SHOOT-ROOT ALLOMETRY AND GROWTH OF NASHI AND TOMATO: EFFECTS OF BUDDING, GIBBERELLINS AND CYTOKININS

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SHOOT-ROOT ALLOMETRY AND GROWTH OF NASHI AND TOMATO : THE EFFECTS OF BUDDING, GIBBERELLINS AND CYTOKININS

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ABSTRACT

Growth of the root and the shoot systems of plants is generally, positively correlated, although the mechanism(s) controlling such relationships is not well understood. A series of experiments were carried out on young nashi trees (*Pyrus serotina*) and tomatoes (*Lycopersicon esculentum* Mill.) to explore this homeostatic phenomenon.

Two nashi cultivars, Hosui and Nijiseiki, were budded on to each of three clonal rootstocks, which differed in vigour (scion-budded trees). Buds from each rootstock was also budded on their own roots (rootstock trees). Growth, measured by individual organ and total plant dry weight, leaf attributes (leaf area, leaf number and leaf size) and root attributes (root length, root number and root volume) over two years after budding, indicated that scion-budded trees were markedly smaller than rootstock trees, irrespective of rootstock vigour. The imbalance of shoot-root ratio occurred following pruning after bud take; this remained in rootstock trees for one year but persisted for two years in scion budded trees. Vigour of all rootstocks appeared to diminish with time and final tree size was not well related to initial rootstock vigour. Neither rootstock nor scion morphological characteristics appeared to be changed by the partner, although presence of the cultivar bud on rootstocks delayed commencement of root activity in early spring. These results indicate that two-year-old (scion budded growth) nashi trees are not appropriate material for studying allometric relationship.

Plant growth regulators, gibberellins and cytokinins, were applied to 6- and 5-week-old tomato seedlings, respectively, in three separate aeroponic experiments. Gibberellic acid was sprayed twice to the shoot (at 2.9×10^{-5} M), while root application was achieved by incorporating GA_3 into the nutrient solution (conc. 5.8×10^{-5} and 2.9×10^{-4} M). Compared to the control, stem elongation, stem dry weight and stem weight ratio (SWR) was increased while root attributes (dry weight and root weight ratio (RWR)), leaf attributes (leaf area, leaf area ratio and leaf dry weight), and consequently total plant dry weight were reduced in GA_3 treated plants.

Gibberellic acid promoted apical dominance. Shoot applied GA_3 was quantitatively more effective than root application, suggesting that the organ in which physiologically active GA(s) originate may be an important component of plant response to environments. In addition, GA_3 effects were additive as indicated by the increasing difference with time in SWR and shoot-root ratio. The increased SWR and reduced leaf weight ratio (LWR) were responsible for an increase in the allometric value between stem and root dry weight (k_S), and a reduction in the allometric value between leaf and root dry weight (k_L), respectively. However, allometric value between shoot and root dry weight (k_T) was unaltered by GA_3. These results suggest no feedback mechanism of *de novo* GA synthesis occurred, and indicate that GA has no role in regulation of shoot-root allometry.

A synthetic cytokinin, benzylaminopurine (BA), was applied to roots at 2.2 $X10^{-8}$, 2.2 $X10^{-7}$ and 2.2 $X10^{-6}$ M. The control gave an intermediate response in all parameters measured, compared to the enhanced response at 2.2 $X10^{-8}$ M BA and the inhibitory response at other BA concentrations. This suggested that BA supplemented, and had a similar effect to, endogenous cytokinins. Benzylaminopurine initially or transiently stimulated shoot and leaf primordia and thus released buds from apical dominance, leading to an increase in leaf attributes (leaf number, leaf area, leaf dry weight and leaf weight ratio (LWR)), increased shoot-root ratio and reduced RWR. Benzylaminopurine had no effect on stem attributes (stem elongation, stem dry weight and SWR). There were, however, no changes induced in k_L and k_T. It is suggested that cytokinins participate in the homeostatic mechanism regulating plant growth allometry.

A model in which both gibberellins and cytokinins integrate to affect plant growth via allometric relationships is proposed. The usefulness of allometric studies to detect and analyse dynamic changes of organs and plant productivity in response to environment, as well as explain mechanisms regulating shoot-root equilibrium is strongly endorsed by this study.

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LIST OF ABBREVIATIONS

BA	=	Benzylaminopurine.
d.wt.	=	Dry weight (g).
GA(s)	=	Gibberellins.
GA_3	=	Gibberellic acid.
k	=	Allometric value or allometric constant or allometric cefficient (the slope of a regression of ln y = ln a + k ln x, where y is either leaf, stem or shoot dry weight and x is root dry weight).
k_L	=	Allometric value for the regression line of ln (leaf d. wt.) = ln a + k_L ln (root d. wt.).
k_S	=	Allometric value for the regression line of ln (stem d. wt.) = ln a + k_S ln (root d. wt.).
k_T	=	Allometric value for the regression line of ln (shoot d. wt.) = ln a + k_T ln (root d. wt.).
LA	=	Total leaf area (cm^2).
LAR	=	Leaf area ratio (ratio of total leaf area to whole plant dry weight, $cm^2.mg^{-1}$).
LWR	=	Leaf weight ratio (ratio of total leaf dry weight to whole plant dry weight, in percentage).
RWR	=	Root weight ratio (ratio of total root dry weight to whole plant dry weight, in percentage).
RGR(s)	=	Mean relative growth rate (refer to page 42, $g.g^{-1}.day^{-1}$).
RGR_L	=	Relative growth rate of total leaf dry weight ($g.g^{-1}.day^{-1}$).
RGR_S	=	Relative growth rate of total stem dry weight ($g.g^{-1}.day^{-1}$).
RGR_T	=	Relative growth rate of total shoot dry weight ($g.g^{-1}.day^{-1}$).
RGR_R	=	Relative growth rate of total root dry weight ($g.g^{-1}.day^{-1}$).
RGR_W	=	Relative growth rate of whole plant dry weight ($g.g^{-1}.day^{-1}$).
RGR_{LR}	=	Ratio of leaf to root relative growth rate (RGR_L/ RGR_R).
RGR_{SR}	=	Ratio of stem to root relative growth rate (RGR_S/ RGR_R).
RGR_{TR}	=	Ratio of shoot to root relative growth rate (RGR_T/ RGR_R).

RGR_{SL}	=	Ratio of stem to leaf relative growth rate (RGR_S/ RGR_L).
se	=	Standard error of mean, unless state otherwise.
shoot	=	Over-ground part of plants, consisting of stem and leaves (g).
SLA	=	Specific leaf area (ratio of total leaf area to whole leaf dry weight, $cm^2.mg^{-1}$).
SWR	=	Stem weight ratio (ratio of total stem dry weight to whole plant dry weight, in percentage).

CHAPTER 1
LITERATURE REVIEW

1.1. PLANT REQUIREMENTS FOR PRIMARY ROOT GROWTH

Vegetative growth in excess of that needed to renew aging spurs and branches can be undesirable in fruit trees after they have filled their allocated area and reached maturity. Since overall vegetative growth is directly related to primary root growth (which will be discussed in more detail later), control of vegetative growth can be achieved by suppressing growth of the roots. This, however, may be detrimental to the health of the tree if root function of such roots is concurrently limited. This, therefore, raises the questions: to what extent is primary growth needed; and to what extent is suppression of growth harmful to the health of the trees?

Apart from anchorage, absorption of water and minerals from soils is the most important function of roots. In fruit trees, regardless of whether secondary thickening has occurred, all roots seem to have the ability for absorption (Atkinson and Wilson 1980). The regions of roots which offer least resistance to water movement are the unsuberized zones, *i.e.*, the zone proximal to the meristematic cell region but distal to the region of extensive cutinization and suberization (Clarkson and Robards 1975). As such regions constitute such a small fraction of the whole root system (*e.g.* even in young fruit trees it may be as low as 15 percent of the total length), the growing parts can not be the only regions for absorption (Atkinson and Wilson 1979). During drought periods or winter when root growth is constrained, water must be taken up through the suberized zone. For example, Kramer and Bullock (1966) found that in a study of roots of loblolly pine and yellow poplar, that in midsummer about 99% of all the roots were suberized. Since midsummer would be the time of maximum transpiration, this must mean that most of the water was entering through suberized roots. The conclusion from this evidence must be that primary root growth is not necessary for water absorption.

Mineral ions are taken up by roots together with water. Like water, it was formerly believed that mineral absorption was likely to be restricted to the young

unsuberized zones of roots near the tip. More recent evidence, however, also shows that ion uptake is not confined to these zones (Russell 1982), although it is well known that after incrustation of suberins on the lamellae at the endodermis walls, which begins a few millimetres away from the tips, *e.g.* 5 mm from the tip in cherry and apple roots (Atkinson and Wilson 1980), and this endodermis restricted the apoplastic pathway drastically. For instance, uptake of labelled nutrients by segments of white roots of cherry trees grown in solution culture was higher only when measured on the basis of surface area or root volume (Atkinson and Wilson 1979). These results demonstrate that, similarly to water uptake, primary roots are not indispensable for ion absorption. In fact, it has been reported that ammonium, potassium, phosphate (Bowen 1969; Burley *et al.* 1970; Clarkson *et al.* 1975) and calcium ions (Atkinson and Wilson 1980) can penetrate, albeit slowly, through zones other than root tips. For phosphorus, the presence of root hairs has also been claimed to increase the uptake substantially (Drew and Nye 1969; Misra *et al.* 1988) because of the increased accessibility of phosphorus inside the soil aggregates. Furthermore, it has been shown that potassium is preferentially absorbed in the root zones further up the root than the zone closest to the tip (Luttge 1983). McCully and Canny (1988) observed that the work of Maertens (1971) with maize indicated that the older zone could take up 15 times the potassium ion of the apical zone. Indeed, it appears that only for calcium uptake, which is widely proposed to be largely restricted to young roots near the tips (Clarkson and Sanderson 1974; Luttge 1983), is the activity of growing root apices necessary. Therefore, in fruit trees, if calcium uptake for plant growth can be accomplished by this pathway during intermittent periods of growth, the question remains to be answered whether prolonged periods of active primary root growth during each growing season is needed for any other reasons.

1.2. PRIMARY ROOT GROWTH, DISTRIBUTION AND ACTIVITY

1.2.1. Root Apices and Primary Root Growth

Healthy primary growth of roots is the first priority for plant establishment and subsequent growth. In roots, primary growth, both cell division and extension, differ from the shoot system in that they occur entirely at the tips

(Wilson 1975) of the main axes and laterals. The initial size of a root tip determines the length of the root's life; large ones become thickened as a part of the framework, whereas thin ones have a short life (Wilson 1975). Root apices, therefore, are of extreme importance in determining the foundation of the root system. When root elongation has completed, the differentiation of the cells, which is also under control of the apex (Luxova 1975), and lateral formation, then follows. Finally, particularly in woody perennials, secondary growth will occur (Esau 1977).

1.2.2. Root Distribution and Plasticity

There are two important strategies by which root systems can contribute to plant survival in unfavorable soil conditions. One is the nature of root ramification and the other is the plasticity of root function. Distribution of roots is of utmost relevance to root activity because absorption of water and nutrients can occur only where roots are in contact with soil particles or solution (Russell 1982). The pattern of root distribution is related to the formation of laterals, which normally occurs at some distance behind main root apices, in partially or fully differentiated tissues (Esau 1977). The lateral primordia are well protected inside the endodermis cylinder (Esau 1977), and are usually unharmed even if soil dries and the cortex withers. Later, with improving conditions, the primordia will resume growth (Russell 1982).

The compensatory response of a root system is a complex issue, and all three factors; distribution, growth and activity, may be involved (Brouwer 1983) in partial or uniform stress conditions. Under partial stress, root morphology and activity of one part of a root system can be altered in relation to the other parts. A reduction in growth (as well as activity and distribution) in one part of the root system is frequently compensated by enhancement in the other part situated in the more favourable conditions (Crossett *et al.* 1975; de Jager 1982; Russell 1982). For example, when only a part of a root system was well supplied with nutrients, not only the absorption rate but also the root growth rate and proliferation of the enriched part increased considerably (de Jager 1982). In contrast, in the deficient

part of the root zone both attributes were markedly decreased, resulting in unchanged absolute growth, and activity, of the total root system.

If plants are subjected to partial water stress partially with one part non-stressed, root growth still occurs even when soil water potential surrounding the other part is as low as -40 bar (Kramer 1988). Under uniform water stress however, depending on the extent of stress and species, root distribution may be enhanced despite the fact that both activity and growth rates are reduced (Brouwer 1963; Zobel 1975; Huck *et al.* 1987). In orchard conditions, stress is usually not localized to parts of the root system; *i.e.*, depletion of water and minerals, is more general throughout the root zone. Nevertheless, the soil varies substantially, resulting in uneven root distribution of individual trees (Rogers and Head 1969), which is similar to what occurs in forest tree plantations (Lyford 1975).

The size, or mass, of a root system does not necessarily determine the activity at which it may perform (Tan *et al.* 1981; Hunt and Burnett 1973; Richards and Rowe 1977 a). For example, uptake of potassium was independent of root size in perennial ryegrass and the specific absorption rate (potassium uptake per unit root dry weight) varied more than 10 fold between the two extreme treatments of light and potassium content (Hunt and Burnett 1973) . Other evidence has shown uptake of water in peach seedlings was not related to the size (*i.e.*, volume) of the root system (Richards and Rowe 1977 a). The rate declined as root volume increased regardless of treatments imposed. These results agree with those of Tan *et al.* (1981), who found no relationship between the portion of roots available for water uptake and the transpiration rate. The observation that root systems do not increase in size when plants change from a non-bearing to a bearing state (Hurd 1978; Hurd *et al.* 1979), indicates that while the activity of roots increases to meet the demand of fruit growth, the size remains the same. These data indicate that given abundant supplies of water and/or nutrients, as found in many contemporary horticultural systems, a small root size can adequately meet demands imposed by the shoot, although a large root size may have advantages under adverse soil conditions (Brouwer 1981).

1.3. INTERNAL FACTORS INFLUENCING PLANT GROWTH AND DEVELOPMENT

1.3.1. Genetic Factors

Inter- and intraspecific differences in root growth rate and distribution pattern clearly emphasize the point that root characteristics are under genetic control (Zobel 1975). Differences in root growth, activity, and distribution, areare commonly found between species (Carpena *et al.* 1988). For example, sorghum and soybean, or tomato and maize, have different root distributions in the same soil (Burch *et al.* 1978; Tan and Fulton 1985). Maize root systems were denser near the surface than were root systems of soybean, regardless of soil type (Tan and Fulton 1985). Variability in rooting behavior has also been found among cultivars of wheat (O'Brien 1979). This variability includes the ability to modify morphology in response to the differing soil conditions (Zobel 1975), such that under the same moisture stress, different cultivated lines of tomatoes showed differences in root intensity and root depth (Zobel 1975; Tan 1988).

Although great variability has been found in the rooting habit of plants, research trends are towards the modification of soil properties, in an attempt to control root growth, rather than breeding new cultivars to obtain a desired root type. This is because both growth and types of roots formed can be influenced markedly by soil properties (Taylor 1986). Nevertheless, important achievements have been made in fruit crop production, in breeding and selecting clones with slow root growth rate, which is one of the most important characteristics in controlling plant size (Tubbs 1973).

1.3.2. Plant Types and Stages of Growth

With the exception of root crops, root growth generally declines with age (Terry 1968; Chalmers and Van den Ende 1975; Nooden 1984). Root growth rate of sugar beet and carrot increases exceeding that of the shoot at later stages of growth, as storage tap roots are gaining weight (Terry 1968; Currah and Barnes

1979). In annuals, the root system of fruit bearing crops accumulates dry matter actively only during the seedling stage up to a certain number of weeks after first anthesis (Hurd 1978; Barraclough 1984). After the plant attains full size, vegetative growth ceases with the development of reproductive organs, after which root size remains constant or may even shrink, *e.g.* in tomatoes (Hurd 1978), cucumbers (Van de Post 1978) and soybeans (Nooden 1984), indicating no further root growth increment on a weight basis (Hurd *et al.* 1979; Nooden 1984). This phenomenon of the cessation of root growth at fruiting coincides with the period when maximum weight of fruits is developing on the plant, and so could be the direct result of competition for photoassimilates. Root growth may resume in wheat after anthesis, or a month later in tomatoes (Hurd 1978; Gregory *et al.* 1978). In the latter, however, only the renewal of root tips occurs, with no net increase in root weight, and the root growth rate remains low throughout (Cooper 1972). In woody trees, root increment diminishes gradually with age (Hermann 1977). In fruit trees, root growth rate decreases sharply when the maximum root size for the species is attained, or when growth is limited by soil factors, or by competition from plants in the vicinity (Rogers and Head 1969; Chalmers and Van den Ende 1975; Chalmers *et al.* 1981). In peach, the annual increment of dry weight can be as low as 0.5-2.0% in large trees older than nine years of age (Chalmers and Van den Ende 1975).

