.0	16.0	24.0	20.0
17	67	80	73.5	17.0	24.0	20.5
18	61	80	70.5	17.0	24.0	20.5
19	65	80	72.5	17.0	25.0	21.0
20	56	80	68.0	15.0	24.0	19.5
21	56	79	67.5	16.0	24.0	20.0
22	60	79	69.5	16.0	23.0	19.5
23	61	80	70.5	16.0	24.0	20.0
24	56	79	67.5	15.0	24.0	19.5
25	61	78	69.5	17.0	24.0	20.5
26	61	81	71.0	17.0	25.0	21.0
27	56	80	68.0	15.0	24.0	19.5
28	48	80	64.0	14.0	23.0	18.5
29	42	80	61.0	13.0	23.0	18.0
30	51	80	65.5	14.0	24.0	19.0
31	56	79	67.5	15.0	23.0	19.0

January

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	55	80	67.5	15.0	24.0	19.5
2	50	80	65.0	14.0	25.0	19.5
3	40	80	60.0	13.0	25.0	19.0
4	32	80	56.0	13.0	25.0	19.0
5	46	80	63.0	13.0	25.0	19.0
6	35	80	57.5	12.0	25.0	18.5
7	40	80	60.0	14.0	25.0	19.5
8	41	80	60.5	13.0	25.0	19.0
9	34	80	57.0	13.0	26.0	19.5
10	33	80	56.5	13.0	25.0	19.0
11	54	80	67.0	13.0	24.0	18.5
12	59	79	69.0	15.0	23.0	19.0
13	40	74	57.0	14.0	26.0	20.0
14	30	72	51.0	12.0	24.0	18.0
15	37	80	58.5	10.0	22.0	16.0
16	42	80	61.0	11.0	21.0	16.0
17	48	78	63.0	12.0	20.0	16.0
18	46	80	63.0	12.0	22.0	17.0
19	66	80	73.0	14.0	22.0	18.0
20	47	80	63.5	14.0	23.0	18.5
21	56	80	68.0	16.0	24.0	20.0
22	53	80	66.5	17.0	24.0	20.5
23	70	80	75.0	17.0	20.0	18.5
24	74	80	77.0	16.0	21.0	18.5
25	74	80	77.0	14.0	20.0	17.0
26	55	80	67.5	12.0	23.0	17.5
27	44	80	62.0	10.0	22.0	16.0
28	30	80	55.0	9.0	22.0	15.5
29	29	80	54.5	10.0	23.0	16.5
30	42	80	61.0	10.0	23.0	16.5
31	38	80	59.0	11.0	24.0	17.5

February

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	40	80	60.0	11.0	25.0	18.0
2	46	80	63.0	13.0	25.0	19.0
3	60	79	69.5	14.0	25.0	19.5
4	66	79	72.5	16.0	25.0	20.5
5	60	79	69.5	16.0	25.0	20.5
6	59	79	69.0	17.0	25.0	21.0
7	36	69	52.5	12.0	24.0	18.0
8	38	80	59.0	10.0	24.0	17.0
9	27	80	53.5	12.0	27.0	19.5
10	54	80	67.0	12.0	26.0	19.0
11	52	80	66.0	15.0	27.0	21.0
12	64	79	71.5	18.0	24.0	21.0
13	61	79	70.0	16.0	25.0	20.5
14	52	79	65.5	16.0	27.0	21.5
15	42	80	61.0	12.0	24.0	18.0
16	52	80	66.0	15.0	25.0	20.0
17	57	79	68.0	16.0	24.0	20.0
18	60	80	70.0	17.0	24.0	20.5
19	60	80	70.0	16.0	25.0	20.5
20	52	79	65.5	16.0	27.0	21.5
21	54	79	66.5	16.0	27.0	21.5
22	43	78	60.5	18.0	28.0	23.0
23	43	80	61.5	12.0	25.0	18.5
24	30	80	55.0	13.0	24.0	18.5
25	38	80	59.0	11.0	24.0	17.5
26	37	80	58.5	11.0	24.0	17.5
27	42	80	61.0	13.0	24.0	18.5
28	56	80	68.0	16.0	25.0	20.5
29	64	79	71.5	16.0	24.0	20.0

