CHAPTER 2

PHENO/PHYSIOLOGICAL MODELS

To enhance competitive fitness, perennial plant species typically display seasonal variation in the production of new leaves, flowers and fruit due to genetically imprinted growth patterns (van Schaik *et al.* 1993). In individual species, biotic influences have generally selected for temporally staggered, or clumped phenological activities. For instance, some species vulnerable to seed predation have developed strongly clumped fruiting sequences by storing carbohydrate reserves to produce larger crops at longer intervals (Janzen 1971); and leaves produced in synchronised flushes sustain less insect damage than those grown asynchronously (Lieberman and Lieberman 1984).

Environmental factors have a major impact on plant growth and dictate seasonal change, within genetically determined limits. For instance, many deciduous species of seasonally dry tropical forests drop all their leaves before the dry season and re-leaf about one month before the onset of rain, thereby minimising the impact of water stress (Frankie *et al* 1974; Wright and Cornejo, 1990). Irradiance and water stress have been identified as the most important environmental factors shaping the phenology of tropical woody plants in natural communities (van Schaik *et al*. 1993). However, with the domestication of fruiting species temperature has become equally important as production has been extended into more hostile environments (Sedgley and Grant 1983; Whiley and Winston 1987; Issarakraisila and Considine 1994).

These introductory remarks are perhaps an over-simplification of the complexity of plant responses and interactions in mixed communities, and ecologists are still grappling to gain a meaningful understanding of the phenological processes and the agents which control them. As horticulturists dealing with monoculture systems we are not concerned with the complexities of mixed communities. However, by recognising and appreciating the evolutionary factors which dictate the organisation of growth and seasonal change in natural plant communities we become better equipped to modify and adapt spatially and temporally separated phenological events for commercial gain.

The significance of phenological modelling to the horticulturist is that it provides a practical holistic approach to understanding plant growth and as such can be utilised as a powerful research and extension tool. It is particularly useful when dealing with the complexities of tree fruit research, where crop performance integrates carry-over effects from previous physiological activity. Yield management involves fundamentally resource (assimilate) allocation between the reproductive and vegetative structures of the tree. In subtropical and tropical evergreen fruit trees, it appears that direct source/sink relationships (spatial separation) are less important than tree phenology, which represents a temporal separation of potentially competing sinks (vegetative vs. reproductive) although exceptions occur. Under appropriate conditions, phenological events can be manipulated so that the impact of potentially competing sinks is lessened (Wolstenholme *et al.* 1990; Whiley *et al.* 1991). Hence the focus of this chapter is devoted to the concepts of phenological modelling and the understanding of significant physiological changes concurrent with growth and quiescence in avocado trees.

2. 1 AVOCADO PHENOLOGY

In this section the development of a phenology model for avocado is discussed, before reporting on more recent developments which are presented as a result of research for this thesis.

The earliest description of seasonal growth of avocado trees and its significance to crop management was by Chandler (1958) and Venning and Lincoln (1958). They observed that shoot growth occurred in cycles (commonly called flushes) separated by periods of relative quiescence. In California, avocado trees generally produced two major shoot flushes each season, in spring and in summer/autumn (Chandler 1958). Trees growing in the tropical regions of Florida and Cuba may have up to four distinct flushes each season of which the first is associated with flowering. With respect to the management of growth of these trees, Venning and Lincoln (1958) concluded that shaping of young trees via tip pruning of succulent shoots could be advantageous through increasing shoot complexity. However, pruning of mature trees was discouraged due to the unpredictable nature of the growth response.

Kotzé (1979) compiled a simple model for the annual growth of avocado (cv. Fuerte) to promote discussion and encourage research initiatives. Tentative suggestions were made with respect to irrigation and the timing of fertiliser applications. However, his model focused on the reproductive cycle from floral initiation through to fruit maturity, and failed to recognise the dynamics of seasonal contributions from competitive and complementary shoot and root growth. A more holistic approach to the dynamics of tree growth was presented by Wolstenholme (1981) who speculated on the interactions between root, shoot and fruit growth. The implications of physiological changes and their effect on the "rhythmic" growth patterns of trees were discussed and conclusions drawn on potential management strategies to improve and sustain avocado yields.

A further significant development in avocado phenology was a detailed account of above-ground growth sequences for 21 avocado cultivars growing in southern Florida (Davenport 1982). His observations on floral development, flowering and fruit set, and vegetative flushes were mostly reported in a single time dimension (seasonal change). Of particular interest were the reported relationships between tree phenology and some associated physiological changes, e.g. observations that leaf senescence was precipitated by flowering, which exposed new opportunities in relating tree physiology and phenology as a research tool. However, the dynamics of root growth were not studied.

The author began whole-tree phenology studies with avocados in the late 1970's and despite prototype models being used to assist with research approaches and as an extension tool, details were not published until 1988 (Fig. 2) (Whiley *et al*. 1988a). By this time the concept had wide recognition as an extension aid by the Queensland avocado industry, and interest in the application of the models was being shown by other avocado producing states in Australia and later internationally. The published models were based on data sets collected in a time sequence from orchard trees, superimposed with the interpretation of research results and drawn as a conceptualised framework to provide management strategies at farm level. The incorporation of root growth patterns, even though these were deduced from simple non-destructive "surface root mat" techniques, was of particular significance to the holistic understanding of rhythmic growth patterns.

The basic phenology model (Fig. 2) is two dimensional, integrating a time scale (*x*-axis) with the magnitude of response (y-axis). It illustrates the sequence of growth events over a full fruiting cycle and the relationship between the reproductive effort and root and shoot growth. Due to the plasticity of phenological responses across environments, the model is a useful tool for providing management strategies to growers in diverse regions. The timing of the key phenological events moves left or right along the *x*-axis in response to warmer and cooler climates dictated by changing latitude or altitude. As orchard management should be timed by growth event rather than by calendar month, strategies which target major phenological changes can be recommended irrespective of where the tree is growing. However, as a cautionary note, experience has shown that at outer environmental extremes (latitudes 12° &