1.3.3. Hormone and Related Factors

1.3.3.1. Auxins and their Oxidation

The high amount of auxin reaching roots accompanied by a low content of auxin oxidase is believed to lead to high root growth rates (Lockard and Schneider 1981 b). Circumstantial evidence indicates that auxins from the shoot (Phillips 1964) moving acropetally towards root tips (Pilet 1977) have an influence on root growth. For example, cambial activity in roots is simulated by auxin from the shoot (Digby and Wangerman 1965; Wilson 1975) and auxins, such as IAA, are well known as strong promoters of lateral root production (Wightman *et al.* 1980). In addition, increased IAA content in the apical zone enhances lateral root initiation (Lachno *et al.* 1982). Other circumstantial evidence, in dwarfing apple

rootstock studies, involves the presence of high concentrations of phenols, which stimulate auxin degradation. These compounds are claimed to contribute, at least partly, to dwarfness of apple trees. Certain phenols enhance the degradation of IAA by functioning as a synergist for IAA oxidase (Lockard and Schneider 1981 a). Although the amount of phenols per gram of bark in vigorous and non-vigorous apple rootstocks was not different (Lockard and Schneider 1981 b), it was found that dwarfing rootstocks contained a higher proportion of bark/wood (Beakbane and Thompson 1940; Lockard 1976). Consequently, higher proportions of total phenols to imported auxin results in a higher rate of auxin destruction, leading to reduced amounts of auxin reaching root tips in the dwarfing rootstock (Gur and Samish 1968). This possible mechanism, however, has been so far demonstrated only in apples. Generalization to other plant species would be difficult, non-woody plants in particular. It could also be argued that the relative thickness of bark is the effect of dwarfness, rather than *vice versa.*

1.3.3.2. Root Cytokinins

It is generally accepted that most cytokinins are synthesized in the roots (Van Staden and Davey 1979). These is also a close relationship between root growth, root meristems (*i.e.*,the sites of cytokinin synthesis) and cytokinin production by the roots (Salama and Wareing 1979; Donchev 1981). In radish roots, cytokinin levels increase with the initiation of cambial activity (Radin and Loomis 1971). Most of the evidence is, however, indirect and derived from the cytokinin content in xylem exudate and overall plant growth rather than root growth itself. This is because vegetative shoot growth and root growth are in general closely correlated (see section 1.5 and 1.6). The level of cytokinin has been shown to be high during the vegetative phase as measured in root exudates (Sitton *et al.* 1967) or activity (Donchev 1981), expressed as equivalents to kinetin concentration (Letham and Palni 1983). The concentration drops sharply when plants attain full size, by which time vegetative growth ceases and the plants enter a transitional or predominately reproductive phase (Sitton *et al.* 1967; Oritani and Yoshida 1971; Hurd 1978; Donchev 1981). Circumstantial evidence from plants grown in hydroponic systems indicated that during this transitional stage, when vegetative growth was unwanted, severe root shedding occurred which would

reduce root cytokinin level instantaneously (Hurd 1978; Tucker 1981). This observation is also consistent with the hypothesis that a relation between the level of endogenous cytokinins and root growth exists.

1.3.3.3. Gibberellins

Whether gibberellin (GA) present in roots is synthesized at the root tips (Butcher 1963; Carr *et al.* 1964; Jones and Phillips 1966; Kende and Sitton 1967) or derived from other parts of plants is still an open question (Crozier and Reid 1971). Nevertheless, a positive correlation was found between GA level in xylem sap and root growth (Reid *et al.* 1969; Ibrahim and Dana 1971; Reid and Crozier 1971). Faster growing plants contain higher levels of GA-like substances in their roots than the same species showing slow growth (Rood *et al.* 1988; Dijkstra *et al.* 1990). For instance, vigorous apple rootstocks have higher GA-like activity in the xylem sap than dwarfing clones (Ibrahim and Dana 1971). The total content of either GA_3 or GA_{4+7} was, however, not correlated with the degree of the root vigour (Yadava and Lockard 1977). This discrepancy may be explained by the fact that not all, but specific GAs, GA_1 and its precursor (*i.e.*, GA_{20}), are active in promoting growth (Rood *et al.* 1988). Therefore, the higher contents of these active GAs may be a better indicator of plant growth or root growth. One notable instance, when root growth and GA content in xylem sap were concomitantly reduced, was reported under flooding conditions (Reid *et al.* 1969; Reid and Crozier 1971). This, however, did not occur under cold stress (Atkin *et al.* 1973; Menhenett and Wareing 1975). On the other hand, the use of anti-GA compounds interfering with GA synthesis, such as the Paclobutrazol (Atkinson *et al.* 1981), has been found to reduce root growth. These data suggest that GA content and root growth are related, particularly with respect to certain growth conditions.

1.3.3.4. Abscisic Acid and Ethylene

Although it is accepted that the major pool of ABA is in leaves (Davies *et al.* 1986), it has been found in roots, especially root caps, which may also be another site of biosynthesis (Pilet 1981). According to Goss and Russell (1980) root growth is negatively related to ABA content. High levels of ABA suppress

the elongation process, and growth of the tips, in response to increasing stress conditions. This suppression was of main root extension (Barlow and Pilet 1984), whereas lateral root initiation was enhanced (Biddington and Dearman 1982).

Like ABA, ethylene at high levels inhibits extension of the main axes and strongly enhances the formation of lateral roots, particularly under anaerobic conditions (Crossett and Campbell 1975). Whether these effects are due to an enhancement of ethylene biosynthesis in response to environmental conditions (Stenlid 1982) is still a matter of debate (Butcher and Pilet 1983; Feldman 1984).

1.4. EFFECTS OF ROOT ENVIRONMENTAL FACTORS ON ROOT GROWTH AND PHYSIOLOGICAL ACTIVITY

Because root growth and distribution are related to the hormone balance in the roots, environmental factors such as the supply of minerals, soil aeration and soil mechanical factors are believed to affect root growth by modulating the balance of hormones (Torrey and Wallace 1975; Marschner 1986). The hormones most often implicated in the response of the root to the rhizosphere are cytokinins and gibberellins (Skene 1975; Goodwin *et al.* 1978).

1.4.1. Nutrient Availability

Increasing soil fertility has a strong positive effect on root growth and distribution (Russell 1982). It is commonly found that roots tend to proliferate in the zone of most suitable nutrient supply (Newbould 1969; de Jager 1982), such as, in fertile topsoil, and bands of richer soil at greater depth in orchards (Rogers and Head 1969). Both Root growth rate and lateral formation are stimulated when roots are well supplied with nutrients (de Jager 1982), while under sub-optimal supply they are markedly reduced (Hackett 1968). Placement of the fertilizers is important in determining root distribution and extension, since laterals can be induced by the local placement of fertilizers (Drew 1975; de Jager 1982; Granato and Raper, Jr., 1989). Potassium and phosphate deficiency reduces the number, total length and volume of root axes and laterals (Hackett 1968). Nevertheless, despite reduced growth and retarded lateral root formation, enhancement of

extension of the main axis is often observed when there is a sub-optimal supply or deficiency of mineral nutrients (Lambers *et al.* 1982).

The level of nutrients in which plants grow (Banko and Boe 1975) and the growth rate of roots is well correlated with the level of root cytokinins (Salama and Wareing 1979). Under conditions of sub-optimal nutrient supply, the growth of roots was reduced and the level of root cytokinins concomitantly declined (Menary and Van Staden 1976; Salama and Wareing 1979; Kuiper *et al.* 1988). A sudden change of full to deficient nitrogen supply (from 100% to 2% N) caused a 50% reduction in internal cytokinin concentration of root tissues within two days (Kuiper *et al.* 1988). In contrast, addition of nitrogen to plants induced a marked increase in the cytokinin content of root sap (Yoshida and Oritani 1974).

1.4.2. Soil Moisture

Water is essential for plant growth because growth must be accompanied by irreversible wall extension and thus enlargement of the cells (Ray 1987). Nevertheless, indirect effects of soil water content, in which physical and chemical properties of soil are also involved, have a considerable impact on root growth. Mechanical impedance and shrinkage of root tissues and soil particles, leading to the discontinuity of soil-root continuum, are the dominant factors (Marschner 1986). Root growth generally declines when soil water potential reduces to -0.5 bar and stops at -15 bars, which approximates the permanent wilting point (Kramer 1988).

Water availability restricts root depth as well as the pattern of distribution (Sharp and Davies 1985). If a uniform soil water potential is maintained throughout the rooting zone, root density is generally highest at the soil surface and decreases downwards. However, the root pattern is reversed when water is lost at the surface (Russell 1982; Sharp and Davies 1985). Local availability of water also regulates the distribution and production of lateral roots. Despite the substantial reduction in overall root activity, growth and development, more fibrous roots are encouraged and roots penetrate deeper into the soil profile of a drying soil (Zobel 1975; Sharp and Davies 1985; Huck *et al.* 1987). In grasses,

the seminal axes become longer and both the length and diameter of laterals formed immediately below the zone of desiccation are much increased (Russell 1982).

Soil drying reduces the synthesis and amount of cytokinins exported to the leaves (Davies *et al.* 1986). There is some indirect evidence of such changes in plants experiencing a water deficit (Itai and Vaadia 1965; 1971). Because transport of other substances, such as nutrients, from roots may also be reduced, it is possible that a multiple chemical signal with several variable components may move from roots to influence shoot physiology under conditions of water stress (Shaner and Boyer 1976).

1.4.3. Aeration

Roots require oxygen for metabolism and hence growth. Conditions which allow a high oxygen diffusion rate, therefore, are suitable for root growth. For each soil type an optimum proportion of air space is required for maximum plant growth. Departing from this point, growth is reduced (Flocker *et al.* 1959). Under conditions of depleted air space (*i.e.*, inundation), growth of roots is reduced (Bradford and Hsiao 1982). If roots are flooded partially or temporarily, root depth, distribution and types of roots formed are altered (Rogers and Head 1969). Herbaceous as well as tree species, which can adapt and survive flooding, create adventitious roots at the stem above the water level where root laterals proliferate (Jackson and Drew 1984; Kozlowski 1984). During recovery from flooding, although the production of root number may increase, even though root shedding may occur (Bradford and Hsiao 1982), root growth is reduced. This also results in trees with shallow root systems where the active roots are in the zone of soil above the water level (Coutts and Philipson 1978; Brouwer 1981). Nevertheless, the overall effect of reduced aeration of the root system is reduced root growth, and consequently plant growth (Kozlowski 1984) even in specifically adapted species (Kordan 1976). The quantity of extractable cytokinin-like substances transported to the shoot fell during flooding of the root system of sunflower (Burrows and Carr 1969). Similar results were obtained with gibberellin-like compounds in the same species (Reid *et al.* 1969; Reid and Crozier 1971).

1.4.4. Temperature

Continuous diurnal and seasonal fluctuation in soil temperature no doubt plays a vital role in regulation of tree root growth and activity as a whole (Barlow and Adam 1989). In general, the range of temperatures in which root apices are able to grow is between 1^{O} and 35-40^{O}C (Barlow and Adam 1989). The optimum temperature for root growth is species and age dependent (Buggee and White 1984). In tomatoes, 25^{O}C is the optimum temperature for the first four weeks but this increases to 30^{O}C for 5-6 week-old plants (Buggee and White 1984). The greater the temperature difference from the optimum temperature the more unfavorable the conditions become for root growth. Near the upper and lower temperature limits rates of cell division and cell elongation are no longer correlated, and root growth and distribution may cease (Aoalsteinsson and Jensen, 1990) because of the premature differentiation of meristematic cells (Erickson 1959).

1.4.5. Mechanical Impedance

Soil physical properties which are most associated with the mechanical impedance of the soil to roots are moisture and porosity (Letey 1985). The relationship between ideal moisture content and aeration for root activity is in the opposite direction of that for moisture content and mechanical resistance (Letey 1985). High moisture content reduces aeration, which is undesirable, but reduces mechanical resistance, which is desirable. In other words, roots penetrate in wetter soil zones because mechanical resistance is low (Greacen and Oh 1972). Root growth starts to decline at approximately -6 bars of soil pressure and ceases below -30 to -40 bars (Richards and Cockroft 1974).

The mechanical impedance for root growth can also be intensified in soil with low porosity (Letey 1985). Porosity is an important characteristic of soil in relation to its water holding capacity, and hence, water availability for root growth and extension. The size of pores determines the potential of water held within them and consequently the suction required to withdraw it (Russell 1982). Heavy soils, in particular, consisting of a large proportion of clay and silt, leaving only

small pores, are difficult for roots to penetrate, especially under dry conditions. Improper cultivation reduces soil porosity and aggravates the situation (Richards and Cockroft 1974; Tardieu 1988). Roots push with pressure to penetrate the barriers and this changes the shape of soil particles surrounding root tips. Root morphology is altered when roots are unable to enter pores that are smaller than their (root) diameter (Goss and Russell 1980; Atwell 1988). Root growth rate declines because roots regulate osmotic potential to counter balance the mechanical pressure (Greacen and Oh 1972). Root growth continues to decline as soil becomes harder until growth ceases. Thus, reduction in growth is not related to nutrient deficiency, which has been demonstrated in experiments under simulated confinement (Hameed *et al.* 1987). In poorly structured soil, the range of water potential over which favourable conditions for root growth occur is narrower, compared to well structured soils. This means that the restriction of root growth occurs earlier, at a higher water content, than the value that would limit root growth on the basis of water availability alone (Letey 1985).

As growth is restricted by mechanical impedance, root morphology is altered. In many crop plants, *e.g.* tomatoes, the main axis is shortened, whereas laterals are thickened (Hameed *et al.* 1987). Root number per unit length of roots and root dry weight per unit length of roots increases (Hameed *et al.* 1987). The increase in root diameter in response to compaction is due to an increase in thickness of the cortex, while the stele remains constant in diameter (Russell and Goss 1974). Cortical and epidermal cell diameters can be increased by up to 50% compared to unstressed cells, while root length is decreased by 5% and 24% in the inner cortex and epidermis (Russell and Goss 1974). In grasses, the pattern of root formation is changed in terms of quantity and the zones in which they are produced. Laterals are formed at a shorter distance behind the apex (Russell 1982) and proliferate in response to compaction (Atwell 1988).

1.4.6. Root Competition

Competition between roots of neighbouring plants of the same or different species is largely a function of competing for nutrients and water (Caldwell 1987). The rate of uptake of a plant, grown in the presence of an active competitor on one

side and a weak competitor on the other side, showed that the uptake of phosphate in the latter situation is considerably higher (Caldwell *et al.* 1985).

The relationship between plant size and spacing implies the existence of competitive interference between plants. For example, in a monospecific stand, there is a positive relationship between the final size of individual plants and the distance to the nearest neighbour (Pielou 1962). In high density plantations of apple trees, Atkinson *et al.* (1976) found that the degree of root overlap increased considerably and in some cases trees were sharing soil space with trees two rows away. In contrast, the root systems of widely spaced trees were almost discrete and only occasionally intermingled at the periphery. Those at narrow spacings had a larger number of the major roots growing downward rather than spreading horizontally and had a greater proportion of finer roots. Thus, the distribution of a plant root system can be expected to change depending on the proximity of its neighbours. This behaviour of roots, however, appears to vary from species to species. Atkinson *et al.* (1976) reported results, similar to those by Rogers and Head (1969) on non-intermingling of roots of apple trees, in widely spaced plantings. In peaches, however, the antagonism between roots of neighbouring trees is much more pronounced and almost no intermingling occurs even at very close tree spacings (Chalmers *et al.* 1986). On the other hand, roots of pear trees, intermingle freely with their counterparts (Rogers and Head 1969). This may be partly due to soil physical properties since poorly structured soil may not allow root extension even when soil moisture is relatively adequate (see section 3.4.5).

For inter-specific plant stands, competition among roots for resources can result if roots of one plant deplete the soil resources more quickly than roots of another, or alternatively, roots of one species deplete resources to levels which other plant roots are still able to extract sufficient quantities for growth and survival (Tilman 1982). Since perennial plants have a long life span and their roots extend considerably further than annuals, overlapping between neighbouring root systems is common (Rogers and Head 1969). It is reported that roots of fruit trees grow well in a grass sward (Rogers and Head 1969). However, the species of grasses present in the orchard appear to be important as Cockroft (1966) showed that growth of fruit trees was more affected by competition for nutrients with

certain grass swards.

In conclusion, plant growth is restricted by the competition for resources from roots of other plants. Whether roots intermingle or avoid each other, they tend to penetrate into deeper zones of the soil profile. But this can occur only to some extent because of unfavorable conditions for growth at deeper levels, and the methods of orchard soil management with which water and nutrients are supplied largely to the top soil. The available root volume of soil for each plant, therefore, is limited resulting in a situation which somewhat resembles root confinement.

1.5. SHOOT-ROOT INTER-RELATION

The interdependence of root and shoot systems arises from the balance required between the supply of nutrients and water by the roots required by the shoot and in return the photosynthates supplied to roots for their growth and activity (Troughton 1974; Wilson 1975; Brouwer 1981). This relationship was initially described as a size equilibrium between shoot and roots corresponding to the need to have an amount of leaves and roots which were functionally equivalent in their capacity to support each other (Brouwer 1963). Many observations have provided general support for this shoot-root size relation. The classical example of this evidence is compensatory growth, which occurs when disturbance by pruning roots or shoots results in a rapid recovery of the pruned part (Maggs 1965; Richards and Rowe 1977 b; Young and Werner 1982), leading back to the original ratio of roots and shoots (Brouwer 1963). Many observations on partial leaf (Buttrose 1966; Kliewer and Fuller 1973) or root removal (Buttrose and Mullins 1968) which resulted in the proportional reduction of growth of the counterpart system also demonstrate this phenomenon.

In particular circumstances, however, the relative size is found to be out of balance over short periods especially in rapid phases of vegetative growth as observed in seedlings of trees (Mullin 1963; Mertens and Wright 1978; Drew and Ledig 1980) and non-fruiting, fruit trees (Williamson and Coston 1989). Thus, during this period at least, high plasticity in both shoot and root activity is evident.

It is therefore important to include a measure of the activities of both plant parts in any description of the shoot-root relationship. Initially, Davidson (1969 a) postulated this functional relationship empirically, in terms of the product of size of the organ and its activity, which he expressed in the form :

root mass x specific absorption rate α shoot mass x specific photosynthetic rate

This model has been supported by many investigations and modified into several forms (Hunt *et al.* 1975; Thornley 1975; Richards 1976; Richards 1978). Hunt and Burnett (1973) and Hunt (1975) preferred the expression :

mass ratio α 1 / activity ratio

They also demonstrated that the relationship held whether a single or a group of mineral element(s) are considered.

Thornley (1975) has stated that for a certain period of vegetative growth the equation can be written as:

root mass x [increment of element(s)/root mass] α constant x shoot mass x [total weight increment/shoot mass]

which later has been simplified to :

increment of element(s) α constant x (total weight increment)

Richards and colleagues using the latter expression of the relationship, have shown that for either water or nutrient uptake, the functional relation exists irrespective of external treatments or plant growth stage (*i.e.*, vegetative or reproductive) (Richards 1976; Richards and Rowe 1977 a; Richards *et al.* 1979 a). This also indicates that the rates of both nutrient and water uptake by roots are a function of shoot demand (Richards and Rowe 1977 a). An increase in the size of the shoot being accompanied by increased root absorption per unit length, rather than the size of the root system *per se*.