March

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	58	79	68.5	16.0	26.0	21.0
2	58	77	67.5	16.0	27.0	21.5
3	60	80	70.0	16.0	27.0	21.5
4	64	79	71.5	18.0	26.0	22.0
5	66	80	73.0	20.0	27.0	23.5
6	66	80	73.0	20.0	27.0	23.5
7	63	80	71.5	18.0	25.0	21.5
8	64	79	71.5	19.0	28.0	23.5
9	70	78	74.0	21.0	25.0	23.0
10	68	78	73.0	21.0	26.0	23.5
11	45	79	62.0	19.0	28.0	23.5
12	72	80	76.0	19.0	23.0	21.0
13	69	79	74.0	20.0	25.0	22.5
14	60	79	69.5	20.0	27.0	23.5
15	72	79	75.5	16.0	25.0	20.5
16	30	79	54.5	14.0	25.0	19.5
17	38	79	58.5	15.0	25.0	20.0
18	34	79	56.5	14.0	27.0	20.5
19	33	80	56.5	15.0	27.0	21.0
20	44	80	62.0	16.0	27.0	21.5
21	68	79	73.5	20.0	28.0	24.0
22	38	79	58.5	19.0	30.0	24.5
23	38	78	58.0	18.0	28.0	23.0
24	51	80	65.5	20.0	28.0	24.0
25	52	79	65.5	19.0	28.0	23.5
26	30	80	55.0	20.0	32.0	26.0
27	49	79	64.0	20.0	29.0	24.5
28	24	78	51.0	16.0	32.0	24.0
29	5	68	36.5	15.0	33.0	24.0
30	24	79	51.5	13.0	28.0	20.5
31	26	80	53.0	14.0	28.0	21.0

April

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	10	80	45.0	14.0	30.0	22.0
2	18	80	49.0	15.0	31.0	23.0
3	30	80	55.0	16.0	31.0	23.5
4	26	78	52.0	17.0	32.0	24.5
5	17	80	48.5	18.0	34.0	26.0
6	15	80	47.5	20.0	31.0	25.5
7	52	80	66.0	17.0	28.0	22.5
8	40	80	60.0	17.0	29.0	23.0
9	24	81	52.5	17.0	32.0	24.5
10	46	80	63.0	17.0	31.0	24.0
11	22	78	50.0	18.0	35.0	26.5
12	2	63	32.5	16.0	37.0	26.5
13	12	80	46.0	17.0	32.0	24.5
14	58	79	68.5	19.0	31.0	25.0
15	58	79	68.5	23.0	30.0	26.5
16	65	80	72.5	21.0	30.0	25.5
17	46	80	63.0	20.0	32.0	26.0
18	30	78	54.0	19.0	31.0	25.0
19	52	80	66.0	20.0	29.0	24.5
20	45	80	62.5	20.0	31.0	25.5
21	35	80	57.5	20.0	32.0	26.0
22	24	80	52.0	19.0	35.0	27.0
23	8	79	43.5	20.0	38.0	29.0
24	2	80	41.0	21.0	41.0	31.0
25	32	79	55.5	23.0	37.0	30.0
26	12	74	43.0	23.0	39.0	31.0
27	21	60	40.5	23.0	38.0	30.5
28	12	59	35.5	20.0	39.0	29.5
29	0	66	33.0	19.0	42.0	30.5
30	12	76	44.0	20.0	37.0	28.5

Abbreviations:

Rhmin	minimum relative humidity (%)
Rhmax	maximum relative humidity (%)
Rhave.	mean relative humidity (%)
Tmin	minimum temperature (degrees Centigrade)
Tmax	maximum temperature (degrees Centigrade)
Tave.	mean temperature (degree Centigrade)

May

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	39	83	61.0	19.0	33.0	26.0
2	14	74	44.0	19.0	36.0	27.5
3	4	80	42.0	19.0	38.0	28.5
4	20	79	49.5	19.0	36.0	27.5
5	10	78	44.0	20.0	37.0	28.5
6	4	80	42.0	21.0	39.0	30.0
7	12	80	46.0	21.0	39.0	30.0
8	16	80	48.0	21.0	37.0	29.0
9	17	77	47.0	22.0	39.0	30.5
10	24	76	50.0	23.0	39.0	31.0
11	0	78	39.0	23.0	43.0	33.0
12	6	80	43.0	24.0	42.0	33.0
13	0	79	39.5	26.0	42.0	34.0
14	22	72	47.0	24.0	38.0	31.0
15	7	72	39.5	21.0	38.0	29.5
16	24	79	51.5	21.0	35.0	28.0
17	47	80	63.5	21.0	34.0	27.5
18	49	81	65.0	22.0	33.0	27.5
19	23	80	51.5	22.0	38.0	30.0
20	28	80	54.0	22.0	37.0	29.5
21	6	80	43.0	23.0	40.0	31.5
22	4	70	37.0	23.0	41.0	32.0
23	4	70	36.8	29.0	42.0	35.5
24	8	80	44.0	23.0	42.0	32.5
25	21	39	30.0	23.0	35.0	29.0
26	20	70	45.0	26.0	34.0	30.0
27	20	70	45.0	24.0	35.0	29.5
28	43	79	61.0	25.0	37.0	31.0
29	5	78	41.3	24.0	37.0	30.5
30	31	78	54.5	24.0	39.0	31.5
31	18	79	48.5	24.0	40.0	32.0