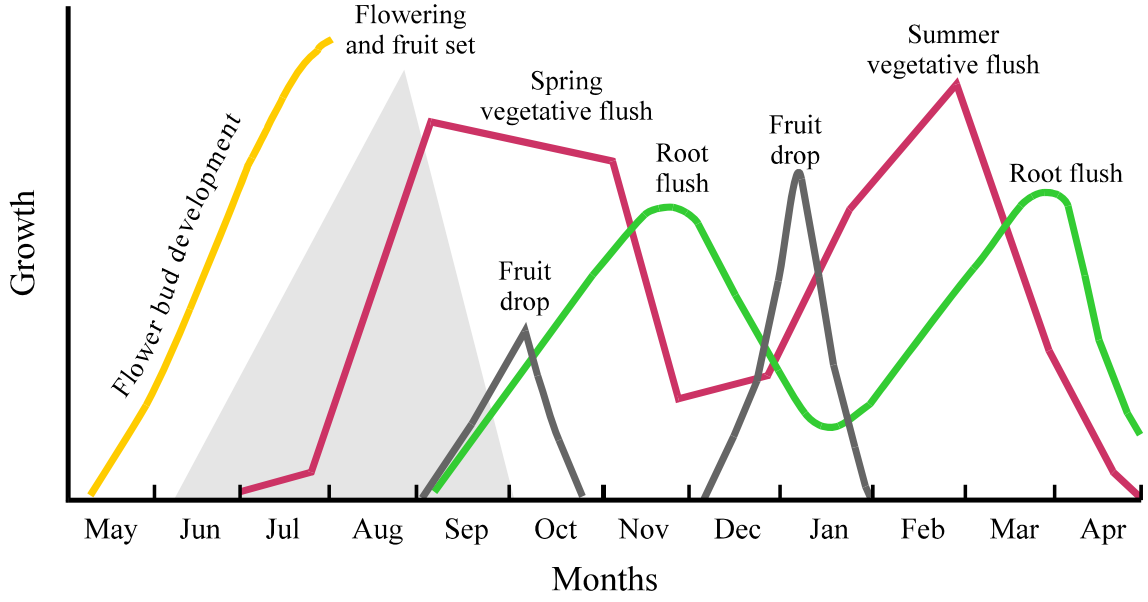

Fig. 2 Phenology model developed for cv. Fuerte avocado growing in a warm, sub-tropical climate at Nambour, S.E. Queensland. Redrawn from Whiley *et al*. (1988a).

33° S in Australia) plasticity may fail wherein there is a requirement to redefine the model. As researchers or managers, we are limited in the control we can exert on displacement along the *x*-axis once a cultivar has been selected for a given environment.

While there is undoubtedly an interaction with prevailing environmental conditions, it is the magnitude of each growth event which can be manipulated through management strategies to have the greatest impact on tree performance. It is largely in this area that horticultural research

research has been focused, defining water, nutritional and crop protection requirements and the time sequence in which they should be applied in relation to phenological events.

2. 2 INTEGRATION OF PHYSIOLOGY WITH PHENOLOGY MODELS

2. 2. 1 Introduction

The previous section has reviewed the development of phenological modelling for avocado and the implications for its use in research and extension programs. However, the model of Whiley *et al*. (1988a) was qualitative and based solely on growth measurements, and as a research tool there were limitations in the interpretation of relationships between phenological events which could only be improved by more detailed physiological knowledge. My objectives with the research reported herein were (i) to re-examine root growth with respect to whole tree phenology; and (ii) to study seasonal changes in net CO_2 assimilation (*A*), leaf nitrogen and chlorophyll concentrations and starch levels, with a view to providing further information on physiological limitations during critical phenological events.

2. 2. 2 Materials and Methods

A commercial ‘Hass’ avocado orchard at Maleny in S.E. Queensland (latitude 26.5^{o}S, altitude 520 m) was chosen for the phenological/physiological study. The climate is cool, mesic subtropical with a high mean annual rainfall of 2000 mm in a summer/wet: winter/dry pattern. The soils of the area are of basaltic origin and are described as krasnozems. Physically they are well drained clay loams (ca. 60% clay fraction) to between 10 to 16 m deep and show no obvious physical limitations to root growth.

Roots were observed from a rhizotron facility especially constructed for the study. It consisted of 10 wooden boxes 1.0 x 1.2 x 2.1 m, each with a 10 mm thick 690 x 845 mm clear plexiglass (poymethyl methacrylate) panel built into the two opposite 1.2 m sides: 20 panels in total (Fig. 3). Disadvantages of this approach to root study have been enumerated by Rogers (1934) and were ameliorated as far as practicable by replication of the viewing panels, planting trees after the facility had been installed and excluding light from the viewing panels. Root measurements obtained with this technique on fruit trees have compared favourably with those obtained by other methods, e.g. tracer uptake (Atkinson 1974) and excavation or water depletion (Atkinson 1978). This is believed to be the first detailed study of this nature and scope and duration (4½ yr) on avocado trees anywhere in the world, incorporating non-fruiting and fruiting trees, and light and heavy cropping.

Holes slightly larger than the boxes were excavated and the rhizotrons installed in October 1988. They were aligned in one row, 4 m apart with the plexiglass panels in each box facing outwards and the top of each window at soil level. To ensure good contact with the plexiglass,

Fig. 3 Installation of rhizotron boxes constructed for root studies on avocado trees, Maleny, S.E. Queensland, Australia.

the top-soil was carefully packed against each of the viewing panels to the same dry bulk density as the surrounding soil (1.1 t m^{-3}). Once in position the rhizotrons were fitted with solid lids with an upper silver surface to block light and reflect heat. Apart from removal for access to the panels each month (ca. 30-45 mins. to collect data) the covers remained closed for the duration of the study. After installation, the soil 3 m either side of the rhizotrons was deep-ripped to 1 m, and planting sites adjacent to each window prepared by incorporating 9 l of chicken manure, 250 g of superphosphate (9% P) and 500 g of dolomite m^{-2} surface area.

During 1988 'Velvick', a Guatemalan race seedling selected in Queensland; 'G755A', a *Persea schiedeana x P. americana* hybrid rootstock, and 'Duke 7', a Mexican race selection both from California (Coffey *et* al. 1988) were clonally propagated using the nurse-seedling technique (Frolich and Platt 1971-72, modified by Brokaw), and were grafted to 'Hass' scions. A number of seedling 'Velvick' rootstocks were also grafted to 'Hass' scions. All propagation material used in this study had been previously tested and certified free of Sunblotch viroid, a potentially serious disease of avocado (da Graca 1985). In March 1989, five 'Hass' trees on each of the four rootstocks were randomly planted in central positions 1 m from the windows. To control weed growth and assist in reducing fluctuations in soil matric potential (ψ_s), trees were mulched with barley straw spread 1 m from the trunk and to a depth of 100 mm, within a week of planting. This mulch was maintained for three years after planting by which time tree canopies provided sufficient ground shade and became self-mulching through the accumulation of leaf litter.