This functional equilibrium also explains the response of the plant when either the root or shoot system is in an unfavorable condition. Since root and shoot activities are flexible to some extent, some adjustment in activity to meet the demand imposed by the other can occur. Beyond this limit, however, the adjustment of relative size must be made to compensate for the low activity imposed by the prevailing conditions. The close linkage between the two systems has been demonstrated to occur in all circumstances (*e.g.* Richards and Rowe 1977 a; Raper, *et al.* 1978). The conclusion that follows from these assumptions, is that there must be a regulatory mechanism controlling the growth distribution between organs of plants through their activities.

1.5.1. Shoot-root Ratio

The simplest quantitative expression of the shoot to root relationship is the ratio of their respective dry weights. This has been used extensively to reflect their functional relationships irrespective of plant size (Brouwer 1962 a; Van Noordwijk and de Willigen 1987). While this is a useful and simple expression for this purpose, it has a number of limitations (Ledig *et al.* 1970; Hunt and Burnett 1973). In particular, as a morphological index, it depends on internal and external factors, and reflects adjustment in the size equilibrium of shoot and root to the prevailing circumstances of imposed treatments or environmental conditions. For a species (or variety) grown under a given environment, the ratio is constant at particular stages (*e.g.* Brouwer 1962 a; Vose 1962; Troughton 1962; Lyr and Hoffmann 1967; Richards *et al.* 1979 a; Hurd *et al.* 1979).

It is important to emphasize, however, that the ratio changes with size and phenological development of the plant (Ledig *et al.* 1970). This is due to the fact that root growth rate generally declines more rapidly than that of the shoot (Brouwer 1962 a; Cooper 1972; Schulze 1983). This gradual change in shoot-root ratio over time is the ontogenic drift, which is the change in plant response, to a specific treatment or environment, as it progresses through its life cycle (Evans 1972). Therefore, it may not be clear if a change in shoot-root ratios is an adaptation to changing conditions, which is different to ontogenic drift, created by the interaction of the growing plant and the environment. With the exception of

root crops, the shoot-root ratio increases during the vegetative phase (Brouwer 1962 a). For example, this occurs in peach trees (Chalmers and Van den Ende 1975), tomatoes (Richards *et al.* 1979 a), wheat (Barraclough 1984) and forest trees (Mullin 1963). The ratio remains constant after plants reach full size or maturity, however, it increases if fruit dry weight is accounted for in the shoot weight (Brouwer 1962 a; Chalmers and Van den Ende 1975; Hurd *et al.* 1979; Richards *et al.* 1979 a; Richards 1983).

A number of environmental factors can modify the ratio markedly (Brouwer 1962 a). In the extreme example of pot-grown apple trees with optimum conditions for growth, the ratio can be as high as 7:1 or higher, while in normal soil condition it is considerably lower (Rogers and Head 1969). Unfavorable conditions which decrease root or shoot growth such as low temperatures (Davidson 1969 a; Buggee and White 1984), nutrient deficiency (Davidson 1969 b), drought (Brouwer 1966; Davidson 1969 b; c; Tan *et al.* 1981; Hubick *et al.* 1986), or inundation of roots (Tang and Kozlowski 1982), or for the shoot such as low irradiance (Troughton 1960) and temperatures (Davidson 1969 a; Szaniawski 1985), the part in the adverse environment is affected to a lesser degree than the other part, leading to a lower or higher shoot-root ratio, respectively (Brouwer 1963; Richards 1983; Szaniawski 1985). By contrast, an increase in nutrient concentration can result in an increase in the ratio (Brouwer 1966; Davidson 1969 b; Kuiper and Staal 1987; Marschner 1986). It should be emphasized, however, that when the ratio adjusts in an inclement environment, this is accompanied by a substantially reduced growth rate of the individual parts and the plant as a whole.

1.5.2. Shoot-root Allometric Relationship

The relationship between shoot and roots can be considered more appropriately as an allometric relation between two plant parts resembling such relationships between organs of animals which have been studied extensively (Reiss 1989). In general, the functional relationship between two size related organs measured at any instant is a constant (Reiss 1989).

The allometric equation is the power function of the two measures in the form of:

$$Y = a\ X^k \qquad (1)$$

Where X and Y are size or function estimates of two organs, and a and k are constants (Gould 1966). The commonly adopted form of the equation (1) has been simplified by taking natural logarithms on both sides. The equation becomes:

$$\ln Y = \ln a + k \ln X \qquad (2)$$

Where ln a and k are constants. A graph of log$Y$ and log$X$ produces a straight line with slope k, the slope of which does not depend upon the units used (Reiss 1989). In the form of equation (2) the allometric constant, or k value, therefore represents the ratio of the mean relative growth rates of the shoot to that of the root, of that system. Since the value of a natural logarithm of any dry weight is its relative growth rate, a plot of both shoot and root relative growth rates derived via this method represents the ratio of those relative growth rates. Thus, the allometric relation actually integrates mass and activity of the shoot and root systems, while the strength of the relation between the two is indicated by the coefficient of determination.

Compared to the functional relationship model discussed earlier (Davidson 1969 a), the allometric equation carries more statistical weight and may, therefore, give more meaningful interpretation and reliability. There has been debate whether least squares regression or reduced major axis regression is more appropriate to use for analysis because both, not one, organ dry weights are variables (Reiss 1989 and references therein). Paradoxically, the results obtained by the two methods are not different. The slope calculated by reduced major axis regression equals the slope calculated by least squares regression divided by r, which is the difference between the methods. The method of maximum likelihood has also been suggested by Causton and Venus (1981). The result, nonetheless, provides relatively similar values with differences, only at the third or higher digit (MacKay, pers. comm.).

Since the allometric constant, or k value, is unaffected by scale or plant size (Hunt and Burnett 1973; Troughton 1960), it is used more widely in

comparisons of growth, altered by treatments or imposed conditions, than shoot-root ratio (Hunt and Burnett 1973). In addition, the value is not influenced by the phase changes of plants, giving a general trend of plant growth and smoothing out the oscillating pattern due to alternating predominance by shoot and root growth. Chalmers and Van den Ende (1975) and Richards (1981), found that k was unaltered if the fruit dry weight was excluded (only vegetative dry weights were counted) from the calculation, but when the fruit weight is included the value increased greatly (Troughton 1960; Troughton 1977; Richards *et al.* 1979 a).

Since the value of k is a measure of the ratio of the relative growth rates of shoot and roots, it follows that it is a primary determinant of shoot-root ratio and a measure of the functional equilibrium between the two systems. If the value is equal to one, which is said to be isometric (Reiss 1989), an equal growth rate occurs between the shoot and root system, and the shoot-root ratio remains constant at unity. If the value is less than one, the root system grows faster than its shoot, or the root growth rate decreases more slowly than the growth rate of the shoot, and *vice versa.* Changes of k, indicating the growth relation between the shoot and the root, therefore, can describe the adaptation of plant growth in response to external treatments and the rhizosphere environment. When growth of roots is indispensable for survival such as in newly transplanted seedlings, or in the situation of hostile root milieu, such as drought or nutrient deficiency, the k value decreases, as a result of plant growth adjusting to provide more root surface area to maintain root activity. In an unfavourable shoot environment such as low irradiance, an increased k value reflects the opposite growth change (Hunt and Burnett 1973). Thus, the change in k value enables one to predict that the shoot-root ratio is decreased in the former and increased in the latter conditions (*e.g.* Davidson 1969 a; Hunt and Burnett 1973). In comparisons of plants grown under different soil fertility, plants growing with the superior soil environment with optimum resources will have a higher k value than those growing on poor soil. In fact, Rogers and Vyvyan (1934) found that the shoot-root ratio of the former can be double of the latter. In fruit trees (and other fruit-bearing plants), the k value is normally greater than one implying the shoot growth rate exceeds that of roots, and the shoot-root ratio increases as the plant grows. This may also indicate a lower requirement for root growth after plants reach maturity.

1.6. MANIPULATION OF ROOT SYSTEMS IN ORDER TO CONTROL PLANT SIZE

In fruit trees, tree vigour is inversely related to fruit productivity, as the two sinks (vegetative organs versus reproductive organs) compete for photoassimilates. Management aims to hasten vegetative growth of young trees to fill their allocated area as quickly as possible. After filling their allocated area and reaching maturity, vigorous vegetative growth is not required for high fruit productivity and efficient functioning of the tree. At this stage, excessive vegetative growth will increase management costs and lower production. The cost of inputs of fertilizers and irrigation to maintain vegetative vigour is not only wasteful but induces light competition which necessitates pruning or results in depressed cropping. If vegetative growth can be retarded without affecting the health of trees, the photoassimilates can be directed into economic yield. Since shoot growth is physiologically linked with root growth, as indicated by the strength of the allometric relation (Wareing 1970; Drew and Ledig 1980), the overall growth of plants can be regulated by controlling root vigour.

1.6.1. Dwarfing Rootstocks

Permanent suppression of root growth can be simply accomplished through the use of dwarfing rootstocks. Although tree size may vary with different soil, growing conditions and management, the relative size of trees growing on rootstocks of varying vigour in a given location still ranges in a predictable order related to rootstock vigour (Parry 1977; Preston 1978). Trees on dwarfing rootstocks are highly productive because the shoot growth is low due to the slow growth rate of the rootstocks (Tubbs 1973). For certain apple rootstocks, *e.g.* M27, shoot growth ceases as early as 5 to 6 years of age (Preston 1978). At present, the use of dwarfing rootstocks may be the simplest way to control plant size, however, extensive use of widely suitable rootstocks is confined to apples. Progress with other fruit crops remains slow. Thus, in many species, growth control can only be accomplished by the alternatives. In addition, rootstocks are expensive. As the name implies, a rootstock provides only the root system, the desired cultivar must be grafted or budded onto the dwarfing root system. This involves a second labour intensive step in propagation.

1.6.2. Root Competition

Root restriction imposed by high tree density has been reported to reduce tree size effectively without affecting crop yields in apples (Atkinson 1978), peaches (Chalmers *et al.* 1981) and calamondrin (*Citrus madurensis* Loureiro) (Salomon 1978). Tree size are in the reverse order to tree density because the amount of roots per tree is reduced and root orientation modified towards the vertical direction (Atkinson 1978). The vigour of trees is directly related to the available volume of soil for root growth (Brouwer 1981; Richards and Rowe 1977 b). The competitiveness of roots of neighbouring trees can limit space available for root growth, and the supply of nutrients and water in the soil (Atkinson 1978). This situation is frequently exacerbated by less than favourable conditions for growth of roots in subsoil. If shading and light competition can be avoided, vegetative growth can be controlled and fruit yield increased. Nevertheless, root competition alone is usually not sufficient to control growth on most horticultural soils (Chalmers, pers.comm.). It becomes quite important, however, when used jointly with other methods for reducing tree vigour such as reduced irrigation (Chalmers *et al.* 1981).

1.6.3. Soil Compaction

In natural plant ecosystems, sites with poor soil physical properties support a markedly reduced population of thriving plants, because such conditions do not allow roots to grow and expand. With highly intensive management, however, root restriction due to poor soil physical properties can be overcome. In soils with shallow topsoil and heavy clay subsoil, under an appropriate cultivation system root volume can be restricted and vegetative growth suppressed, leading to an increase in fruit yield (Olsson and Cockroft 1980).

1.6.4. Root Pruning

Root pruning has been shown to restrict root growth, although, temporarily. Hence, the plant size can be suppressed for only a limited period (Richards 1986). For instance, Schupp and Ferree (1989) showed that annual root

pruning of apple trees could reduce shoot growth by up to 44%. To maintain plant size by this method, however, a portion of the root system must be removed repeatedly at regular intervals. For instance, Buttrose and Mullins (1968) have demonstrated that in grapes a removal of 25% of roots is needed to retain a constant plant size. This is because photoassimilates are mobilized in favour of root growth, in order to regain the pre-pruning shoot-root equilibrium (Brouwer 1963; Harris *et al.* 1971; Richards and Rowe 1977 a). In this situation, the vegetative sink potential of roots is stimulated (Schupp and Ferree 1989). As a consequence, the competitive potential of the vegetative portion of the plant is increased. Plant size is controlled, but this is accomplished with no change, or often a decrease, in crop yield. Photoassimilates are diverted to the pruning site, at the expense of flower and fruit production (Richards 1986). For 15 year old Melrose on semi-dwarf apple rootstock (M26), pruning at full bloom reduced shoot growth substantially (Schupp and Ferree 1988). Leaf area was decreased via the reduction in both shoot leaf-size, and number, but not spur leaves. Although fruit yield was not significantly reduced, and fruit number and quality were improved, fruit size was markedly suppressed (Schupp and Ferree 1988). From the practical view point, a number of factors, such as time and severity of pruning, varietal response with respect to vigour and age of trees, and proximity to trees and depth of pruning, also have to be taken into account (Schupp and Ferree 1988; 1989). If the technique is to be applied for commercial benefit, further research is needed.

1.6.5. Root Confinement

The situation in which plant size is reduced because roots are overcrowded in potted plants is commonly seen but has not been used as a method for controlling the size of crop plants until recently. Nevertheless, it has been shown that size of plants can be controlled through the use of limited root volume (Richards and Rowe 1977 a; Carmi and Shalhevet 1983; Hameed *et al.* 1987; Ruff *et al.*1987). In field situations, root barriers restricting peach tree root systems to a limited soil volume for each tree drastically reduced root growth and tree size (Richards 1986). Precocity was also enhanced but fruit loads were slightly lower. Further studies would also seem necessary to make this technique feasible in orchards.

1.6.6. Water and Nutrient Management

Irrigation and nutrition regimes can be tuned to control plant size effectively, while fruitfulness can be enhanced. Chalmers *et al.* (1981, 1984) have successfully controlled vegetative vigour with trickle irrigation applied with a deficit watering regime during rapid vegetative growth, and close plant spacing. Vegetative growth was reduced by 80% in peach and 70% in pear (Chalmers *et al.* 1984). The water deficit implemented to control root growth was introduced during the initial period when fruit growth was relatively insensitive to the treatment, and after harvest. The amount of water applied was determined from the evaporation rate and rainfall data calculated over the effective planting square of the tree (Chalmers *et al.* 1986). This system, however, has so far been effective, only in areas where the climate is suitable as interference of natural precipitation should be minimal during the treatment periods. Similar strategies may be employed with nutrient supply (Hansen 1980; Hart *et al.* 1990).

1.7. POSSIBLE MECHANISMS FOR REGULATING SHOOT-ROOT GROWTH EQUILIBRIA

The concept of correlative growth between the shoot and root system can be considered as an adaptive mechanism for environmental variation and change. When soil properties change, root function can adjust to meet the demands for shoot activity. However, adjustment of potential root activity by growth occurs only to some extent, as can be seen in the recovery of size of root systems after severe pruning or the gradual adaptation in size of plant root system to drought. This form of adjustment can only occur at the expense of growth and activity of the shoot and total production by the plant must decline. In natural systems this adjustment is dynamic but slow. If a change in environmental conditions persists, the plant adjusts its root growth so that a new shoot-root ratio is obtained to suit in the new environment. For example, apple trees excavated from a loam soil at East Malling had a shoot-root ratio of about 2:1, irrespective of different tree size induced by different rootstocks. By contrast, trees of the same cultivar excavated from a poor, sandy soil had a shoot-root ratio of about 1:1 (Rogers and Vyvyan 1934). The latter group of trees had a relatively larger root system per unit plant

size and consequently were in a better position to cope with the more demanding root environment. This and many similar results suggest, as does the allometric relation between shoot and root size, that the plant has a balancing or homeostatic mechanism which regulates the relative size of shoot and root systems for a particular root environment.

Two major models have been postulated to describe this mechanism. The most widely accepted model proposes that shoot and root systems produce hormonal messages that mediate growth of the reciprocal organ. This model was first advanced by Went (1938) and is supported by numerous other researchers. The other model is a physical mechanism involving water transport in plants and cell turgor pressure (Passioura 1988 b; Boyer 1989).

1.7.1. Potential Signals

1.7.1.1. Turgor Pressure and Water Potential

Based on the vast amount of evidence relating water stress to growth, it has been proposed that water potential regulates shoot-root communication. Growth of cells depends directly upon turgor pressure which expands cells that have extensible cell walls (Hsiao 1973). Turgor changes with respect to water entering cells in response to the concentration of the cell solutes. The solutes in enlarging cells are concentrated because they are used for respiration and to build new materials (Boyer 1988). Thus, water moves along water potential gradients, from the cells closest to the xylem, the other end of which connects to the roots and hence the soil. The xylem water potential, therefore, can be changed with the changes in transpiration or soil water potential. Consequently, water potential and turgor may be the signals that communicate levels of water stress for roots to the shoot (Boyer 1989). When the soil is drying, root water potential is lower, and it is suggested that this message is transmitted through the xylem via cells adjacent to the xylem to the growing cells of the shoot and stomata (Nonami and Boyer 1987). The reduced water entering the cells results in a reduced growth rate and induces stomatal closure. This also affects the photosynthetic mechanism of the leaf, probably through reduced stomatal conductance in the case of mild drought stress, while in severe stress both stomatal aperture and chloroplast reactions are affected

(Sharkey and Seemann 1989).

Leaf growth, however, may be reduced in response to soil drying with no change in leaf turgor (Munns 1988; Passioura 1988). Boyer (1988) argued that this is because the water potential of cells decreases with increasing distance from the xylem. In other words, growing cells have a much lower water potential than xylem cells and they will therefore be less affected by a drop in xylem water potential. Hence, the turgor of growing cells is unchanged, unless the xylem water potential becomes very low or is persistently reduced. Cell growth is reduced because there is less or no water entering the cells. Stomatal conductance has also been demonstrated to be unaffected by leaf turgor but related to soil water potential (Davies *et al.* 1986; Schulze 1986; Passioura 1988 a, b). Furthermore, stomatal conductance can be modified in the absence of the roots within a few minutes (Ehret and Boyer 1979). These observations indicate other mechanisms must be involved (Sharp and Davies 1989). Blackman and Davies (1985) and Passioura (1988 a) noted that the signals sent by roots to the leaves in response to root environments may be hormonal, rather than physical in nature.