June

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
24	79	51.5	25.0	37.0	31.0
20	79	49.5	27.0	41.0	34.0
23	79	51.0	27.0	42.0	34.5
0	60	30.0	29.0	45.0	37.0
1	60	30.5	25.0	45.0	35.0
29	79	54.0	25.0	42.0	33.5
61	79	70.0	30.0	36.0	33.0
60	79	69.5	29.0	36.0	32.5
59	80	69.0	30.0	35.0	32.5
60	71	65.5	29.0	35.0	32.0
61	80	70.0	29.0	33.0	31.0
53	80	66.0	28.0	33.0	30.5
60	80	69.8	32.0	34.0	33.0
43	79	61.0	28.0	36.0	32.0
32	80	55.8	28.0	40.0	34.0
23	81	51.5	26.0	40.0	33.0
9	80	44.5	26.0	40.0	33.0
18	72	45.0	22.0	39.0	30.5
12	69	40.5	24.0	39.0	31.5
29	72	50.3	25.0	37.0	31.0
22	80	51.0	26.0	36.0	31.0
21	79	50.0	27.0	37.0	32.0
21	79	49.8	29.0	39.0	34.0
25	80	52.0	32.0	37.0	34.5
50	80	64.5	28.0	37.0	32.5
31	80	55.5	27.0	37.0	32.0
61	80	70.3	28.0	31.0	29.5
54	80	66.5	28.0	35.0	31.5
33	62	47.5	25.0	38.0	31.5
4	80	41.8	23.0	43.0	33.0

July

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	21	80	50.3	25.0	40.0	32.5
2	28	80	54.0	29.0	39.0	34.0
3	20	80	49.5	27.0	40.0	33.5
4	9	78	43.0	26.0	41.0	33.5
5	23	80	51.5	26.0	40.0	33.0
6	62	80	70.5	27.0	33.0	30.0
7	62	79	70.3	30.0	36.0	33.0
8	60	80	70.0	29.0	36.0	32.5
9	61	79	70.0	29.0	37.0	33.0
10	63	68	65.5	29.0	39.0	34.0
11	49	80	64.0	29.0	38.0	33.5
12	29	79	54.0	29.0	39.0	34.0
13	32	79	55.5	30.0	39.0	34.5
14	51	79	65.0	29.0	38.0	33.5
15	46	80	63.0	30.0	38.0	34.0
16	59	78	68.5	30.0	36.0	33.0
17	39	80	59.5	27.0	38.0	32.5
18	10	74	42.0	27.0	43.0	35.0
19	16	79	47.5	28.0	42.0	35.0
20	18	80	49.0	26.0	41.0	33.5
21	26	80	53.0	29.0	42.0	35.5
22	12	67	39.5	26.0	43.0	34.5
23	18	68	43.0	27.0	43.0	35.0
24	21	78	49.5	28.0	43.0	35.5
25	21	80	50.5	29.0	43.0	36.0
26	15	80	47.5	30.0	46.0	38.0
27	18	79	48.5	30.0	40.0	35.0
28	18	60	39.0	29.0	43.0	36.0
29	31	68	49.5	29.0	43.0	36.0
30	29	57	43.0	30.0	43.0	36.5
31	29	64	46.5	30.0	46.0	38.0