At the time of planting, under-tree mini-sprinklers (10 l hr^{-1}) were installed at each site to supplement natural rainfall. Soil matric potential was monitored 0.5 m from rhizotron walls using permanently installed tensiometers at 30 and 75 cm depth. During dry periods tensiometers were checked at weekly intervals and irrigation given to maintain $\psi_s \leq 40$ kPa at 30 cm and ≤ 50 kPa at 75 cm depth. Trees were fertilised according to the schedule for tree age developed for avocados growing in S.E. Queensland (Banks 1992). The exception to this program was the additional 4 g m^{-2} of canopy of Solubor (22% elemental B) soil-applied in spring and summer each year due to known boron deficiencies and the high buffering capacity of the soil at this site (A.W. Whiley, unpublished data).

Root measurements were made only of the white, unsuberised “feeder” roots. Data were collected at monthly intervals by tracing the outline of roots visible at the soil-panel interface onto transparent sheets of acetate with a black indelible pen. Only those portions of roots that were visible at the interface were recorded. No distinction was made between roots of different diameters. Only some of the white “feeder” roots became suberised (browning) after which they were no longer measured. The information on the acetate sheets was digitised by scanning to an electronic file using a Hewlett Packard ScanJet IIc. Root lengths were determined by computerised image analysis (Sci-Scan Image Analysis System, Delta T, UK). This method gave a total length (m) of visible white root at the soil-panel interface (0.58 m^2 vertical window area) each month.

Beginning in 1991 trunk girth measurements were taken during July of each year in positions demarcated by white acrylic paint marks, above and below the graft union. In 1992, the first year of heavy cropping, the diameter and height of the trees were measured and the canopy volume calculated using the models for a half sphere and a cylinder. This was the only year that canopy measurements were taken as trees began to crowd in 1993 and side canopies had to be pruned.

Reproductive and vegetative phenology data were collected for four seasons at monthly intervals, or more frequently when necessary, using the system of Whiley *et al*. (1988a). Floral bud development was ranked on a 0 to 10 scale where 0 = no visible development and 10 = opening of the first flower. Flowering was judged by recording the first and last dates of anthesis and estimating the time that 50% of the flowers had opened. All qualitative estimates were made independently by two people and the mean of the scores used for fitting the data. Fruit drop in spring was estimated by counting fruit on three tagged shoots on each of five trees at weekly intervals from the end of anthesis until numbers were relatively stable. The weekly data were calculated as a percentage of the total fruit that dropped from the tagged shoots. In summer, fallen fruit under each tree were counted and removed at weekly intervals. These data were calculated as a percentage of the total number of fruit on the tree at harvest, reflecting the crop loss after a substantial growth investment (30-40% of full size). At the completion of anthesis three indeterminate and three determinate inflorescences on each of five trees were tagged and individual fruit lengths on each shoot measured with electronic callipers at weekly

at weekly intervals for the first five months after fruit set and then monthly until harvest. When harvesting the two “on” crops (1992 & 1994), fruit which developed on either indeterminate or determinate shoots were recorded separately.

For nitrogen and starch analysis, the most recently matured summer-flush leaves were selected at monthly intervals from May until December 1992. Thirty leaves were randomly collected from each tree and equally divided into sub-samples; one for nitrogen and the other for starch analysis. Leaves for nitrogen analysis were washed in a solution of mild detergent (1 ml l^{-1}) and acetic acid (0.6 ml l^{-1}), rinsed in distilled water, dried at 52^{o}C for three days, milled and re-dried at 105^{o}C immediately prior to determinations. Nitrogen was measured using a Kjeldahl digest of sulphuric acid, sodium sulphate and selenium catalyst (M^{c}Kenzie and Wallace 1954). The digestate was diluted prior to automatic colorimetric analysis using the indophenol reaction with salicylate and sodium dichloroisocyanurate (Berthelot 1959).

Wood samples were collected for starch analysis from the large roots radiating from the crown of the rootstock and from the scion region of the trunk after June 1992, when it was judged that trees were large enough to support a monthly program of this nature. For each organ, samples were obtained from five sites around the tree by first removing a plug of bark and then drilling 40 mm into the wood with a 9 mm diameter bit. The drilled shavings from each hole were bulked for analysis.

Starch samples were placed in a cool, insulated box for transport back to the laboratory and within 3 hrs of collection, were transferred to a convection oven at 60^{o}C and dried to constant mass. Dried samples were ground at 100 mesh in a Udy Mill (Udy Corporation, USA) and stored in an airtight container. Starch was determined by a two stage enzymatic hydrolysis of the starch to glucose and the concentration measured colorimetrically using a coupled glucose oxidase/peroxidase/chromogen system as described by Rasmussen and Henry (1990).

Photo-assimilation studies were carried out from March to December 1992 on ‘Hass’ trees growing in the rhizotron and grafted to cloned ‘Velvick’ rootstocks. When summer-flush shoots were nearing maturity, five fully expanded sun-exposed leaves were tagged on the northern sides of trees. At the time of selection the leaves were ca. 40 days old and fully

expanded, (Chapter 3) and to lessen "sink" effects were at least 0.5 m from the nearest fruit. Net CO_2 assimilation (*A*) was measured at monthly intervals with a LICOR LI-6200 portable photosynthesis meter configured as a closed system (LICOR, Nebraska, USA) and using a LI-6000-11, 1 l chamber. All measurements of *A* were made at or above PPFs of 1200 µmol quanta m^{-2} s^{-1} and between 0830 to 1030 h, a low stress time of day (Whiley *et al*. 1988b). Photosynthetic rates were derived from LI-6200 Software Version 2.00.

Chlorophyll concentrations were determined from five leaves on the northern side of the same trees used for photo-assimilation studies. Two discs totalling 1.0 cm^2 were sampled from either side of the midrib of each leaf and the discs pooled for each tree. Chlorophyll was extracted with 85% acetone from the discs kept in darkness at 25^oC for 48 h. Measurements were made spectrophotometrically as described by Proctor (1981).

An automatic weather station (Monitor Sensors, Caboolture, AUST.) was positioned at the site to record rainfall and air and soil temperatures. The soil temperature sensor was installed at 450 mm below the surface in a position equi-distant between the top and bottom of the recording field. Data presented in the figures are the means ± SEs of pooled values from five trees.