1.7.1.2. Nutrient Molecules

Nutrient molecules may also be signals controlling the activity of a metabolic system in water deficient plants. As inorganic nutrients are transported through the transpiration stream from the roots, reduced water potential in the roots could reduce the nutrient flux. It has been demonstrated that the rate of nitrogen addition regulates plant relative growth rate (Duarte *et al.* 1988). Reduced nitrate flux through roots has been shown to cause a reduction in the activity of nitrate reductase in maize shoots exposed to dehydration (Morilla *et al.* 1973). Because nitrate reductase is a short-lived enzyme, it must be synthesized continually, and synthesis is induced only in the presence of the substrate (nitrate). It was found, however, that under nitrogen deficient conditions, poor incorporation of nitrogen in leaves, rather than the unavailability of the nutrient limited growth (Lambers *et al.* 1982). Therefore, it was proposed that the mechanism linking nutrient levels to regulation of shoot-root ratio was communicated hormonally rather than as a nutrient stress.

1.7.3. Hormonal Signals

Went (1938) proposed intuitively that chemical messengers or 'rhizocalines' from the roots and 'caulocalines' from the shoot formed the communicating link between the two parts which controlled plant growth. Of the five groups of hormones studied to date, cytokinins (Wareing 1970; Skene 1975; Goodwin *et al.* 1978) have been most intensively studied as the root-produced hormones, followed by gibberellins (Carr *et al.* 1964; Phillips and Jones 1964; Kende and Sitton 1967; Torrey 1976; Goodwin *et al.* 1978). As extensively reviewed by Van Staden and Davey (1979), considerable circumstantial evidence strongly indicates that roots, the tips in particular (Short and Torrey 1972), are the prime producers of cytokinins, which are exported to the shoots via the xylem (Kende 1964; Van Staden and Davey 1979 and references therein). Gibberellin activity has also been detected from the base of excised root tips (Jones and Phillips 1966), as well as *in vitro* root tips continually maintained in cultured forms for many years (Butcher 1963).

Auxin is considered to be the major candidate for the shoot-produced hormone as far as communication with the roots is concerned (Wareing 1977). Although auxin has been found in root tissues (Goldsmith 1977), it is now known that the major amount of auxin is synthesized in the shoots; near apices and young leaves (Thimann and Skoog 1934) or young shoots (Hatcher 1959), and transported basipetally in stem and acropetally towards the tips in roots (Goldsmith 1977). This polarity of movement of auxin fits in well with the mechanism in relation to shoot-root communication (Golsmith 1977; Goodwin 1978).

There is also a good example of cooperative levels of cytokinins and auxin controlling an integrated system of growth and development of plants in tissue culture (Murashige and Skoog 1962). Shoot initiation and growth was promoted by the high ratio of cytokinins/auxin, while a low ratio favoured root growth and development. The apical meristem of oat seedling coleoptiles was promoted when BA was applied at the apex of shoots or through the cut base in culture medium, whereas root excision reduced auxin secretion by coleoptile tips (Jordan and Skoog

1981). Auxin has an enhancing effect on root lateral formation (Webster and Radin 1972), and root cambial activity (Hejnowicz and Tomaszewski 1969; Wilson 1975). In addition, there is a positive relationship between auxin transport and growth of roots (Cane and Wilkins 1970; Hillman and Phillips 1970; Hejnowicz, 1968; Konings 1969), and root cambial activity (Wilson 1975).

On the other hand, there seems to be limited circumstantial evidence on the involvement of other hormones in the regulation of shoot-root equilibrium. Abscisic acid is believed to have a specific role in shoot-root communication as far as water stress is concerned (Hubick *et al.* 1986, Sharp and Davies 1989). The abscisic acid pool was once considered to be largely in the leaf mesophyll (Heilmann *et al.* 1980), and was supposed to antagonise effects with cytokinins, especially on stomatal conductance (*e.g.* Blackman and Davies 1983; Zhang *et al.* 1987 b). Recently, however, evidence has been obtained that ABA can be produced in root tissues (Walton *et al.* 1976; Lachno and Baker 1986). Subsequently, Sharp and Davies (1989) suggested that root ABA may have a different role from ABA emanating from the leaves and directly involve the mechanism of root controlled shoot growth via the control of stomata. Since this work has been largely based on plants under water stress, the extent to which ABA functions as an inhibitor of photosynthesis in leaves (Sharkey *et al.* 1989) and in intact plants, in general, still needs to be assessed.

The hormone model proposes that the rate of primary growth in the shoot depends on the rate of primary growth of the root, and *vice versa*, through hormonal feedbacks, and can be mediated by environmental factors such as, moisture and nutrient conditions of soils (Brouwer 1963; Wilson 1975; Brouwer 1983) or levels of light falling on the leaves (Loveys and Wareing 1971). Circumstantial evidence has so far supported this view. Results from a number of studies indicate that root hormones are involved in many developmental processes of the shoot. It has been demonstrated that senescence of detached leaves can be retarded if they are rooted (Chibnall 1954). Foliar application of exogenous cytokinin also delayed this aging process (Nooden 1984). Kende (1964) demonstrated that compounds in xylem exudate which were related to senescence co-chromatographed with zeatin. This effect of cytokinins on arresting senescence

has been suggested to involve the regulation of protein synthesis (Chibnall 1954) or chlorophyll formation in such leaves (Dei 1983).

Shoot activity may also be controlled by the cytokinin activity in the roots. Cytokinins enhanced transpiration (Biddington and Thomas 1978) and stomatal opening in grass leaves (Jewer and Incoll 1980; Blackman and Davies 1983). Bud break from dormancy is related to the activity of cytokinins, which has been detected in xylem sap of trees, *e.g.* in apples (Luckwill and Whyte 1968), *Populus* X *robusta* (Hewett and Wareing 1973), and oak (Smith and Schwabe 1980). Cytokinin activity was maximal just prior to bud burst (Hewett and Wareing 1973) or at full bloom (Luckwill and Wareing 1968), and disappeared from the sap when shoot growth had ceased (Luckwill and Wareing 1968) or in the dormant state (Hewett and Wareing 1973; Qamaruddin *et al.* 1990). The control of lateral shoot production (Kender and Carpenter 1972; Richards 1980; Greene and Autio 1989), and apical dominance (Woolley and Wareing 1972 a) are also influenced by the compound. Shoot growth has also been shown to be regulated by a mechanism involving the root cytokinins. Cessation of shoot growth coincided with the time when cytokinin level was low (Kende 1964; Sitton *et al.* 1967; Grochowska and Karaszewska 1978; Hurd 1978; Donchev 1981).

Under unfavourable root environments, root cytokinin production was suppressed, and so was shoot growth. These situations include deficient nutrient levels (Woolley and Wareing 1972 a; Menary and Van Staden 1976; Kuiper and Staal 1988), saline stress (Itai *et al.* 1968), drought (Itai and Vaadia 1965), waterlogging (Buurrows and Carr 1969), heat stress (Itai *et al.* 1973; Caers *et al.* 1985) and cold stress (Atkin *et al.* 1973). Reports on the relation between gibberellin levels in xylem sap and stressed root environments, however, have been mainly confined to flooding (Reid *et al.* 1969; Reid and Crozier 1969; 1971). In addition, qualitative changes in cytokinins due to stresses have also been reported (Walker and Dumbroff 1981). In contrast, improving root conditions results in an increased cytokinin content. Yoshida and Oritoni (1974) showed that cytokinin level was increased by nitrogen fertilization. Kuiper and Staal (1987) obtained similar results. The cytokinin content was correlated positively with the internal nutrient level in the plant tested. From this evidence, it is generally accepted that

the production of cytokinins within root tissues, may be environmentally determined and since shoot growth is correlated with that of roots, overall plant growth may be controlled by the production of cytokinins within the roots.

Application of synthetic cytokinins (Railton and Reid 1973; Richards and Rowe 1977 b) or GA_3 (Carmi and Heuer 1981) to the shoot of plants, in which roots were stressed, can restore shoot growth partially or fully. These results indicate that in such conditions, shoot growth is suppressed by the lack of root hormones. In contrast, Kulaeva (1962) showed that rooted leaf-cuttings did not respond to exogenous cytokinin while derooted leaves did, indicating a response to applied cytokinin is dependent on the absence of the root system. In other words, the supply of cytokinins from the roots is optimum, or sufficient, in the normal plants, but deficient in the derooted plants.

The implication of the preceding discussion is that the activity of the root tip with respect to its capacity to produce hormones determines the level of cytokinins and, perhaps, gibberellins in plants. Various models propose that the hormone activity of the root tip and consequently the quantity of the hormone exported from the root itself adjusts according to the rhizosphere environment (Skene 1975; Blackman and Davies 1985; Kuiper and Staal 1987). This influences growth of shoot apices (Woolley and Wareing 1972 b), shoot growth and development ((Itai *et al.* 1968, 1973; Reid and Crozier 1971; Richards and Rowe 1977 b; Walker and Dumbroff 1981; Blackman and Davies 1985; Kuiper *et al.* 1988), production of auxins in the shoot tips (Jordan and Skoog 1971), ABA in the leaves (Davies *et al.* 1986), stomatal conductance (Jewer and Incoll 1980; Incoll and Whitelam 1977; Blackman and Davies 1983; 1985) and perhaps transpiration rates (Biddington and Thomas 1978; Blackman and Davies 1983), the latter two of which lead to changes in photosynthetic rate. As a consequence of the altered rate of shoot growth, the quantity of auxins exported to roots increases. This completes the feed back loop, which would continue to increase in activity until a factor in the root or shoot environment becomes limiting.

Considering the range of root and shoot environments normally encountered during the growing season by crop plants, Chalmers (1987) proposed

that the root environment limits growth in the majority of situations. If this is correct, it follows that the hormonal signal produced by the root system in response to the limiting root environment will limit overall growth and production by the whole plant. Extending the preceding argument, it is logical to assume, and indeed there is considerable explicit evidence in plant ecology, that the influence of the rhizosphere has dominated evolution of the correlative growth mechanism of roots and shoots. If this is correct it is also likely that the activity of the root system will remain the rate limiting process in an experimental system (using natural light and CO_2 levels) in which the physical and chemical limitations of the rhizosphere have been minimized.

Few attempts have been made to investigate the functional relationship between shoot and root systems of trees. This is mainly due to the difficulty of establishing the suitable plantation for experimentation and in maintaining the operations involved for the time required for trees to become mature. Apart from excavation, accurate measurement of root parameters remains difficult and time-consuming to obtain due to tree size (Wilson 1975). Thus, only seedlings of annuals or trees, mostly in pots, have so far been used for these types of studies. On the account of this difficulty, two parallel experiments were proposed for the studies. The first experiment was to follow the growth of a slower growing perennial fruit trees, *i.e.*, nashi, to investigate the allometric relationship between the shoot and root system, and to provide information leading for future study. In the second experiment, tomato seedlings were used to provide rapid turnover of plant generations to allow for modification and testing of the hypothesis of plant growth regulation via root hormones.

Since in the first study, establishing experimental trees required two years, which followed by two years of investigation and measurements. The main objectives were:

1). To study the distribution of photoassimilates (and carbohydrate reserves) in young nashi trees grafted onto three clones of seedling rootstocks.

2). To determine quantitatively the dimensions of the root and the shoot.

3). To investigate the dynamics of allometric growth between the shoot and root system.

4). To investigate the respective roles of primary growth rates of shoot and roots in regulating the growth of nashi trees in the early years.

In the parallel group of experiments, a similar approach to growth analysis was followed. In addition, however, the involvement of the two key hormones in the shoot-root allometric relationship was studied. Synthetic analogues of plant growth hormones can be applied in various ways to mimic effects of endogenously produced hormones. This approach has been used to gather circumstantial evidence that hormones regulate plant growth including the correlative mechanism (*e.g.* Wareing 1970; Richards and Rowe 1977 b; Kuiper and Staal 1987). Such evidence has often been questioned, however, on the grounds that, although the predicted response has been elicited, no evidence can be provided, that a parallel change in the analogous endogenous hormone causes that effect in normal (non-experimental) plants. Nevertheless, in studying whole plant models, such as inter-organ communication, few alternative options are available. In order to minimize this criticism, in this study, I have also sought to include treatment methods in which the synthetic analogue was delivered to the point of action, employing the natural pathway from the roots. By this approach, one could safely assume, that the synthetic chemical was moving with, and was probably combined with the pool of endogenous hormone. Therefore, in this work I have studied and analysed the growth responses of plants in which synthetic gibberellins and cytokinins have been applied via root systems and translocated to the shoots. Further, I employed a system of aeroponic irrigation which eliminates soil barriers, including, physical impedance, aeration, water and nutrient supply to avoid as far as possible confounding of treatment effects. Finally, I have employed a concentration range which, not only, spans the important published data, but also extends to lower concentrations to reduce the chance that normal physiological concentrations and response to the endogenous hormone were not grossly perturbed. In these ways, I have aimed to ensure, as far as possible, that the synthetic analogue enters and becomes part of the endogenous hormone pool, and only marginally supplements the natural concentrations.

CHAPTER 2
SHOOT-ROOT ALLOMETRY OF TREES ON DIFFERENT NASHI CLONES : A PRELIMINARY OBSERVATION

2.1. INTRODUCTION

Concepts of growth of a grafted (or budded) tree have generally been described in terms of a rootstock and scion relationship, rather than as a coordination of growth and function between organs of the plant (Tubbs 1973). It has been demonstrated, in pears on quince rootstocks (Tubbs 1977 b), apples (Vyvyan 1955; Tubbs 1980) and other fruit species (Tubbs 1977 b), that plant size is controlled by the genetics of the graft partners. The resultant relative growth rate of a young compound tree is the arithmetic mean of the two individual rates of its components when grown on their own roots, at the same age and site, with only negligible contribution of the interaction between the two (Tubbs 1980). The prediction of growth rate for such trees, therefore, can be made using the growth data of the individual partners.

An attempt has also been made to quantify the influence of the genetic contribution as well as the effect due to position of the grafted partners. Lefort and Legisle (1977), working with only one character, *i.e.*, length of *Vitis* vine, for a single growing season, proposed a biometrical model composed of the simple influence of, and interaction between, the two grafted partners, and the position effect. While this genetic model seems to answer the question of uncertainty arising from grafting two clones of different growth rate, it appears that generalization cannot be made from this analysis for all species.

On the other hand, the vigour of trees can be altered by other characteristics in mature trees (Tubbs 1973), which may not be explained by such genetic model. For example, Quince C as a rootstock for pear cultivars showed no dwarfing effect until this attribute was induced by precocious fruiting of the scion (Tubbs 1977 a). Although varieties may differ in the proportion of stem and root in their first year as a seedling (Maggs 1958), this difference decreases in mature

trees (Rogers and Vyvyan 1934). These results imply that the growth of trees is modified, to some degree, by the environment. It has been observed that growth characteristics of a clone as a rootstock can be changed when it acts as a scion (Tubbs 1977 b), and the stem-root ratio varies between different sites (Rogers and Vyvyan 1934). Thus, the functional balance of plant shoot and root systems is no less important than their genetic composition in controlling plant growth, as well as yield.

It is accepted that plants cannot survive unless they can maintain functional and size balances between their various organs (Pearsall 1927; Brouwer 1963; Wareing 1970). This requires an extensive network of feedback mechanisms by which functioning of various organs can be continuously correlated and adjusted to each other (Wareing 1970). This assumption of growth coordination seems to hold for annuals, perennials and compound fruit trees alike (Brouwer 1963; Wareing 1970). The aim of the study is to observe growth and development, and examine the allometric relationship, in young nashi trees. The method of measurements of dry weight and certain other attributes will enable the progressive changes with seasons to be analysed and described. The allometric relationships and related growth patterns have been studied in mature compound fruit trees throughout their growing stages (Chalmers and Van den Ende 1975). However, such an investigation has never been performed for very young grafted (or budded) trees.

2.2. MATERIALS AND METHODS

2.2.1. Experimental Procedures

The three nashi (*Pyrus serotina*) rootstock clones used were initially found as seedlings growing in bags at a commercial nursery. Visually, they indicated differing degrees of vigour as three year-old plants. Rootstock #2 seemed to be most vigorous, while #1 appeared to be least vigorous. Multiplication of these clones *in vitro* was carried out at the nursery and in February 1986 one hundred propagules of each clone were obtained and repotted into 8" volume planting bags. Each bag contained a mixture of 65% peat, 35% sand, optimum quantities of complete fertilizers, and slow released fertilizers (Osmocote 14-6.1-11.6 and 18-2.6-10). After two subsequent re-pottings, individual trees were transplanted into 50-litre black polyvinyl bags in January 1987. The potting medium was composed of Manawatu river sand mixed thoroughly with the same rate of fertilizers. Thereafter, the similar rate of fertilizers were supplied by top dressing and drilling, coinciding with the addition of 24 g dolomite twice annually.

Fifty four trees, selected for uniformity, from each clone were transferred to an experimental plot at the Fruit Crops Unit, Massey University, in December 1987 (Fig. 2.1). The trees were arranged in three double rows, running north-south, with an initial spacing of 80 cm X 125 cm on levelled-ground. This area was covered with a black polyethylene sheet, extending well beyond the bags on both sides of the rows to control weeds. The space between trees became larger as trees were harvested. Each plant was supplied with water through a drip emitter (capacity of 4 litres/hour) connected to a short sub-lateral (0.5 cm inner diameter) drawing water from the main irrigation laterals (1.9 cm internal diameter). The irrigation system was connected to the main orchard system which was scheduled using residual soil moisture. Due to the low water holding capacity of the sand, additional water was supplied to the experimental trees manually as needed, especially during dry period which coincided with a failure of the irrigation system. The emitters were frequently checked and changed if malfunctioning. In addition to holes in the base of the bag, four holes were made in each bag five centimetre above ground level to avoid water-logging. Routine orchard pest management was provided.