August

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	14	79	46.5	30.0	46.0	38.0
2	30	79	54.5	31.0	40.0	35.5
3	43	77	60.0	30.0	39.0	34.5
4	20	79	49.5	31.0	39.0	35.0
5	60	67	63.5	31.0	37.0	34.0
6	60	79	69.5	30.0	36.0	33.0
7	16	80	48.0	31.0	43.0	37.0
8	30	80	55.0	29.0	39.0	34.0
9	64	80	72.0	28.0	36.0	32.0
10	48	79	63.5	29.0	38.0	33.5
11	28	78	53.0	29.0	41.0	35.0
12	37	79	58.0	29.0	39.0	34.0
13	60	78	69.0	30.0	38.0	34.0
14	62	78	70.0	29.0	38.0	33.5
15	62	78	70.0	29.0	38.0	33.5
16	61	78	69.5	29.0	35.0	32.0
17	60	78	69.0	30.0	35.0	32.5
18	64	79	71.5	29.0	35.0	32.0
19	62	78	70.0	30.0	35.0	32.5
20	60	79	69.5	30.0	37.0	33.5
21	62	79	70.5	28.0	36.0	32.0
22	60	79	69.5	28.0	34.0	31.0
23	29	58	43.5	27.0	35.0	31.0
24	61	78	69.5	28.0	35.0	31.5
25	63	78	70.5	28.0	35.0	31.5
26	63	78	70.5	28.0	35.0	31.5
27	64	80	72.0	28.0	34.0	31.0
28	60	80	70.0	25.0	34.0	29.5
29	60	79	69.5	25.0	35.0	30.0
30	59	79	69.0	26.0	34.0	30.0
31	37	79	58.0	26.0	38.0	32.0

September

ste	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	41	79	60.0	26.0	39.0	32.5
2	38	79	58.5	22.0	36.0	29.0
3	36	80	58.0	21.0	38.0	29.5
4	14	80	47.0	21.0	40.0	30.5
5	26	80	53.0	25.0	38.0	31.5
6	40	79	59.5	26.0	38.0	32.0
7	31	80	55.5	26.0	36.0	31.0
8	56	79	67.5	26.0	36.0	31.0
9	40	79	59.5	26.0	38.0	32.0
10	51	79	65.0	25.0	37.0	31.0
11	61	79	70.0	26.0	35.0	30.5
12	60	79	69.5	26.0	35.0	30.5
13	59	79	69.0	28.0	34.0	31.0
14	64	79	71.5	27.0	34.0	30.5
15	64	78	71.0	27.0	35.0	31.0
16	65	78	71.5	28.0	35.0	31.5
17	65	80	72.5	27.0	36.0	31.5
18	64	80	72.0	26.0	35.0	30.5
19	63	80	71.5	25.0	34.0	29.5
20	64	79	71.5	25.0	35.0	30.0
21	64	79	71.5	26.0	34.0	30.0
22	62	78	70.0	26.0	34.0	30.0
23	60	78	69.0	25.0	34.0	29.5
24	60	80	70.0	24.0	34.0	29.0
25	60	80	70.0	22.0	34.0	28.0
26	48	79	63.5	22.0	34.0	28.0
27	52	77	64.5	23.0	36.0	29.5
28	46	80	63.0	21.0	38.0	29.5
29	36	80	58.0	20.0	39.0	29.5
30	41	80	60.5	22.0	37.0	29.5

October

Date	Rhmin	Rhmax	Rhave	Tmin	Tmax	T.ave.
1	50	80	65.0	24.0	37.0	30.5
2	55	79	67.0	25.0	35.0	30.0
3	55	78	66.5	22.0	35.0	28.5
4	32	71	51.5	21.0	34.0	27.5
5	6	66	36.0	18.0	36.0	27.0
6	30	78	54.0	18.0	37.0	27.5
7	54	80	67.0	19.0	34.0	26.5
8	60	80	70.0	23.0	34.0	28.5
9	58	79	68.5	23.0	34.0	28.5
10	42	80	61.0	20.0	34.0	27.0
11	50	79	64.5	19.0	34.0	0.0
12	48	80	64.0	20.0	34.0	27.0
13	56	80	68.0	20.0	34.0	27.0
14	58	80	69.0	21.0	34.0	27.5
15	58	80	69.0	21.0	34.0	27.5
16	43	80	61.5	20.0	34.0	27.0
17	10	79	44.5	20.0	39.0	29.5
18	24	79	51.5	20.0	38.0	29.0
19	22	79	50.5	20.0	36.0	28.0
20	28	78	53.0	20.0	34.0	27.0
21	22	80	51.0	18.0	36.0	27.0
22	22	80	51.0	13.0	34.0	23.5
23	24	82	53.0	13.0	33.0	23.0
24	7	75	41.0	10.0	34.0	22.0
25	10	80	45.0	10.0	35.0	22.5
26	22	78	50.0	12.0	35.0	23.5
27	22	81	51.5	14.0	34.0	24.0
28	55	80	67.5	16.0	33.0	24.5
29	62	80	71.0	19.0	31.0	25.0
30	50	80	65.0	17.0	33.0	25.0
31	40.0	80.0	60.0	16.0	34.0	25.0