2. 2. 3 Results and Discussion

Some trees on 'Duke 7' and 'G755A' rootstocks died in the second and third years of the project (Verticillium wilt). Therefore only data for trees propagated on cloned and seedling 'Velvick' rootstocks are presented.

Rootstocks and Root Phenology

Twenty-seven months after planting an over-growth of the scion, expressed by a scion/rootstock girth ratio of > 1.0, was detected in trees grafted to cloned 'Velvick' rootstocks (Table 1). The over-growth in this scion/rootstock combination persisted for the duration of the study indicating mild incompatibility. In contrast, trees grafted to seedling 'Velvick' were near normal (slightly favouring the rootstock) with respect to scion/rootstock relationships. The compatibility of graft unions between the same species is ultimately a function of biochemical events (Leakey 1985). In *Pinus contorta*, scion overgrowth has been attributed to translocation incompatibility wherein a degree of phloem degeneration and necrosis is evident (Copes 1975). Compatibility of this type does not necessarily indicate that the combination is without merit and indeed it may be exploited for horticultural gain.

The first roots were visible at the soil-panel interface in some boxes by March 1990, but due to insufficient numbers recording did not begin until July 1990 when all windows were colonised. Note that where time is plotted as the abscissa in Figs. 4 & 5 it refers to time elapsed since 1 June 1990 (June is early winter in the southern hemisphere); thus each calendar season refers to a three month period, e.g. spring is from September through November.

Table 1 Scion/rootstock girth ratios of cv. Hass trees grafted to cloned and seedling 'Velvick' rootstocks. The ratios were calculated from girth measurements taken above and below the graft union. Data are mean values of five trees ± standard errors.

Rootstock	Scion/rootstock ratio			
	1991	1992	1993	1994
Cloned 'Velvick'	1.15 ±0.04	1.21 ± 0.04	1.20 ± 0.05	1.17 ± 0.01
Seedling 'Velvick'	0.94 ± 0.02	0.97 ± 0.01	0.98 ± 0.01	1.00 ± 0.01

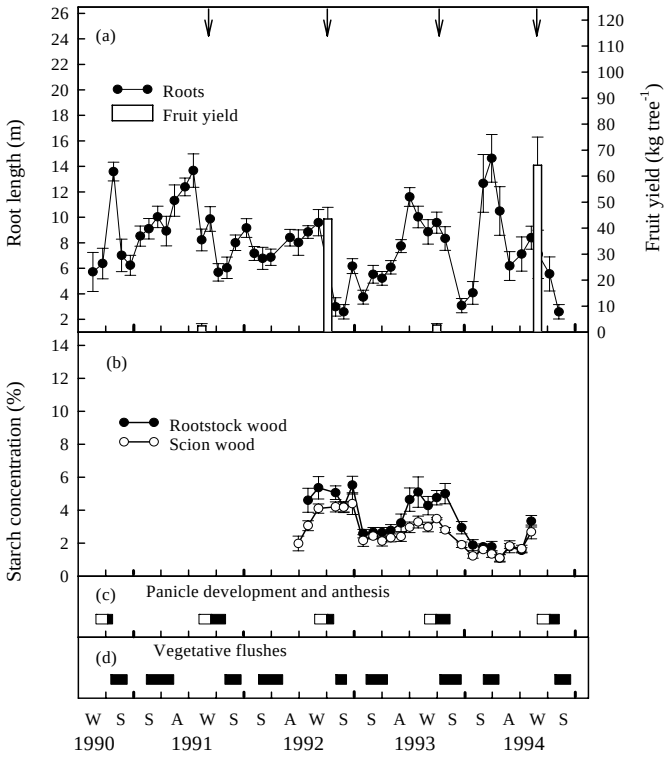

Fig. 4 Root growth and starch cycling over a 4½ yr period in cv. Hass grafted to cloned 'Velvick' rootstock as they relate to above ground tree phenology and yield where: (a) is seasonal changes in root length per 0.58 m^2 vertical window area, and annual fruit yield (arrows indicate harvest times); (b) is seasonal changes in starch concentration of the rootstock and scion portions of the tree; (c) are periods of inflorescence development represented by the open bars, and anthesis represented by the closed bars; and (d) are periods of shoot growth. Root length, yield and starch data are mean values of five trees ± vertical SE bars.

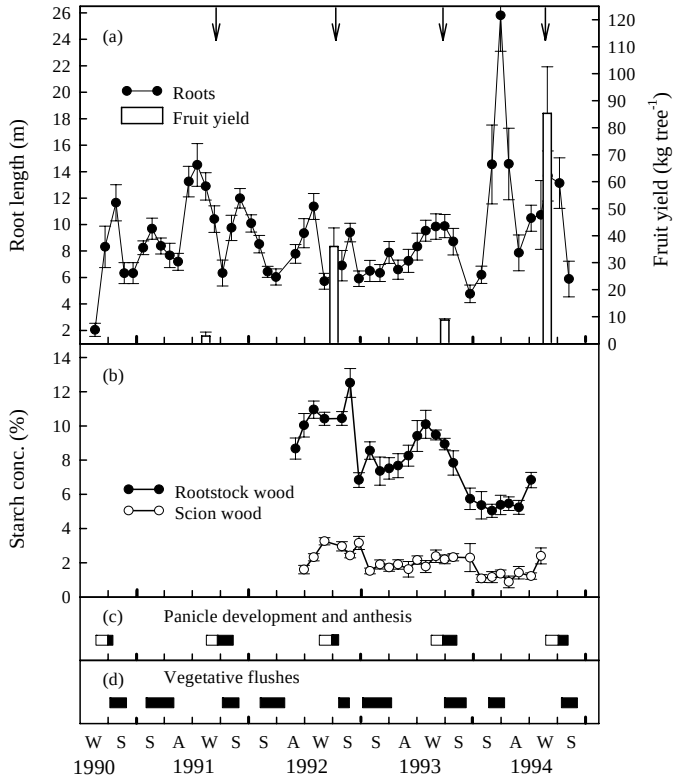

Fig. 5 Root growth and starch cycling over a 4½ period in cv. Hass grafted to seedling 'Velvick' rootstock as they relate to above ground tree phenology and yield where: (a) is seasonal changes in root length per 0.58 m^2 vertical window area, and annual fruit yield (arrows indicate harvest time); (b) is seasonal changes in starch concentration of the rootstock and scion portions of the tree; (c) are periods of inflorescence development represented by the open bars, and anthesis represented by the closed bars; and (d) are periods of shoot growth. Root length, yield and starch data are mean values of five trees ± vertical SE bars.