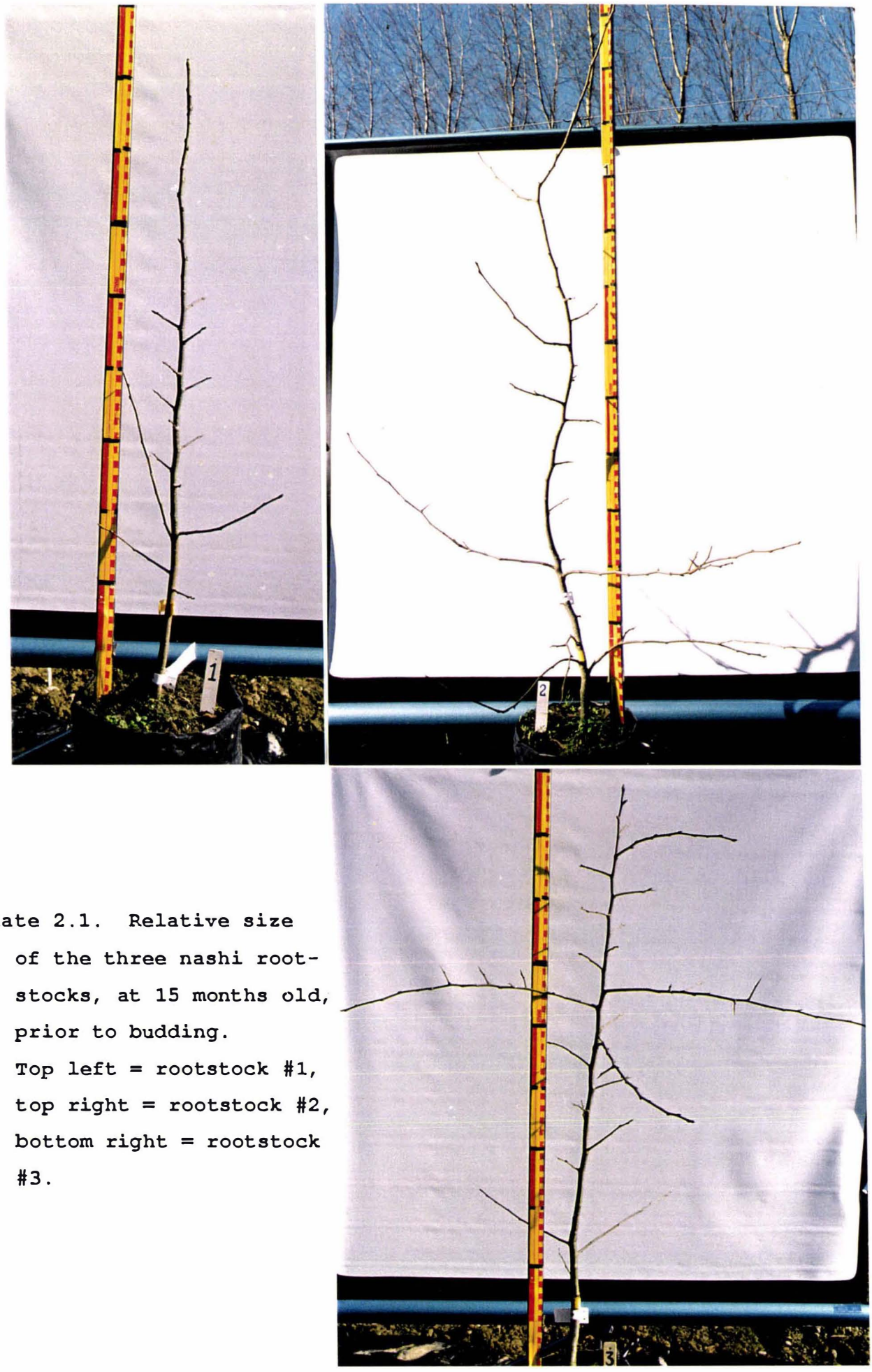


Plate 2.1. Relative size of the three nashi rootstocks, at 15 months old, prior to budding.
Top left = rootstock #1, top right = rootstock #2, bottom right = rootstock #3.

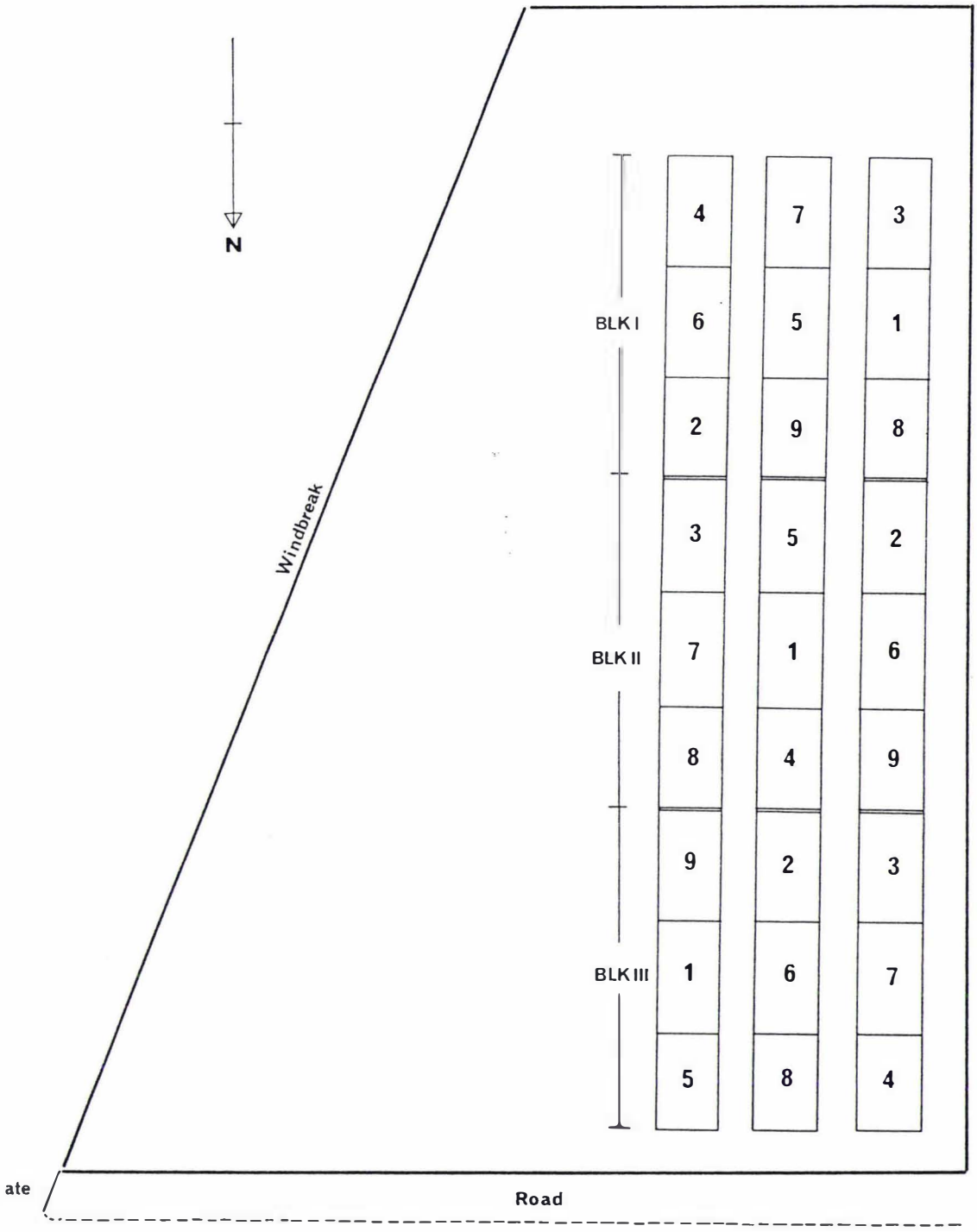


Figure 2.1. Nashi experimental layout, the number in each square indicates the scion/rootstock combination :

1 = rootstock#1/rootstock#1	2 = Hosui/1	3 = Nijiseiki/1
4 = 2/2	5 = H/2	6 = N/2
7 = 3/3	8 = H/3	9 = N/3

The three rootstocks were T-budded in March 1987 with the scion cultivars Hosui and Nijiseiki (henceforth called scion-budded trees). In addition, each rootstock clone was budded with the same rootstock clone to provide a budded rootstock plant as a control (henceforth called rootstock trees). This gave nine combinations of rootstock and scion. Single trees of each scion clone were used as the source of buds. Budding was completed in August when the rootstocks were topped. There was no visible signs of incompatibility for any bud combinations. The trees were allowed to grow untrained with the minimum amount of supporting wire required to prevent wind damage, and were unpruned for the course of the experiment. Measurement of rootstock diameters, 5 cm under the bud, was made three months after budding to assess vigour. Butt cross sectional areas calculated from these data showed a significant difference between rootstocks. Rootstock #2 was largest (166 $\pm$ 3.6 sq.mm.), followed by rootstock #3 (128 $\pm$ 3.4 sq.mm.), and rootstock #1 (107 $\pm$ 3.3 sq.mm.) was smallest.

2.2.2. Experimental Design

Serial harvests were planned as a split-plot design with three blocks, each covering one-third of all rows (Fig. 2.1). In each block, a group of six trees of each budded combination represented a plot unit (factor A). Time was the sub-plot factor (factor B) with five levels or harvest dates, with one extra (spare) tree allowed for each plot. With this arrangement, each harvest could also be considered as a randomized complete block design (RCBD) experiment on its own.

Three trees of each rootstock clone were selected at random, prior to budding in February 1987, and used as an initial sample to determine the dry weight of plant parts at that time. It was planned to harvest one plant per treatment per block to make a total of 27 trees per harvest. During the two year course of the experiment, harvests were performed one year after budding and later at intervals of three months, *i.e.*, the first week of February, May, August and November, as these times were at the transitions between seasons.

2.2.3. Collection of Data

Water rinsing allowed each plant to be harvested with the minimum of sand attached to the root system. This process was slow and approximately three days were required for one complete harvest, *i.e.*, one block per day. Thorough rinsing was performed carefully in the laboratory to minimize the loss of fine fibrous roots.

Leaves (when present), stem and roots were separated for each plant. The root system was kept in cold water in a cool room at 5°C. Following measurements of shoot parameters which generally required two days, roots were further separated into the subsurface crown, and real roots. The crown was chopped into pieces, not larger than 1 X 2.5 X 1.5 cm. After root volume was determined by water displacement (Bohm 1978), roots were cut into lengths not exceeding 2.5 cm and laid onto a sampling tray (44 X 60 cm) with enough water to facilitate an uniform distribution. For a large root sample, three to five trays were needed to accommodate the sample. Five to ten percent of the total root sample was subsampled at random and submerged in cold fresh water, which was kept in a 1-litre can at 5°C until root number and root length were determined. The cold water was replaced every two days to keep the samples fresh. Towards the end of the experiment, subsamples taken from 4-5 very large samples (which more than three trays were needed to facilitate subsampling) was as low as 2.5% of total root length.

The parameters measured in the study were:

Shoot :

- Total stem dry weight
- Leaf dry weight
- Leaf Number
- Leaf area

Root :

- Root length
- Root number
- Root dry weight

- Root volume

Leaf area was determined by Licor Area Meters, model LI-3100 (Lambda Instruments Corp., USA). Root length was estimated by Comair Root Length Scanner (Richards *et al.* 1979 b) (Hawker de Havilland Victoria Ltd., Australia), calibrated using the formula:

$$A = -0.2246 + 0.9655\,E + 0.00123\,E^2,$$

Where A = adjusted estimate of root length,
and E = root length measured by the scanner.
Root number was determined by counting the root joint at which the roots branched. For each subsample, this was conducted by examining a small portion of a subsample suspended in water in a petri-dish against a dark background (Richards and Rowe 1977 a). The time consumed for root number determination was approximately two weeks. During this period, therefore, roots had to be kept in such a way that no alteration of parameters occurred. According to the recommendation in the root length scanner manual, the storage life of roots can be extended to 6-10 weeks if kept under the storage conditions described in this study. On the other hand, the subsamples were only 2.5 to 10% of the roots, and the effect of any losses to other root data would have been small. Each plant part was oven-dried separately at 70^{o}C for two to four weeks, to constant weight, before being weighed.

2.2.4. Data Analyses

2.2.4.1. Mean Analyses and Comparisons

Analysis of variance (ANOVA) and least significant difference test (Lsd) were performed on individual harvests (as a single RCBD). In this experiment, serial harvests provided data on developmental changes, along with seasonal changes and increments of plant size. All ANOVA performed in this study (and subsequent studies) were based on the random effect model of analysis of variance.

2.2.4.2. Estimations of K-values

Dry matter data of aerial (leaf, stem or total shoot) parts of all harvests were transformed into natural logarithms, (ln Y), together with all the root dry weight data, (ln X), enabling a graph of ln Y against ln X to be drawn for each treatment and resulting trends were observed (Reiss 1988). Statistical tests of the apparent linearity were carried out by fitting the following least squares equation to the data:

$$\ln Y = \ln a + k \ln X$$

where
- ln a — is a constant or intercept of the regression line at the y-axis.
- k — is the slope of the regression line, henceforth called the k-value.
- ln Y — is the logarithm of leaf, stem or shoot (both leaf and stem) dry weight.
- ln X — is the logarithm of root dry weight.

In this study, ln and log will be used interchangably, but in all instances will refer to the natural logarithm. The k value was calculated for the pooled data only, since there was insufficient replications for each treatment at individual harvests.

To resolve any differences between k-values, an unprotected means comparison was carried out using a t-test (Steel and Torrie 1980).

2.2.4.3. Calculation of Mean Relative Growth Rates (RGR) and their Variances

Mean relative growth rates (RGR) between two consecutive harvests were calculated by the method described by Venus and Causton (1979), using non-pairing replicate plants of the two harvests. The mean RGR is given by :

$$E(RGR) = 1/(t_2-t_1).[E(\ln W_2) - E(\ln W_1)]$$

and $$V(RGR) = 1/(t_2-t_1).[V(\ln W_2) + V(\ln W_1)],$$

where
- $E(RGR)$ is the expected value of the relative growth rate.
- $V(RGR)$ is the expectedvariance of the relative growth rate;
- t_1, t_2 are harvest times 1 and 2 respectively.
- $E(\ln W_2)$, $E(\ln W_1)$ are the expected values of logarithmic dry weights at times 1 and 2 respectively.
- $V(\ln W_2)$, $V(\ln W_1)$ are the expected values of variance of the logarithmic means at times 1 and 2 respectively.

Because the samples collected at each harvest were independent of one another, there is no covariance between $\ln W_1$ and $\ln W_2$.

2.3. RESULTS

2.3.1. Differences in Leaf Attributes

Leaf data were recorded only three times; in late summer (early February 1988), late spring (November 1988) and in the following summer (February 1989). Some leaves had abscissed before the final harvest was completed on February 18, 1989. This premature leaf fall may have been due to drought during the previous month (January), which coincided with a failure of the irrigation system. Caution was therefore exercised in interpreting these data for the final harvest.

By the end of the first season (February 1988), rootstock 2/2 had significantly higher leaf area than plants in other treatments (Table 2.1). Leaf area and leaf number increased markedly between the first and the second growing season. Leaf expansion of the rootstock trees started earlier and proceeded at a more rapid rate than the scion-budded trees, which increased in growth rate towards the end of the season. By the end of the growing period (summer), the rootstock trees had attained a significantly greater leaf areas compared to the scion-budded trees. Rootstock 2/2 had the greatest leaf area, while the cultivars worked onto this rootstock, conspicuously, showed the lowest leaf area.

Leaf number was the decisive factor causing the difference in leaf area between treatments (Table 2.1). Dissimilarity in the number of leaves was so great that even at the final harvest the trend appeared not to be affected by the loss of leaves in the premature leaf fall (Table 2.1). Leaf number of rootstock trees was significantly higher than scion-budded trees. Nonetheless, the reverse trend was true for leaf size. Of the cultivars, Hosui had larger leaves than Nijiseiki which is characteristic of the cultivars. Between rootstocks, the larger leaf size of rootstock 2/2 resulted in the higher leaf area over other rootstocks, although this difference was non-significant.

2.3.2. Differences in Root Attributes

In general, the rootstock trees had much larger root systems than scion-budded trees (Table 2.2). A significant difference was, however, detected at only

TABLE 2.1. *Seasonal changes in leaf attributes during second year of growth of nashi trees*

Time	Scion/rootstock	Leaf area ($X10^3 cm^2$)		Leaf number		Leaf size (cm^2)	
		**		**		**	
February	1/1	5.46	a	489	b	11.0	a
1988	H/1	2.66	a	43	a	64.4	c
	N/1	2.90	a	60	a	52.2	c
	2/2	9.91	b	327	b	30.1	b
	H/2	3.25	a	34	a	62.8	c
	N/2	2.69	a	36	a	55.0	c
	3/3	4.21	a	392	b	10.9	a
	H/3	2.84	a	70	a	51.1	c
	N/3	2.71	a	51	a	53.7	c
	se	0.70		51		2.7	
November		**		**		ns	
1988	1/1	16.17	b	2460	c	6.6	
	H/1	6.10	a	233	a	28.6	
	N/1	4.61	a	173	a	26.8	
	2/2	22.49	b	1085	b	21.6	
	H/2	6.99	a	184	a	34.6	
	N/2	-		-		-	
	3/3	16.84	b	2085	c	8.0	
	H/3	10.03	a	379	a	27.2	
	N/3	5.68	a	228	a	24.9	
	se	1.28		133		18.5	
February		ns		*		*	
1989	1/1	15.33		1774	b	13.0	a
	H/1	11.56		247	a	80.6	b
	N/1	11.81		160	a	74.0	b
	2/2	18.94		784	ab	29.2	ab
	H/2	9.26		378	a	70.1	b
	N/2	7.15		102	a	70.0	a
	3/3	12.76		2462	b	6.2	a
	H/3	19.53		502	a	38.7	ab
	N/3	12.46		375	a	34.2	ab
	se	2.71		390		10.4	

- Each mean figure from 3 replications with $df_{(error)} = 16$.
- Mean separation within column by Lsd ($p \leq 0.05$).