Experiments ended

Appendix 2: Samples of statistical calculations (software: Costat)

```
GLM ANOVA PROCEDURE

BARTLETT'S TEST OF HOMOGENEITY OF VARIANCES
11.04.1998    5:06 pm
Using: C:\COHORT3\200DT96\TTWTNOX.DT
Variable: col120
Factors:
 1: poll          with      3 treatments
 2: tree          with      3 treatments

Warning: Groups with s2<=0 ignored (e.g. 3)
X2 = 10.508248311      df = Number of means - 1 = 6
P  = 0.1048172 ns


GLM ANOVA
11.04.1998    5:06 pm
Using: C:\COHORT3\200DT96\TTWTNOX.DT
.AOV Filename: 2WCR      - 2 Way Completely Randomized
  Variable: col120
  1st Factor: poll
  2nd Factor: tree
0 rows of data with missing values removed.
18 rows remain.
```

Source	df	Type III SS	MS	F	P
Main Effects					
poll	2	1268.207778	634.10389	4.9068066	.0362 *
tree	2	207.9744444	103.98722	0.8046713	.4770 ns
Interaction					
poll * tree	4	199.9888889	49.997222	0.3868872	.8130 ns
Error	9	1163.065	129.22944<-		
Total	17	2839.236111			
Model	8	1676.171111	209.52139	1.6213131	.2431 ns

```
R^2 = SSmodel/SStotal = 0.59035988749
Root MSerror = sqrt(MSerror) = 11.3679129327
Mean Y = 18.3722222222
Coefficient of Variation = (Root MSerror) / abs(Y Mean) * 100% = 61.875547%


Least Significant Difference (LSD)

Factor: poll
Error mean square = Variance = 129.229444444
Degrees of freedom = 9
Significance level = 5%
LSD 0.05 = 14.8471427941
```

Rank	Trt#	Mean	n	Groups of not significantly different means
1	2	25.35	6	a
2	1	23.2	6	a
3	3	6.56666666667	6	b

```
Least Significant Difference (LSD)
Factor: tree
Error mean square = Variance = 129.229444444
Degrees of freedom = 9
Significance level = 5%

LSD 0.05 = 14.8471427941
```

Rank	Trt#	Mean	n	Groups of not significantly different means
1	3	21.7833333333	6	a
2	1	19.6	6	a
3	2	13.7333333333	6	a

```
CORRELATION
11.04.1998   5:27 pm
Using: C:\COHORT3\200DT96\RIPE.DT
For: 2 variables (ThT160,, %Bsr160r.all)
Broken down by: Main factors only
If:


X variable: ThT160
Y variable: %Bsr160r.all

          poll    tree     Rep       Corr (r)      S.E. of r     P(r=0)
-------------------------------------------------------------------------------
           all     all     all -0.4096772223 0.24380386929 0.1150543 ns        1
             1     all     all 0.28315709973 0.47953677046 0.5866158 ns
             2     all     all -0.9123858185  0.2363275398 0.0307188 *
             3     all     all -0.2752557638 0.55504782512 0.6540107 ns
           all       1     all -0.3875033801  0.5322409011 0.5192573 ns
           all       2     all -0.3714894375   0.536033456 0.5381213 ns
           all       3     all -0.7393031054 0.33668639649 0.0930855 ns


POLYNOMIAL REGRESSION
11.04.1998   5:28 pm
Using: C:\COHORT3\200DT96\RIPE.DT
Variables:
  x = ThT160
  y = %Bsr160r.all
Keep if #1=2
Regression equation:
y = 314.615708907
  + -0.1450574761*x^1

R^2 = 0.8324478818

Source                      SS       df            MS              F     P
-------------------------------------------------------------------------------
Regression       200.070523911        1 200.070523911 14.9048765969 .0307 *
  x^1            200.070523911        1 200.070523911 14.9048765969 .0307 *
Error            40.2694760893        3 13.4231586964
-------------------------------------------------------------------------------
Total                   240.34        4

     Variable      Coef.  Std Error  t(Coef=0)      P      +/-95% CL
-------------------------------------------------------------------------------
    Intercept  314.61571  60.300636  5.2174526  .0137 *    191.90354
          x^1  -0.145057   0.037573  -3.860683  .0307 *    0.1195741

degrees of freedom for two-tailed t tests = 3

              X      Y observed      Y expected        Residual
-------------------------------------------------------------------------------
           1568            83.8   87.1655863824   -3.3655863824
         1648.5            74.9   75.4884595564   -0.5884595564
         1616.5            77.5   80.1302987916   -2.6302987916
           1540            94.5   91.2271957132   3.27280428678
         1648.5            78.8   75.4884595564   3.31154044361
```