There were strong seasonal variations in total measured root length of both rootstocks (Figs. 4 & 5). These appeared independent of soil temperatures at 450 mm depth which varied by 7.5^{o}C between summer (23.5^{o}C) and winter (16.0^{o}C). Typically, two peaks of root growth occurred over a one year period; the first of the new season in spring and generally concomitant with spring flush, and the second beginning in late summer and peaking in winter immediately prior to anthesis (Figs. 4 & 5). The pattern was more pronounced in trees grafted to seedling 'Velvick' rootstocks and was not always apparent in trees growing on the cloned material.

Similar bimodal periodicity for avocado root growth has been previously described by Whiley *et al*. (1988a) and Ploetz *et al*. (1992), although in both cases the extension of the second growth phase through winter to anthesis was not indicated. It is likely that roots observed in the surface mat technique used by Whiley *et al.* (1988a) suffered desiccation during the dry winter months giving the impression of growth cessation, while the young trees used by Ploetz *et al*. (1992) may not have developed root cycles typical of mature fruiting trees. The two-peak annual cycle has similarities with deciduous fruit crops (Head 1967; Rogers and Head 1969), however the major difference is extension of the second growth period of avocado roots into winter in this cool, mesic subtropical environment. With avocado major points of interest are alternation between shoot and root flush peaks; the prolonged winter root growth in deeper, warmer and moister soil zones; and the pronounced reduction in feeder root growth (die-off of feeder roots) during flowering and fruit set.

The bimodal periodicity observed in this study is likely due to competition between shoots and roots for photo-assimilates in this complex, much branched tree. In photosynthate translocation studies with avocado (Chapter 5) it was found that when leaves were exposed to ^{14}C during active shoot growth 43% was recovered in the new shoots while only 5% was recovered from roots. In contrast, when leaves were exposed during a period of shoot quiescence, 32% of the ^{14}C was recovered from the roots and only 5% from the most recent shoot flush (Whiley and Schaffer 1993).

The greatest root lengths were recorded during the first two years of the study when they reached ca. 14 m per 0.58 m^2 of window observation area for a month, and again in the fifth year when root length of the seedling 'Velvick' rootstock reached 25.8 m per 0.58 m^2 of window observation area. At other times root length was lower with maximum recordings from ca. 9 to 11 m for any one observation time. Root lengths during the first two years of the study may be due to either greater root activity at the peripheral zone of the tree's canopy, which was approximately aligned with the side of the rhizotrons 18 months after planting; or proportionally greater root growth in non-fruiting trees. The latter is supported by the root patterns determined for 'Hass' trees grafted to cloned 'Velvick' where during the 1991/92 season, trees carried ca. 44 kg of fruit and maximum root lengths measured were ca. 9 m (Fig. 4). In contrast, the 1992/93 crop was small (ca. 3 kg $tree^{-1}$) and the maximum root length at the

soil-panel interface reached 11.6 m. Differences were not as clear with ‘Hass’ trees grafted to seedling ‘Velvick’ rootstocks though root growth on average during the fruiting years was greater than those trees on cloned rootstocks; 8.0 ± 0.3 m compared with 7.1 ± 0.4 m respectively (Figs. 4 & 5). Trees on both rootstocks showed strong root growth following spring shoot maturation in 1993 despite trees carrying a heavy crop. This is likely due to the vigorous shoot growth which was observed following anthesis. However, root growth during the late summer and winter was markedly suppressed, which is probably related to fruit lipid accumulation (Kaiser and Wolstenholme 1994) and growth of fruit which occurs during this period.

The lower impact of fruiting on seedling rootstock may be due to the greater vigour of these trees. The effect of cropping on root growth of trees has been reported on many occasions and the outcomes have generally been consistent. Head (1969) found reduced periodicity and magnitude of new root growth in fruiting apple trees with the major summer growth peak eliminated in some years. Similarly, Ryhakov and Dzavakjanc (1967) and Dzhavakyants (1971) reported that cropping in apples reduced the number of root growth peaks from two in vegetative trees to one per season. Others finding adverse effects of cropping on root growth include Maggs (1963), Avery (1970), Cannell (1971) and Atkinson (1977). This is not surprising when considered in the context of the “priority sinks” philosophy. Here developing seeds (fruit) have a large “sink strength” or “mobilising ability” to attract photo-assimilates and are usually more competitive than other plant organs, of which roots are generally acknowledged as among the weakest sinks of the plant (Cannell 1971; Chalmers and van den Ende 1975; Lenz 1979). For example, the proportion of the annual increment of dry mass allocated to the root system decreased from 20% in young peaches, to 1% in fruiting peach trees (Chalmers and van den Ende 1975).

There were seasonal changes in the starch content of major roots and the scion trunks of both scion/rootstock combinations (Figs 4 & 5). Accumulation occurred during the autumn and winter when shoots were quiescent with concentrations falling rapidly during or just after anthesis (see Chapter 6 for more information). However, it is very noticeable that the starch concentration in the large woody roots of the seedling 'Velvick' was always about double that in the cloned 'Velvick' rootstock. There was also a direct relationship between the root starch concentration of seedling 'Velvick' roots and root length (Fig. 6). This relationship would be expected as more photo-assimilates are translocated to the roots during relatively quiescent periods in the aerial portions of tree, thereby increasing the growth of roots, and remobilised to stronger aerial sinks at critical stages of phenological development, e.g. flowering, fruit set and seed growth.

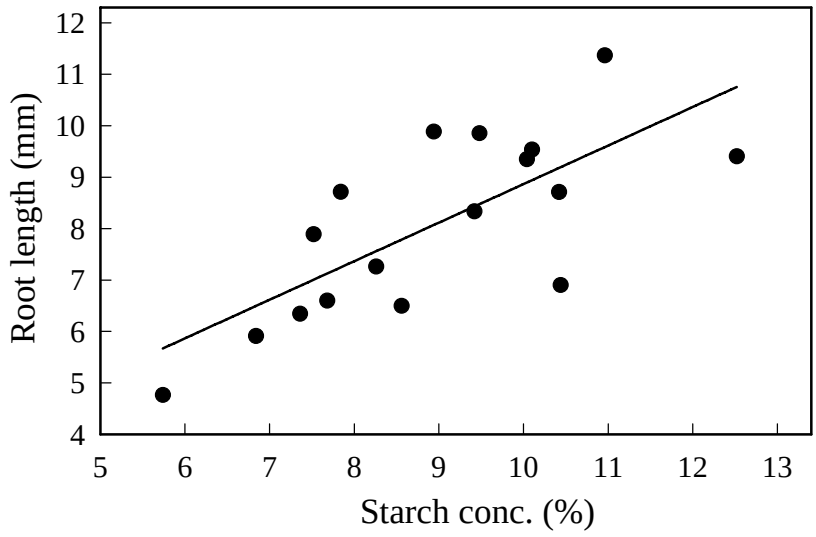

Fig. 6 Relationship between starch concentration in the rootstock and root length measured at the soil-panel interface. The regression is represented by the equation $y = 1.37 + 0.75x$, $r^2 = 0.55$*.