TABLE 2.2. *Seasonal changes in root attributes during second year of growth of nashi trees*

Time	Scion/rootstock	Root length (m)		Root number x10 ^{3}		Root volume (cm^3)	
		**		**		**	
February	1/1	324	a	18.8	a	338	a
1988	H/1	273	a	17.2	a	213	a
	N/1	213	a	9.9	a	265	a
	2/2	1214	c	128.4	b	783	b
	H/2	501	ab	20.1	a	255	a
	N/2	723	b	45.6	a	305	a
	3/3	327	a	27.9	a	377	a
	H/3	303	a	30.8	a	333	a
	N/3	271	a	28.7	a	328	a
	se	52		10.9		37	
		**		*		ns	
May	1/1	1219	a	42.7	ab	720	
1988	H/1	279	a	23.3	ab	245	
	N/1	535	a	31.5	ab	373	
	2/2	2386	b	34.0	ab	721	
	H/2	708	a	21.9	ab	387	
	N/2	1227	a	45.8	ab	527	
	3/3	846	a	62.7	b	803	
	H/3	398	a	25.8	ab	380	
	N/3	403	a	20.3	a	377	
	se	215		7.4		118	
		ns		ns		ns	
August	1/1	791		44.1		404	
1988	H/1	1293		55.5		539	
	N/1	959		45.6		557	
	2/2	1572		52.3		697	
	H/2	480		34.9		297	
	N/2	1258		37.8		443	
	3/3	1708		67.0		818	
	H/3	938		47.0		502	
	N/3	617		46.3		455	
	se	397		12.5		138	
		ns		ns		**	
November	1/1	869		51.0		913	b
1988	H/1	488		41.0		275	ab
	N/1	560		41.9		241	a
	2/2	1420		52.4		1935	d
	H/2	1318		66.2		480	ab
	N/2	-		-		-	
	3/3	959		58.0		1392	c
	H/3	632		54.2		609	ab
	N/3	437		43.4		220	a
	se	213		8.2		83	

TABLE 2.2. (continued)

Time	Scion/rootstock	Root length (m)	Root number x10 ^{3}	Root volume (cm^3)	
		ns	ns	**	
February	1/1	4294	192.4	1820	b
1989	H/1	1821	127.9	823	a
	N/1	1354	108.1	757	a
	2/2	8865	172.7	2157	b
	H/2	3250	106.9	705	a
	N/2	2101	124.3	517	a
	3/3	3208	148.6	1905	b
	H/3	2361	144.3	1168	a
	N/3	4100	122.0	1190	a
	se	1449	23.3	164	

- Each mean figure from 3 replications with $df_{(error)} = 16$.
- Mean separation within column by Lsd ($p \leq 0.05$).

one harvest. After one year of growth, the root size of rootstock 2/2 (measured as length, number and volume of roots), was greater than other combinations. Root length of most tree combinations increased throughout autumn, then decreased through winter and spring. This trend probably reflected root shedding, followed by elongation again during summer. In contrast to root length, root number decreased during autumn, increased again in early spring, and then seemed to decrease in early summer (Table 2.2). This final decline maybe due to competition with shoots for photoassimilates, before rapid production over the following period. Root volume, like root length, also increased over the autumn period but not in winter (Fig. 2.2). By early summer, all rootstock trees had increased in root volume, while the scion-budded trees had remained inactive. By the end of the second season, the rootstocks had attained an appreciably larger root volume. Thus, in the end, root size of rootstock trees had increased markedly, by whatever parameter measured.

Of the root parameters investigated, root volume demonstrated the greatest discrimination between treatments (scion-budded versus rootstock trees), particularly at the two final harvests (Table 2.2). Root volume is perhaps a better indicator of root activity than either root length or root number as it combines differences of both parameters.

2.3.3. Progression of Changes in Absolute Growth

The trees derived from buds of the same rootstock clone showed much stronger growth than the cultivars (Table 2.3), despite all tree combinations started from a single bud as a scion. By the end of the first year (February 1988), the size of all rootstock trees was larger than the scion-budded trees (Table 2.3). Rootstock 2/2, in particular, resulted in all parameters measured being larger size. During autumn and winter there was only a small size increase in most trees. Growth of rootstocks commenced earlier in spring than the scion-budded trees, in which growth occurred later in summer (Fig. 2.3 to 2.7). Thus, it was not unexpected that the difference in growth between the rootstocks and the scion-budded trees was highly significant only during active growing periods, *i.e.*, at February 1988, November 1988 and February 1989 harvests.

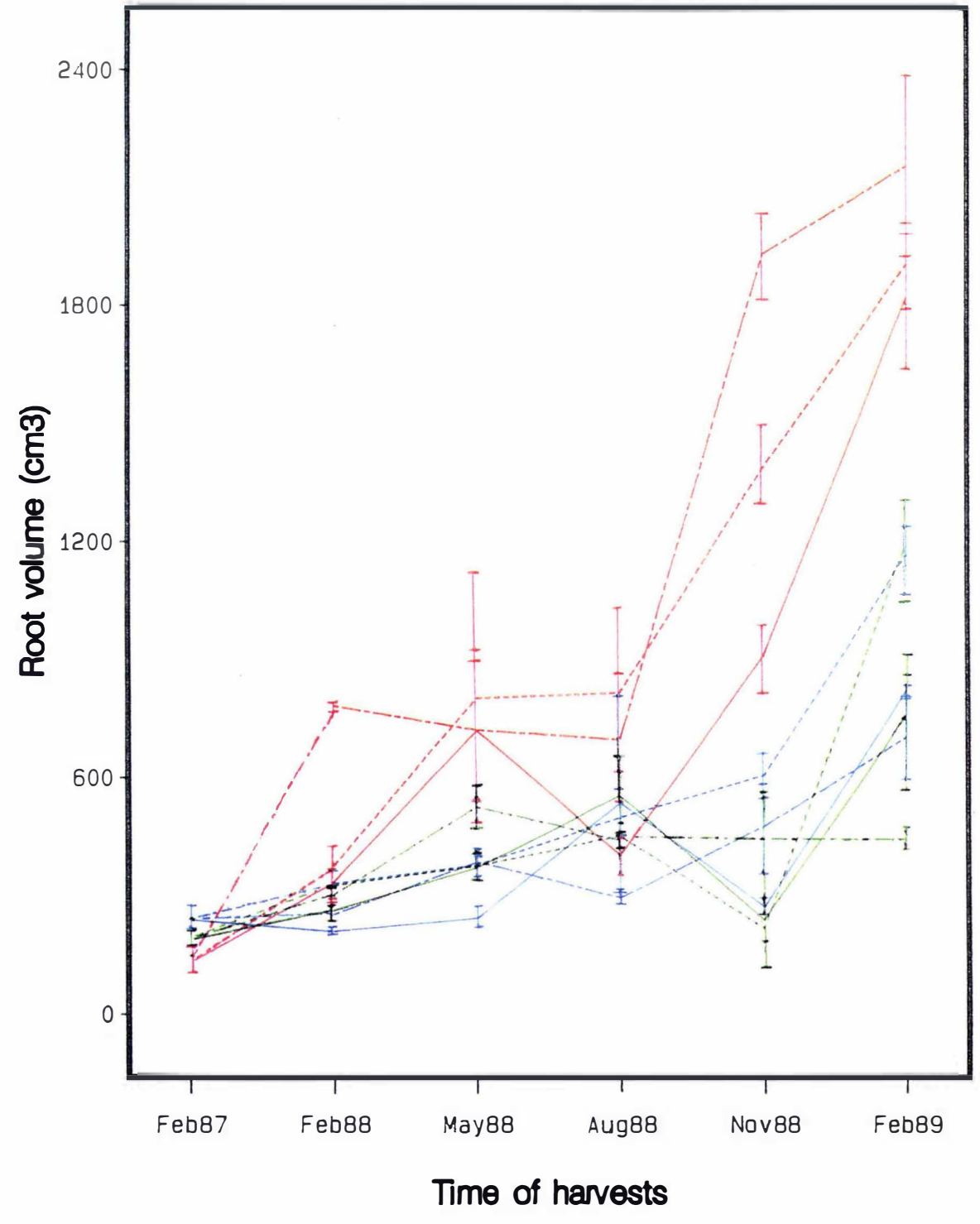

2400
1800
1200
600
0
Root volume (cm3)
Feb87
Feb88
May88
Aug88
Nov88
Feb89
Time of harvests
Treatment
1/1
H/1
N/1
2/2
H/2

TABLE 2.3. *Seasonal changes in dry weight of plant parts and whole plant during second year of growth of nashi trees*

Time	Scion/rootstock	L_w*1	S_w*2	T_w*3	R_w*4	W*5
		**	**	**	**	**
February	1/1	62 a	187 a	249 a	82 a	331 a
1988	H/1	39 a	97 a	136 a	65 a	202 a
	N/1	47 a	103 a	150 a	85 a	235 a
	2/2	137 b	341 b	478 b	204 b	682 b
	H/2	40 a	95 a	135 a	90 a	225 a
	N/2	34 a	46 a	81 a	87 a	167 a
	3/3	54 a	165 a	219 a	119 a	337 a
	H/3	38 a	91 a	129 a	100 a	228 a
	N/3	42 a	83 a	124 a	107 a	231 a
	se	10	30	34	10	48
			ns	ns	ns	ns
May	1/1	-	259	259	201	459
1988	H/1	-	111	111	92	202
	N/1	-	124	124	126	250
	2/2	-	201	201	194	396
	H/2	-	129	129	128	256
	N/2	-	183	183	159	342
	3/3	-	225	225	285	510
	H/3	-	101	101	150	251
	N/3	-	82	81	145	226
	se	-	50	50	34	82
			ns	ns	ns	ns
August	1/1	-	141	141	131	272
1988	H/1	-	218	218	215	433
	N/1	-	156	156	190	346
	2/2	-	203	203	171	373
	H/2	-	91	91	107	198
	N/2	-	109	109	110	219
	3/3	-	259	259	241	500
	H/3	-	129	129	156	285
	N/3	-	145	145	155	300
	se	-	37	37	44	77
		**	**	**	**	**
November	1/1	140 b	329 b	470 b	217 a	687 b
1988	H/1	47 a	127 a	175 a	72 a	247 a
	N/1	30 a	99 a	130 a	81 a	210 a
	2/2	206 c	414 b	620 c	379 b	999 c
	H/2	34 a	181 a	215 a	137 a	352 a
	N/2	-	-	-	-	-
	3/3	164 b	382 b	546 bc	445 b	991 c
	H/3	71 a	191 a	262 a	167 a	429 a
	N/3	42 a	75 a	116 a	103 a	220 a
	se	10	34	26	30	57

Table 2.3. (continued)

Time	Scion/Rootstock	L_w *1	S_w *2	T_w *3	R_w *4	W *5
		ns	**	*	**	**
February	1/1	200	838 b	1039 b	603 ab	1642 b
1989	H/1	144	496 a	639 a	251 a	890 a
	N/1	168	368 a	536 a	245 a	781 a
	2/2	265	689 ab	953 ab	672 b	1626 b
	H/2	118	385 a	503 a	191 a	695 a
	N/2	90	225 a	315 a	174 a	488 a
	3/3	174	502 a	676 a	763 b	1439 ab
	H/3	235	455 a	690 a	401 ab	1091 a
	N/3	172	302 a	474 a	401 a	875 a
	se	34	70	95	67	150

- Each mean figure from 3 replications with $df_{(error)} = 16$.
- Mean separation within column by Lsd ($p \leq 0.05$).
- *1 = Leaf dwt.,
  *2 = Stem d.wt.,
  *3 = Shoot d.wt.,
  *4 = Root d.wt.,
  *5 = Whole plant d.wt.

Figure 2.3. Temporal changes in leaf dry weight of nashi trees during the first two years after budding. I = standard error of means.

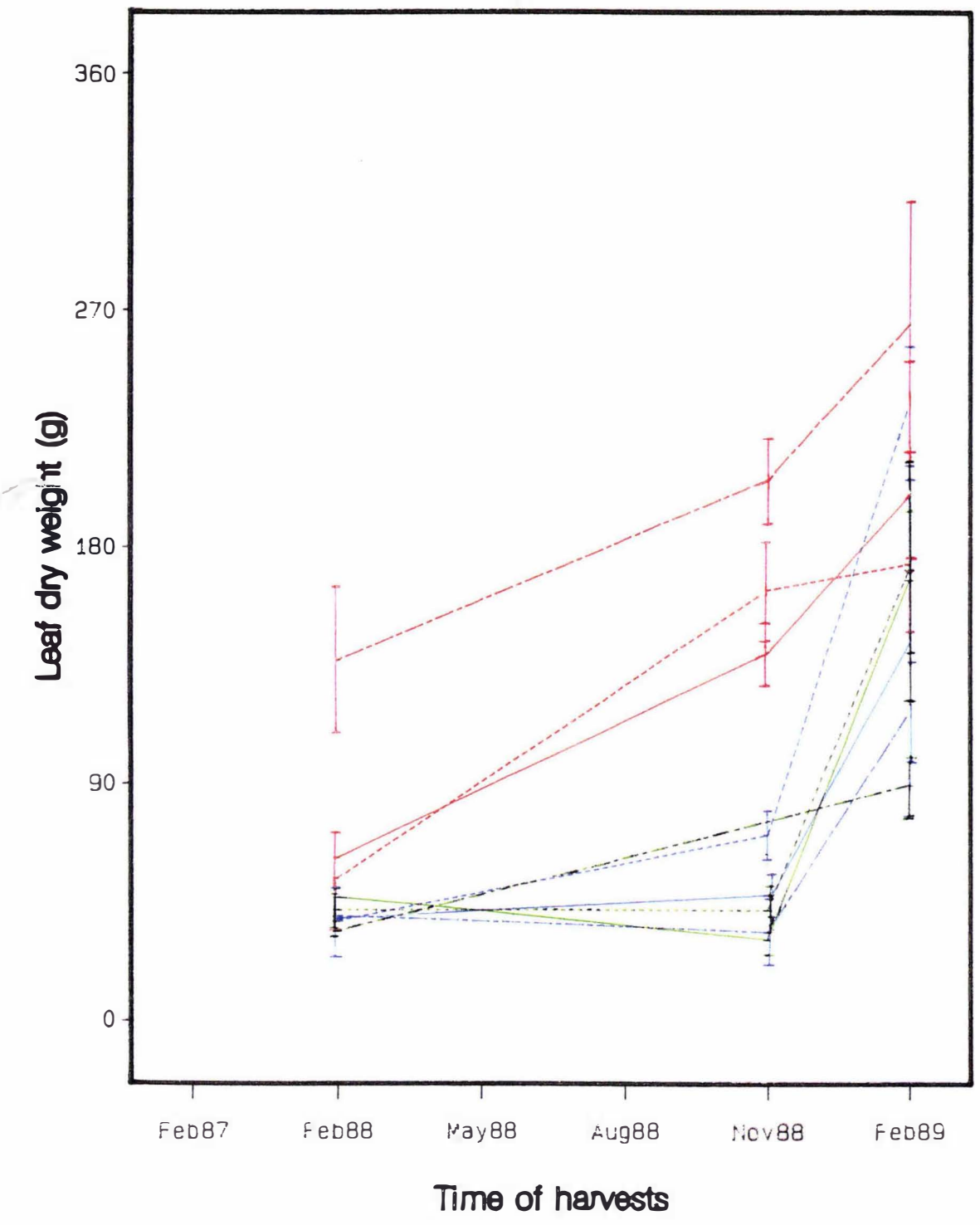

360
270
180
90
0
Leaf dry weight (g)
Feb87
Feb88
May88
Aug88
Nov88
Feb89
Time of harvests
Treatment
1/1
H/1
N/1
2/2
H/2
N/2
3/3
H/3
N/3

Figure 2.4. Temporal changes in stem dry weight of nashi trees during the first two years after budding. I = standard error of means.

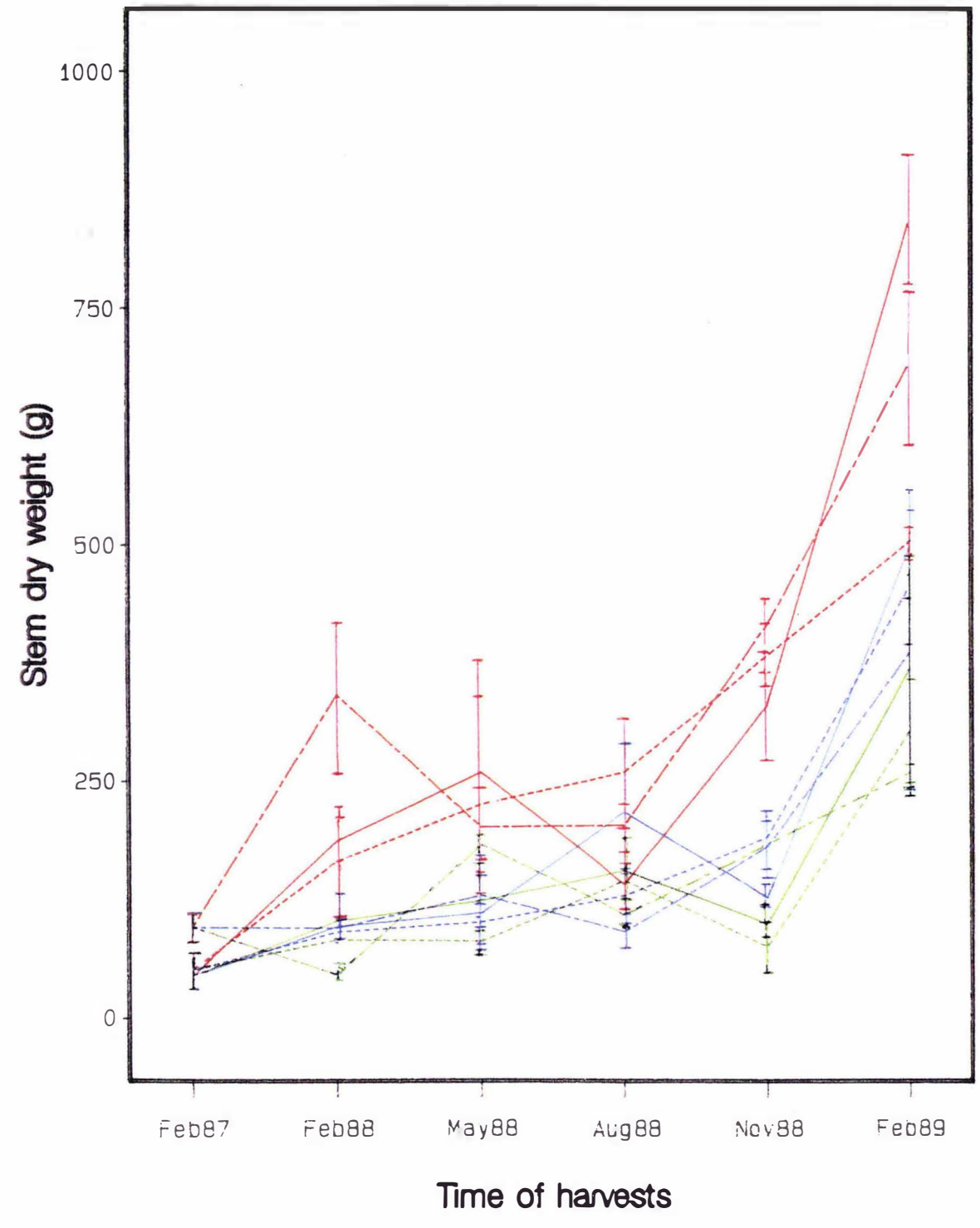

1000
750
500
250
0
Stem dry weight (g)
Feb87
Feb88
May88
Aug88
Nov88
Feb89
Time of harvests
Treatment
1/1
H/1
N/1
2/2
H/2
N/2
3/3
H/3
N/3

Figure 2.5. Temporal changes in shoot dry weight of nashi trees during the first two years after budding. I = standard error of means.