Differences in starch concentrations between the two rootstocks may be explained by mild incompatibility between the cloned 'Velvick' rootstock and the 'Hass' scion (Table 1). It is possible that the movement of translocate to roots was impeded due to phloem degeneration (Copes 1975) resulting in less root growth, particularly when trees had a substantial crop load,

e.g. 1992 (Figs. 4 & 5). The outcome of less starch moving to the roots was a higher concentration maintained in the scion which was ca. 30% more than the concentrations measured in the 'Hass' scions on the seedling rootstocks.

The mild incompatibility and reduced vigour of the cloned 'Velvick' root system is most likely responsible for the smaller stature of these trees when compared with those on seedling 'Velvick' rootstock. When canopy measurements were taken in September 1992, ca. 30 months after planting, 'Hass' trees grafted to clonal or seedling 'Velvick' rootstocks had canopy volumes of 12.44 ± 1.38 m^3 and 16.98 ± 1.22 m^3, respectively. When the 1992 yield performance of trees on the two rootstocks was compared on a canopy volume basis, 'Hass' grafted to clonal 'Velvick' rootstocks produced 3.57 ± 0.31 kg m^{-3} of fruit which was significantly greater than the 2.12 ± 0.42 kg m^{-3} produced by trees grafted to seedling 'Velvick' rootstocks. These data are supported by a long-term rootstock experiment on the same site where 'Hass' grafted to clonal 'Velvick' rootstocks have continued to have the highest production efficiency on a canopy volume basis when compared with clonal 'Duke 7' and seedling 'Velvick' rootstocks (A.W. Whiley, unpublished data). In this case, mild incompatibility at the scion/rootstock interface and the resultant reduced tree vigour has been an effective horticultural tool in the repartitioning of assimilates to give higher fruit yields.

The central axis or primary inflorescence of avocado is usually terminated by a vegetative bud which at the finish of anthesis grows out into a new shoot (Chandler 1958). However, in some cases the inflorescence is terminated by a panicle sub-unit. The two types are known as either indeterminate or determinate compound inflorescences, respectively (Thorp *et al*. 1994). Compared to other major Mexican/Guatemalan race cultivars, 'Hass' produces a greater proportion of determinate inflorescences which in years of heavy cropping can become a problem due to exposed fruit becoming sunburnt. In their study Thorp *et al.* (1994) reported that in 37% of the floral shoots of 'Hass' the terminal meristem remained reproductive and gave rise to determinate compound inflorescences.

In this study fruit on both indeterminate and determinate inflorescences grew rapidly in length for the first 150 days after fruit set and thereafter the growth rate substantially diminished (Fig. 7). This latter stage of diminished growth coincides with rapid lipid accumulation in the fruit (Kaiser and Wolstenholme 1994). At 40 days after set, determinate fruit were already larger than those set on indeterminate inflorescences and during the first 150 days they maintained a higher growth rate (slope of curves). This growth advantage was still apparent at maturity where determinate fruit were ca. 18% longer than those set on indeterminate inflorescences.

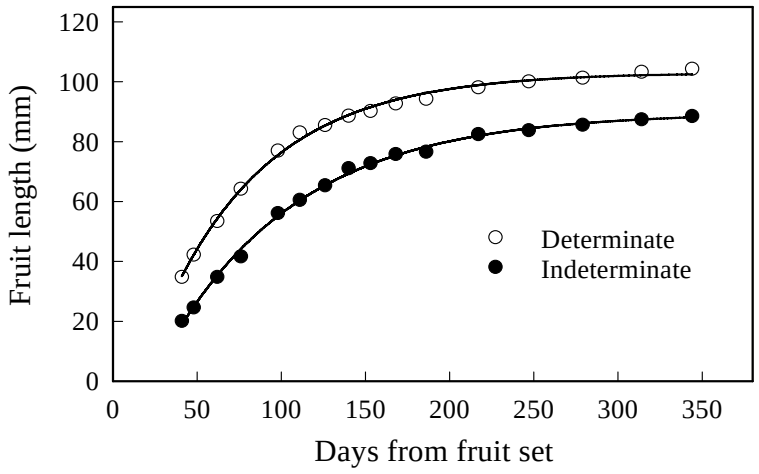

Fig. 7 The growth of cv. Hass fruit on indeterminate and determinate terminals from 40 days after fruit set through until maturity. Growth was determined by measuring the increase in fruit length. The regression for determinate fruit is represented by the equation $y = 103.05 - 130.23(0.984^x)$, $r^2 = 0.99$; and the regression for indeterminate fruit is represented by the equation $y = 89.67 - 118.62\ (0.988^x)$, $r^2 = 0.99$. The curves are significantly different in placement and shape as judged by *t* tests ($P < 0.001$). Data points are mean values of fruit from three terminals on each of five trees.

The growth advantage of fruit on determinate shoots is thought to be due to spatial separation from shoots which develop concurrently with fruit set on indeterminate inflorescences. Using mid-bloom foliar sprays of paclobutrazol to suppress ‘Hass’ spring shoot growth from

indeterminate inflorescences, Wolstenholme *et al*. (1990) reported increased fruit size when shoots matured. This resulted in larger fruit at maturity compared with fruit from the unsprayed control trees.

The yield data for 1992 and 1994 showed that the greatest percentage of fruit harvested from trees on either rootstock was from determinate shoots, > 80% for trees grafted to cloned 'Velvick' and > 60% for trees grafted to seedling 'Velvick' (Table 2). There were significant differences in the indeterminate/determinate yield ratios between rootstocks which was lowest for cloned 'Velvick' for the two years that data were collected.

Mechanisms for the production of determinate shoots have not been elucidated but the author

Table 2 Effect of rootstock on the ratio of indeterminate/determinate fruit on cv. Hass. The ratios were calculated from the 1992 and 1994 crops which were "on" years for these trees. Data are mean values from five trees ± standard errors; percentage determinate fruit are given in parenthesis.

Rootstocks	Indeterminate/determinate fruit ratio	
	1992	1994
Cloned 'Velvick'	0.22 ± 0.06 (83.4)	0.17 ± 0.01 (86.0)
Seedling 'Velvick'	0.91 ± 0.33 (60.8)	0.48 ± 0.05 (67.8)

has observed that trees infected with *Phytophthora cinnamomi* Rands, which causes Phytophthora root rot, usually have a higher percentage of determinate inflorescences, suggesting that root damage or stress (lack of vigour) is a primary cause. In this study trees grafted to clonal 'Velvick' rootstocks carried ca. 20% more of their crop on determinate inflorescences than trees on seedling rootstocks (Table 2). Of the physiological variables measured, the major difference between trees was in root starch concentrations. There is little doubt that roots play an important role in the regulation of flowering and promotion of bud

development through the timely supply of growth regulators (Jackson 1993). It is suggested that the lower assimilate concentration in cloned compared with seedling 'Velvick' roots may have resulted in a reduced capacity of cloned roots to stimulate terminal vegetative buds in the inflorescences thereby leading to a greater proportion of determinate inflorescences. This mechanism would have ecological significance, in that trees in a cropping cycle with depleted reserves would enhance their ability to set and carry more fruit by reducing competition with indeterminate flowering shoots.

Pheno/physiological Models

Leaf starch concentrations of mature summer leaves increased rapidly from March reaching peak concentration in June/July (winter), when there was a sharp decline which coincided with inflorescence development and anthesis (Fig. 8a). The level declined again in November during the onset of leaf senescence. The leaf nitrogen concentration remained relatively stable from April until July, a period of extended quiescence in the canopy of the tree (Fig. 8a). However, there was a sharp decline during the growth of inflorescences. Leaf N concentrations showed recovery during anthesis but declined once more during fruit set and spring shoot growth. The leaf concentration flux of starch and nitrogen showed significant changes which could be related to critical stages of tree phenology. The fall in concentration of both products coincided with inflorescence development and it is likely that remobilisation occurred to support the proximal reproductive sink. The decline in leaf N concomitant with fruit set and shoot growth has similarly been reported in citrus where it was concluded that young vegetative flushes draw nitrogen from reserves in old leaves (Erner 1988).

Net CO_2 assimilation (*A*) of sunlit summer-flush leaves reached its highest rate in April (18.3 μmol CO_2 m^{-2} s^{-1}) and then slowly declined through to May (Fig. 8b). By June there was a rapid decline in *A* which remained at ca. 10.2 μmol CO_2 m^{-2} s^{-1} through to October. There was a small recovery in *A* by November followed by a rapid decline as leaves senesced. Except for a lag phase going into winter the pattern of chlorophyll concentrations in leaves substantially mirrored *A*. Levels increased from March to April but then remained stable through to July. There was a sharp decrease in August and concentrations remained low until October when

there was a rapid increase through to November, then subsequently a fall as leaves senesced (Fig. 8b).

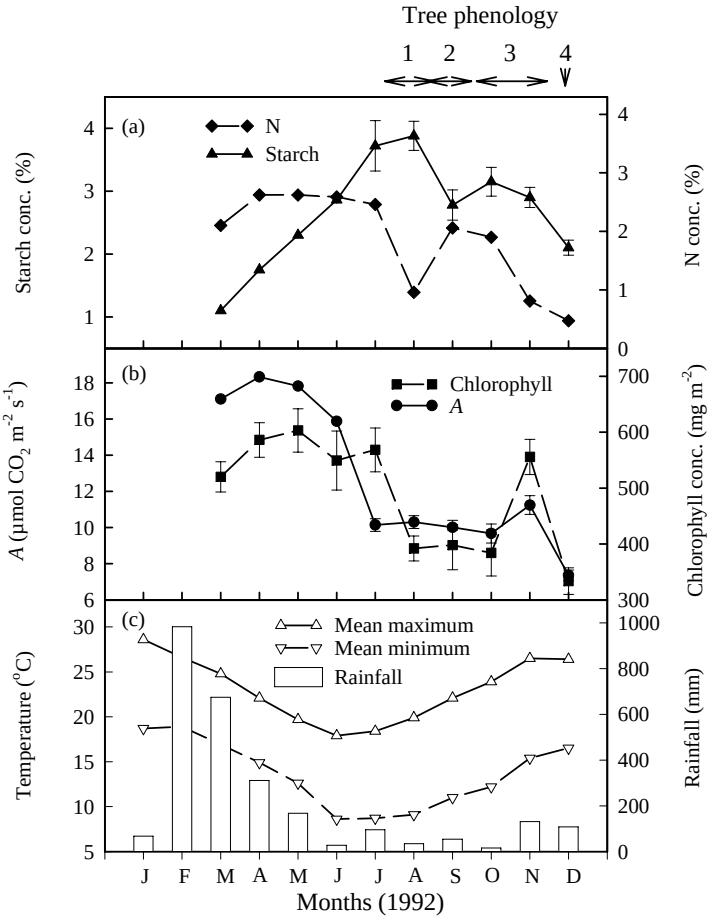

Fig. 8 Seasonal changes in nitrogen, starch and chlorophyll concentrations and net CO_2 assimilation (*A*) of summer grown leaves of cv. Hass in relation to phenology (1 = inflorescence development; 2 = anthesis; 3 = fruit set and shoot growth; 4 = leaf senescence) and temperature where: (a) are mean leaf nitrogen and starch concentrations (n = 5); (b) is the total chlorophyll concentration and *A* (n = 3); and (c) are the mean monthly temperatures and the exceptionally high rainfall recorded at the experimental site. Data are mean values of five trees ± vertical SE bars which are obscured by symbols at some points.

The autumn decline in *A* can be attributed to at least three factors. There was an increase in vapour pressure deficits (VPD) over the months that measurements were taken rising from <

1.0 kPa to ≈ 2.4 kPa. VPDs are known to affect *A* in most crops due to reduced stomatal conductance (g_s) (Schultze 1986). Bower *et al.* (1978) indirectly related lower *A* in avocado to an increase in VPD, i.e. they showed an inverse relationship between g_s and VPD. Over the duration of this study taking measurements before 1030 h reduced variation in VPD but nevertheless some effect may have occurred.