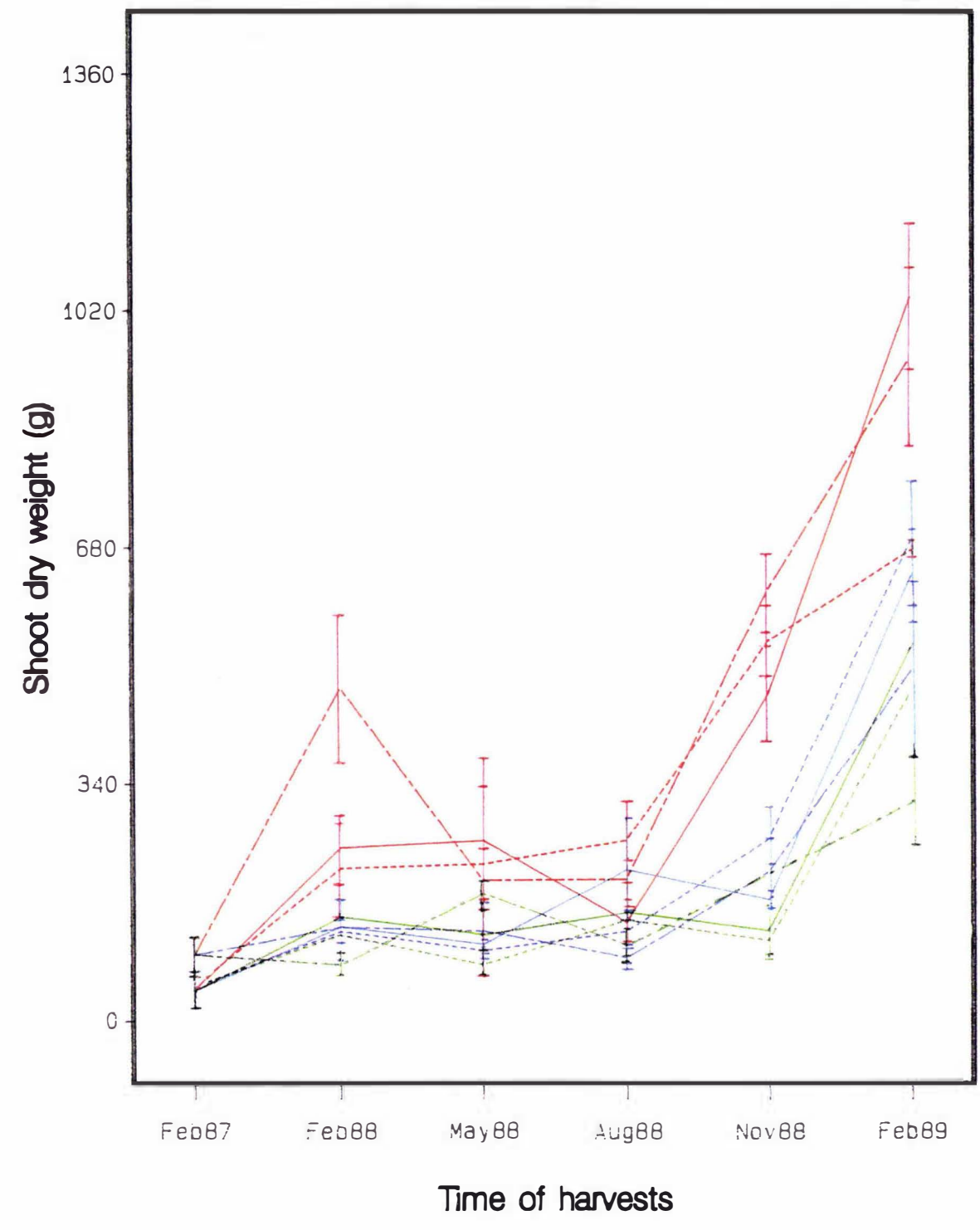

1360
1020
680
340
0
Shoot dry weight (g)
Feb87
Feb88
May88
Aug88
Nov88
Feb89
Time of harvests
Treatment
1/1
H/1
N/1
2/2
H/2
N/2
3/3
H/3
N/3

Figure 2.6. Temporal changes in root dry weight of nashi trees during the first two years after budding. I = standard error of means.

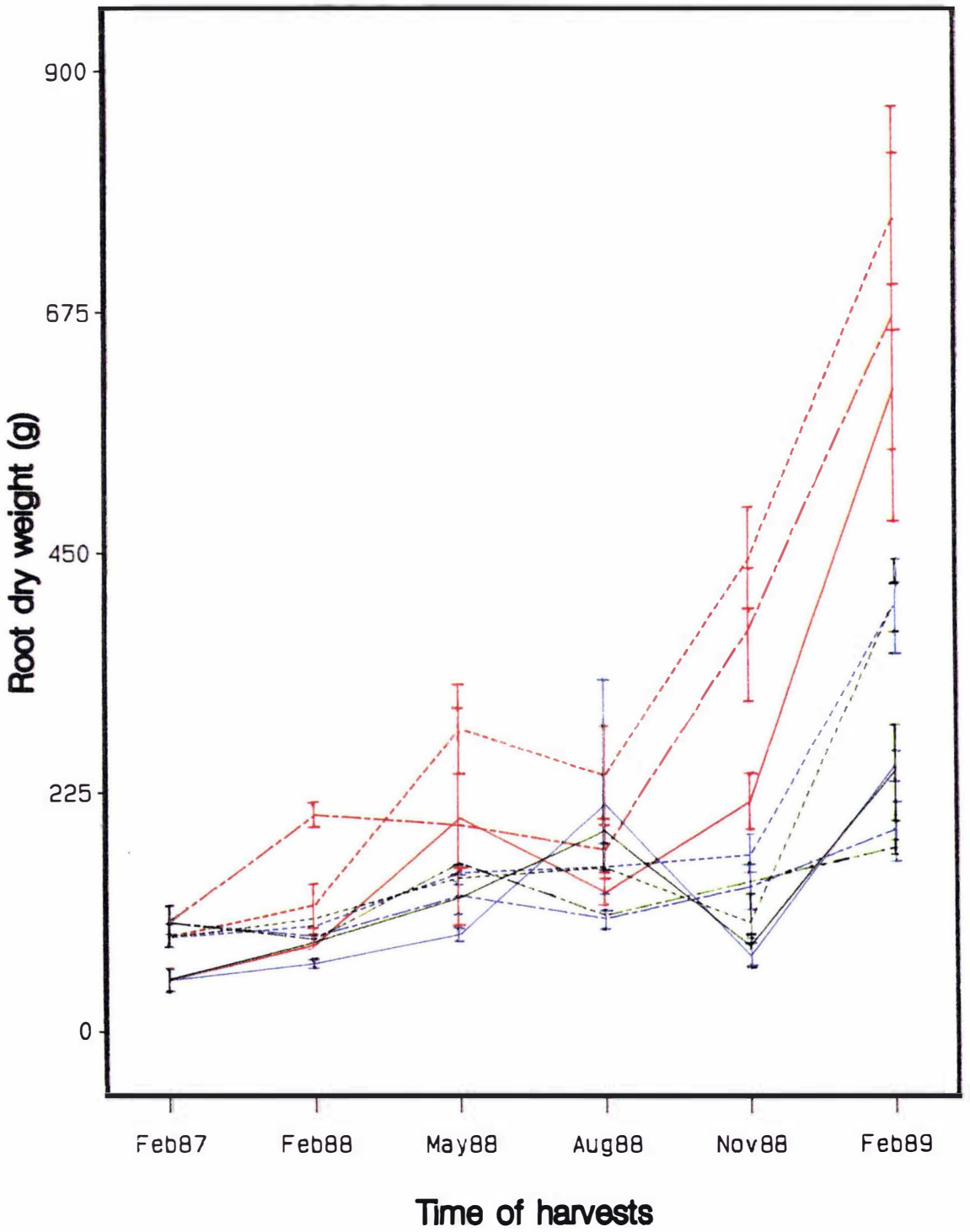
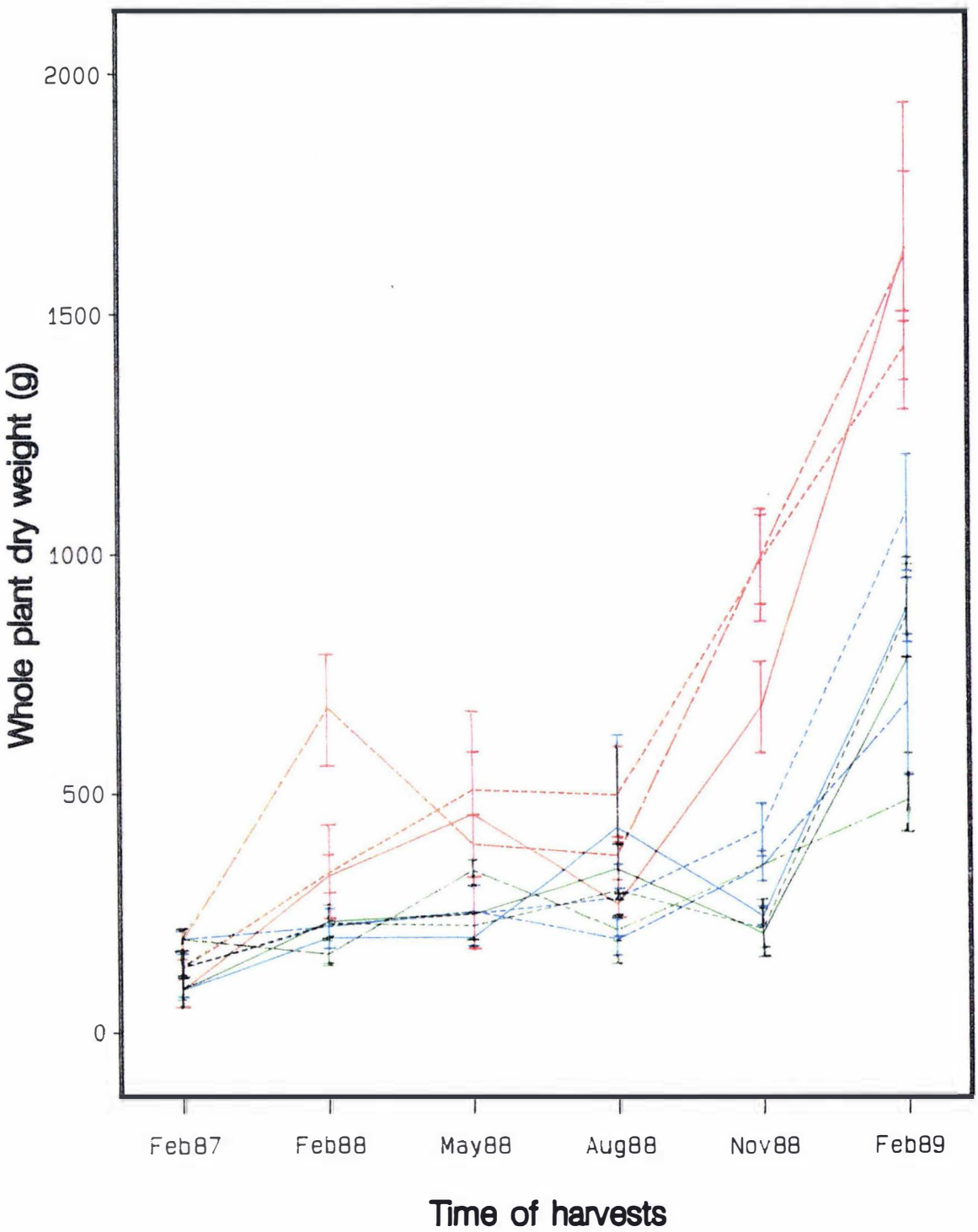

900
675
450
225
0
Root dry weight (g)
Feb87
Feb88
May88
Aug88
Nov88
Feb89
Time of harvests
Treatment
1/1
H/1
N/1
2/2
H/2
N/2
3/3
H/3
N/3

Figure 2.7. Temporal changes in total dry weight of nashi trees during the first two years after budding. I = standard error of means.


2000
1500
1000
500
0
Whole plant dry weight (g)
Feb87
Feb88
May88
Aug88
Nov88
Feb89
Time of harvests
Treatment
1/1
H/1
N/1
2/2
H/2
N/2
3/3
H/3
N/3

The pattern of changes in all organ and total dry weights indicated earlier spring growth and activity of the rootstock trees. The leaf development (Fig. 2.3) was significantly different due to early bud burst and rapid leaf expansion of the rootstocks, while in the scion-budded trees leaf expansion rate increased measurably, later in the season.

The stem and root dry weights generally continued to increase during autumn but decreased over the winter period (Fig. 2.4 and 2.6), which was also reported by Vyvyan (1931) in apple seedlings, and Bhar *et al.* (1970) in plum trees. The development of the canopy appeared to be totally under scion control. Rootstocks did not influence lateral production or main shoot length (data not presented). The main shoot of the scion-budded trees was generally very long; up to two metres, with few laterals. The rootstocks, by contrast, had a considerably shorter main shoot with profuse branching. This contrast resulted in a vast difference in total shoot length between the two groups. When leaves were included in the data analysis, the pattern of changes in shoot (leaf plus stem) growth was similar to that of stem, reflecting the influence of the latter which was the major component of the tree, being approximately 45 to 55 % of total dry weight in general (Table 2.4). Root growth of scion-budded trees decreased (Fig. 2.6), along with shoot growth (Fig. 2.5), in spring, while rapidly increasing in the rootstock trees. At the end of the second growing season, plants could be placed into two distinct groups of root size (Fig. 2.6). One consisted of the rootstocks and the other of the scion-budded trees. Roots of the scion-budded trees were also grouped with respect to rootstocks, as was also apparent in root volume (Fig. 2.2). In this respect, root volume appeared to more reliably represent root size, measured by dry weight (Fig. 2.6), than either root length or number (Table 2.2).