An increase in leaf starch levels was concomitant with the initial decline in *A* which may be the effect of end product feedback-inhibition. Schaffer *et al*. (1987) concluded that accumulation of leaf starch in avocado resulted in the inhibition of *A*. However, the sharp drop in July is more likely due to an inhibition of photosystem II activity brought on by exposure to low temperature stress (Chapter 3) (Smillie and Hetherington 1983). Smillie *et al*. (1988) reported that many tropical species develop photo-inhibition damage once temperatures fall below 12^{o}C. In this case leaves had been exposed to mean minimum temperatures of < 10^{o}C for one month prior to measuring the low *A* values (Fig. 8c). The winter fall in chlorophyll concentration is also more likely to be linked to temperature than to declining N concentrations. The one month lag in relation to the decline in *A* is consistent with photo-oxidation of chlorophyll, which develops after longer exposure to cold temperatures and an excess of absorbed light beyond that utilised in photosynthesis (van Hasselt 1974; Demmig-Adams and Adams III 1992) (see Chapter 3). The partial recovery in both *A* and chlorophyll concentrations is consistent with the release from photo-inhibition conditions (Smillie *et al*. 1988) and did not occur until October when mean minimum temperatures rose above 12^{o}C. However, this was at a time when leaf N concentrations were rapidly declining thereby restricting the full potential of *A* recovery (DeJong 1982; Syvertsen 1984). Furthermore, it is believed that there is strong competition between reproductive and vegetative sinks at this time for available photo-assimilates, either current or from stored sources (Biran 1979; Wolstenholme *et al*. 1990). The horticultural implications of these results are further developed in Chapter 7 (section 7. 2) of this thesis.

The phenology model developed for ‘Hass’ at Maleny (Fig. 9) has similarities to the earlier

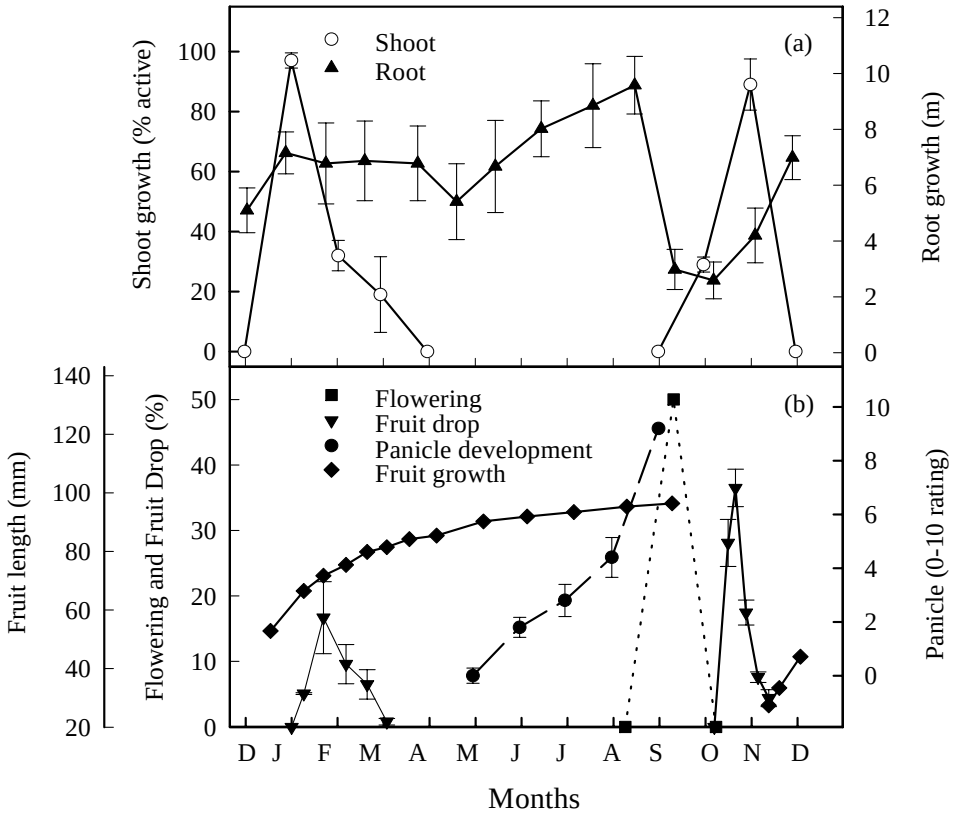

Fig. 9 Phenology of cv. Hass on cloned ‘Velvick’ rootstock growing at Maleny, S.E. Queensland where: (a) is the seasonal relationship between shoot and root growth; and (b) is the relationship between floral development and fruiting. Data points are mean values from five trees ± vertical SE bars which are obscured by symbols at some points.

schematic model proposed by Whiley *et al*. (1988a) for ‘Fuerte’ (Fig. 2). The main differences between the two models are firstly the delay of phenological events in relation to the time dimension, e.g. anthesis for ‘Fuerte’ was early June to late September; for ‘Hass’ from early August until early October; and secondly the extended root growth through winter culminating in a sharp decline concomitant with inflorescence development and anthesis. The shift in the time frame of growth events illustrates the plasticity of the phenological response which is driven by genotypic/environmental interactions. For instance, ‘Fuerte’ is an early maturing

cultivar and when studied was growing in a warm coastal environment compared with the later maturing ‘Hass’ growing in a cool, subtropical highland region. Modification by environmental factors may implement more significant changes to the model as shown by Kaiser and Wolstenholme (1994). In their studies with ‘Hass’ growing in the cool, mesic subtropical Natal midlands, one extended period of shoot growth was recorded over the spring and summer months in contrast to the bimodal periodicity reported for ‘Fuerte’ (Whiley *et al*. 1988a) and ‘Hass’ in this study (Fig. 9). Such changes require careful consideration of likely implications when research hypotheses or management strategies are being tested.

Differences in root growth patterns between the ‘Fuerte’ model (Whiley *et al.* 1988a) and ‘Hass’ (Fig. 9) can be explained by the different techniques used to collect the information. For ‘Hass’, studies were more quantitative and carried out from the surface to a depth of 820 mm thereby integrating results from a more representative zone of root activity than that used for ‘Fuerte’. The extended period of root growth during summer through to mid-winter and the starch dynamics of scion/rootstock interactions have tree performance and management implications worthy of further research. Some pertinent issues will be discussed in subsequent chapters of this thesis