It is of interest that the root growth of rootstocks dominated increase in size, while in the scion-budded trees, the shoot was the major contributor to the increased size of the total plant. For example, between the two growing seasons the increase in roots of rootstock 1/1 was 7.4 fold but only 4.2 fold in the shoot (Table 2.3). By contrast, the increases in N/1 trees were by factors of 2.88 and 4.7 for the roots and shoot respectively. Although these combinations gave the

TABLE 2.4. *Seasonal changes in dry weight distribution during second year of growth of nashi trees expressed as a ratio of plant organ to total plant dry weight or to root dry weight*

Time	Scion/rootstock	Leaf weight ratio %	Stem weight ratio %	Root weight ratio %	Shoot-root ratio	Stem-root ratio
		ns	*	*	*	**
February 1988	1/1	18.6	56.3 b	25.1 a	3.02 b	2.27 b
	H/1	19.4	48.1 ab	32.5 ab	2.10 a	1.49 a
	N/1	20.5	42.2 a	37.3 b	1.71 a	1.56 a
	2/2	19.7	48.9 b	31.4 ab	2.22 ab	1.58 ab
	H/2	18.4	43.7 a	37.9 b	1.77 a	1.26 a
	N/2	20.6	33.1 a	46.3 b	1.05 a	0.63 a
	3/3	15.3	46.2 a	38.6 b	1.71 a	1.28 a
	H/3	15.7	38.2 a	46.0 b	1.39 a	0.81 a
	N/3	18.0	35.7 a	46.3 b	1.16 a	0.77 a
	se	1.2	2.9	3.4	0.26	0.20
			*	*	ns	ns
May 1988	1/1	-	54.5 b	45.5 a	1.22	1.22
	H/1	-	54.6 b	45.4 a	1.21	1.21
	N/1	-	49.6 b	50.4 a	0.98	0.98
	2/2	-	45.4 ab	54.6 ab	0.87	0.87
	H/2	-	48.0 b	52.0 a	0.98	0.98
	N/2	-	53.8 b	46.2 a	1.17	1.17
	3/3	-	43.9 ab	56.1 ab	0.78	0.78
	H/3	-	40.1 ab	59.9 ab	0.67	0.67
	N/3	-	35.4 a	64.6 b	0.55	0.55
	se	-	3.2	3.2	0.12	0.12
			ns	ns	ns	ns
August 1988	1/1	-	51.3	48.7	1.10	1.10
	H/1	-	53.0	47.0	1.15	1.15
	N/1	-	46.1	53.9	0.89	0.89
	2/2	-	53.9	46.1	1.19	1.19
	H/2	-	46.5	53.5	0.87	0.87
	N/2	-	50.0	50.0	1.01	1.01
	3/3	-	51.4	48.6	1.06	1.06
	H/3	-	44.7	55.3	0.86	0.86
	N/3	-	48.8	51.2	0.96	0.96
	se	-	4.3	4.3	0.16	0.16

(continued)

TABLE 2.4. (continued)

Time	Scion/rootstock	Leaf weight ratio %	Stem weight ratio %	Root weight ratio %	Shoot-root ratio	Stem-root ratio
		ns	**	ns	*	ns
November	1/1	20.7	47.4 b	31.8	2.15 b	1.50
1988	H/1	19.5	51.4 b	29.1	2.37 b	1.73
	N/1	14.5	46.8 b	38.7	1.47 b	1.23
	2/2	21.0	42.6 b	36.4	1.64 b	1.18
	H/2	9.3	50.8 b	39.8	1.73 b	1.45
	N/2	-	-	-	-	-
	3/3	16.5	38.6 ab	44.8	1.24 a	0.86
	H/3	16.6	44.1 b	39.3	1.56 a	1.13
	N/3	19.0	33.2 a	47.8	1.11 a	0.71
	se	2.3	2.5	3.6	0.21	0.15
		ns	**	**	**	**
February	1/1	12.0	51.2 b	36.8 b	1.72 bcd	1.39 b
1989	H/1	16.3	55.2 b	28.5 a	2.52 d	1.93 b
	N/1	22.0	45.6 b	32.4 ab	2.11 cd	1.43 b
	2/2	15.5	43.6 b	40.9 bc	1.47 abc	1.10 ab
	H/2	18.0	54.8 b	27.2 a	2.68 d	2.05 b
	N/2	15.6	49.9 b	34.5 ab	1.88 bcd	1.41 b
	3/3	12.2	35.0 ab	52.8 c	0.90 a	0.67 a
	H/3	21.5	41.7 ab	36.8 b	1.72 bcd	1.13 b
	N/3	19.3	34.1 a	46.6 c	1.18 ab	0.75 ab
	se	2.2	2.8	2.3	0.15	0.15

- Each mean figure from 3 replications with $df_{(error)} = 16$.
- Mean separation within column by Lsd ($p \leq 0.05$).

extreme values for this response, the effect was generally apparent among other treatments. This result indicates that in the presence of the cultivars, less photoassimilate was allocated to roots than in rootstocks. Meanwhile, it was also noted that rootstock 2/2 had declined in vigour by the end of the second year of growth (Table 2.3). The total increment was only 2.4 fold for rootstock 2/2 compared to 5.0 and 4.3 in rootstock 1/1 and 3/3 respectively. By this time, the difference in plant size between rootstocks as seedlings had disappeared or had become small. It appears, therefore, that the vigour of rootstock 2/2 may have been associated with the juvenile stage and was not persistent. On the other hand, this may be related to the difference in response of rootstocks to water stress at mid-summer of the second year of growth. These results suggest that evaluating *P.serotina* rootstocks for their vigour potential during the early years of growth does not provide useful information regarding their potential for that purpose. The apparent vigour shown for these growing conditions, at this age also provided no information in relation to the growth of the same or older age plants under other growing conditions.

2.3.4. Differences in Partitioning of Carbohydrate Reserves and Organ Weight Ratios

Since there were substantial differences in plant size as a result of the first year of growth, comparisons of the weight ratios, of organ dry weights to total plant dry weight, should give some insight to differences in photoassimilate and reserve distribution over the period studied for the two groups of trees.

No significant difference was obtained for root weight ratio (RWR) and stem weight ratio (SWR) between the rootstocks and scion-budded trees (Table 2.4). Initial growth of leaves appeared to be largely at the expense of reserves in the roots, as RWR decreased more markedly than SWR in the presence of leaves. Other studies on seasonal changes in carbohydrate distribution reported similar utilization of root reserves (Priestley 1963; Hansen and Grauslund 1973). Excluding leaves, RWR and SWR were approximately equal (Table 2.4). The portion of root reserves in the rootstocks was smaller than the scion-budded trees during the first growing period. This may be the result of greater use of reserves

and greater growth increment of the former. This difference disappeared during the dormant period. The RWR of scion-budded trees decreased, whereas it increased in the rootstocks by the end of the second year of growth. The RWR of rootstocks was larger than for the scion-budded trees on the same rootstock. This may imply that growth of the rootstocks not only had started earlier but also ceased sooner than the scion-budded trees. Considering the vigour potential of the two cultivars, the more vigorous, Hosui, appeared to grow more strongly than Nijiseiki, irrespective of the rootstock. These results indicate that the recognized vigour potential of scion had emerged after two years of growth.

Shoot-root ratio (which included leaves) fluctuated with seasons (Fig.2.8), as did stem-root ratio (Fig. 2.9). As mentioned above, in the presence of leaves the shoot shared a greater fraction of tree dry weight than the root system. The shoot-root ratio during the active growth period was high while it was lower during dormancy (Table 2.4). Since leaves are an annual component of the trees, variation due to leaves may be eliminated by using the stem-root ratio. Nevertheless, part of the fluctuation was due to the movement of root reserves, which were utilized in new leaf production. Thus, it remained apparent in stem-root ratios.

At the end of the first growing season, the shoot-root ratio of rootstock trees was higher than the scion-budded trees of the same rootstock. This occurred because residual root tissues of scion-budded trees remained the major weight constituent and the top grew only a little. In contrast, at the end of the second growing season, shoot-root ratio had declined in the rootstock trees whilst it had increased in the scion group (Table 2.4; Fig. 2.8). This suggests that compared to root growth, shoot growth rate increased more rapidly in the latter than the former, which was in agreement with the RGR(s). This response was not significant, however, except for rootstock 2/2, which differed significantly to H/2 and N/2 at this time. This decline in shoot-root ratio in rootstocks was due to the more advanced development of the rootstock trees entering the rest period. The evidence of low leaf weight ratio in these trees, which varied between 12 and 16% at February 1989, compared to 23 to 29% at the end of the first year of growth may support this proposition (Table 2.4).

Figure 2.8. Temporal changes in shoot-root ratio of nashi trees during the first two years after budding. I = standard error of means.

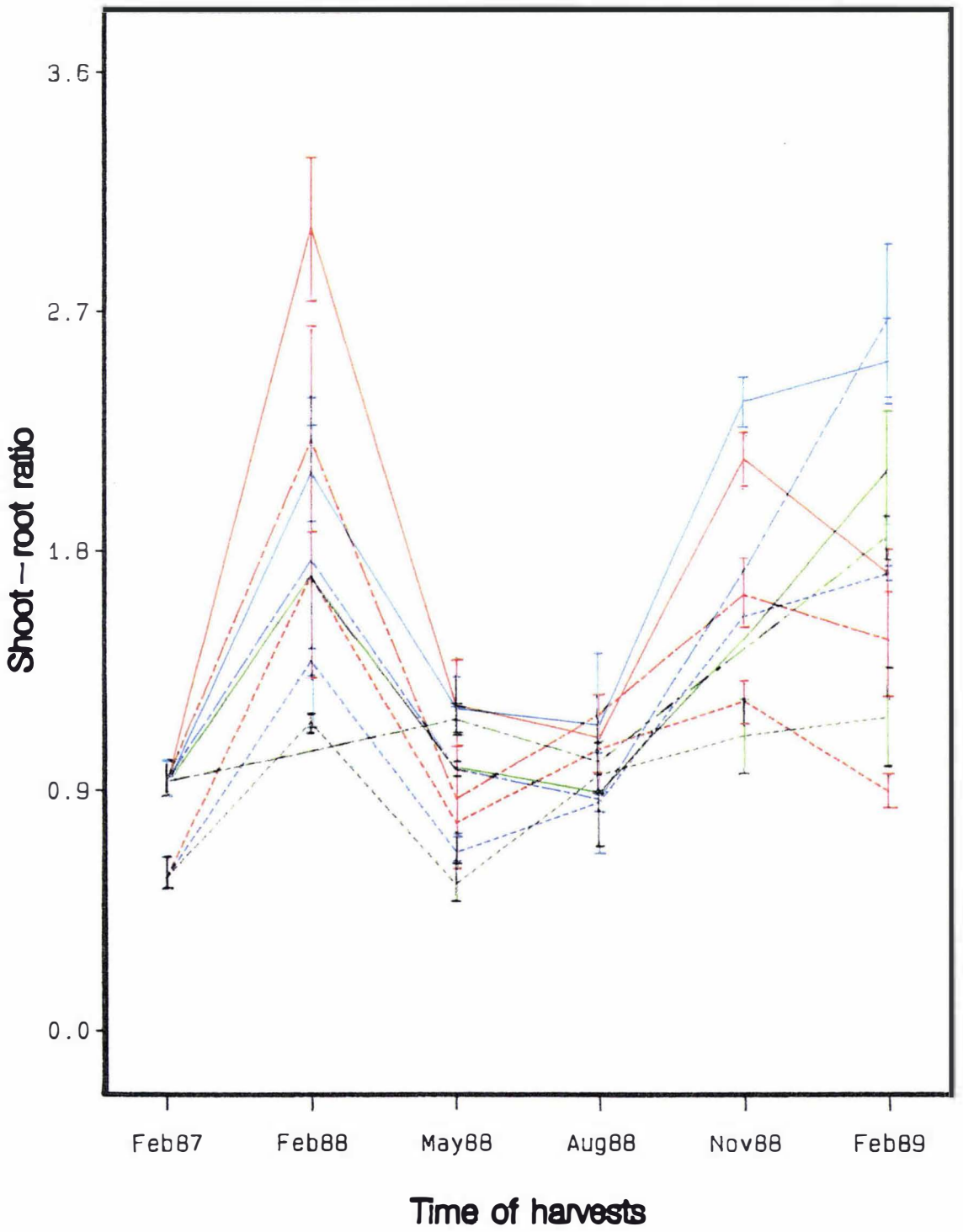
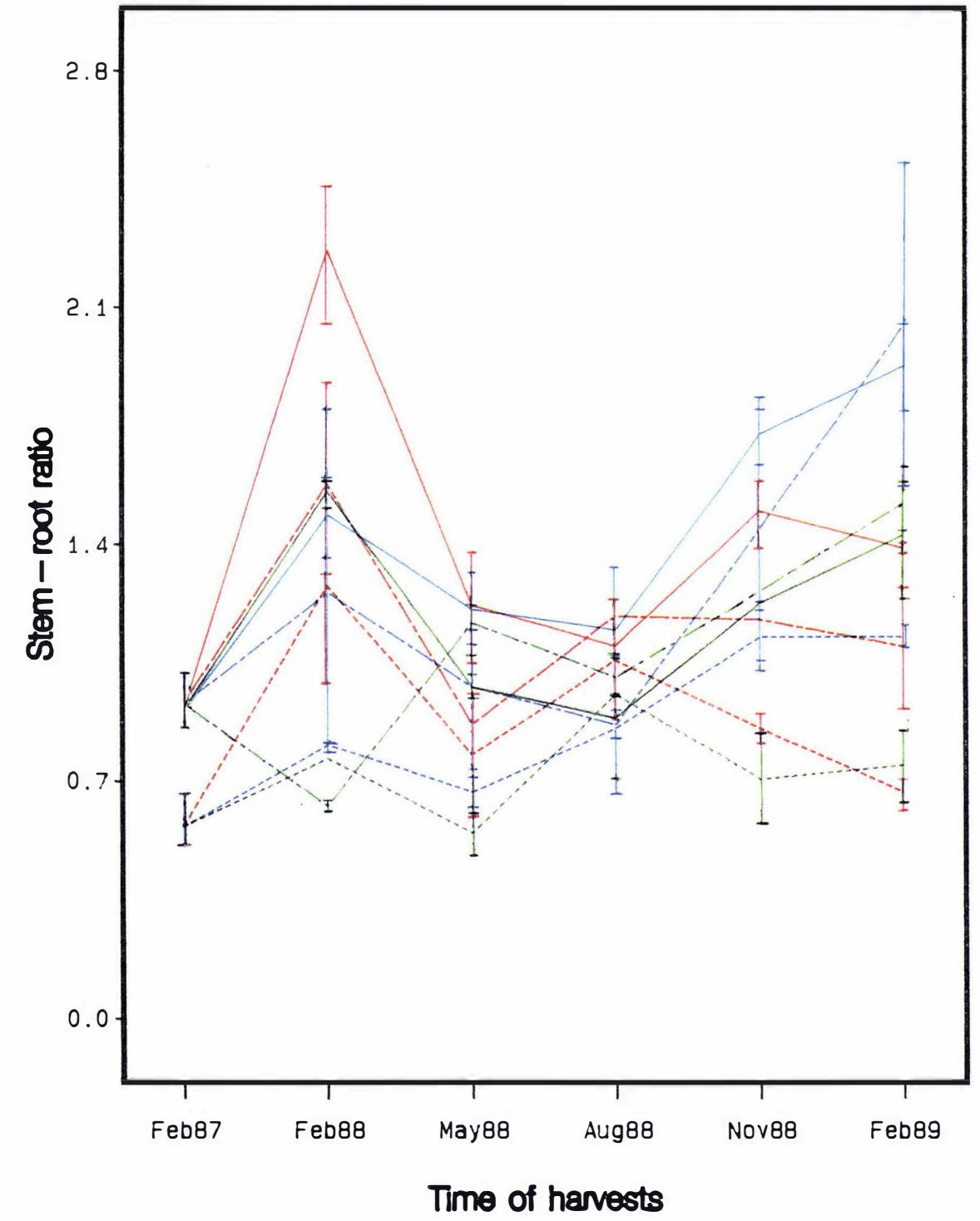

3.6
2.7
1.8
0.9
0.0
Shoot-root ratio
Feb87
Feb88
May88
Aug88
Nov88
Feb89
Time of harvests
Treatment
1/1
H/1
N/1
2/2
H/2
N/2
3/3
H/3
N/3

Figure 2.9. Temporal changes in stem-root ratio of nashi trees during the first two years after budding. I = standard error of means.


2.8
2.1
1.4
0.7
0.0
Stem-root ratio
Feb87
Feb88
May88
Aug88
Nov88
Feb89
Time of harvests
Treatment
1/1
H/1
N/1
2/2
H/2
N/2
3/3
H/3
N/3

at February 1989, compared to 23 to 29% at the end of the first year of growth may support this proposition (Table 2.4).

It could be argued that the decline of shoot-root ratios of the rootstocks may partly be attributed to the early loss of leaves. The leaf fraction was reported to be around 22% of total tree weight during the early years of fruit tree development (Vyvyan 1957), which agrees with the result of this study. Adjustment of the leaf fractions by adding 5% of root weight back into shoot weight may correct for this error. This adjustment, however, made no substantial difference in the pattern of distribution. Thus, it appears that the decline in shoot-root ratios, of the rootstocks, was real.

Shoot growth of rootstocks appeared to be more rapid than scion-budded trees in the first year only (Table 2.4). In contrast, during the second year, shoot growth of the scion-budded trees was faster. The results appear to indicate that the development of the latter was delayed, again supporting the hypothesis that the scion cultivars determined shoot-root performance and not *vice versa*. Similar results were obtained by Barden (1979), who found no effect of rootstock on shoot attributes in 1-year-old apple seedlings.

2.3.5. Differences in Relative Growth Rates

The seasonal pattern of tree growth does not allow one to determine relative growth rates at different times during the season. Nevertheless, the RGR(s) were calculated for the period between the end of two growing seasons (Table 2.5). Despite having the largest size after the first season, the whole plant RGR (RGR_W) of rootstock 2/2 declined during the second year, reflecting declining vigour with age. In general, the RGR(s) of the rootstock 2/2 and cultivars worked on it were lowest. Root RGR (RGR_R) of the rootstocks were higher than the scion-budded trees, while the Hosui shoot RGR (RGR_T) was higher than Nijiseiki on the same rootstock.

The RGR results, in general, are in agreement with the preceding results of organ weight ratios. During the second season, RGR_T of the rootstocks was

TABLE 2.5. *Relative growth rate of organs and whole plant of nashi trees during second year of growth*

Time	Scion/rootstock	RGR_L *1 $g.g^{-1}.y^{-1}$		RGR_S *2 $g.g^{-1}.y^{-1}$		RGR_T *3 $g.g^{-1}.y^{-1}$		RGR_R *4 $g.g^{-1}.y^{-1}$		RGR_W *5 $g.g^{-1}.y^{-1}$	
		*		*		*		*		*	
February 1988- February 1989	1/1	1.11	b	1.51	b	1.44	b	1.99	b	1.61	b
		(0.302)		(0.155)		(0.170)		(0.115)		(0.151)	
	H/1	1.16	b	1.64	b	1.56	b	1.37	a	1.50	b
		(0.330)		(0.119)		(0.041)		(0.068)		(0.015)	
	N/1	1.42	bc	1.32	b	1.35	ab	1.07	a	1.25	al
		(0.258)		(0.246)		(0.377)		(0.316)		(0.356)	
	2/2	0.74	ab	0.72	a	0.73	a	1.15	a	0.88	a
		(0.266)		(0.269)		(0.268)		(0.302)		(0.268)	
	H/2	0.80	ab	1.21	ab	1.13	ab	0.70	a	0.98	a
		(0.227)		(0.389)		(0.361)		(0.178)		(0.259)	
	N/2	0.32	a	1.31	ab	1.04	ab	0.68	a	0.90	a
		(0.278)		(0.394)		(0.374)		(0.320)		(0.301)	
	3/3	1.34	bc	1.29	ab	1.30	ab	1.90	b	1.56	b
		(0.339)		(0.361)		(0.355)		(0.223)		(0.357)	
	H/3	1.91	c	1.69	b	1.76	b	1.39	a	1.61	b
		(0.305)		(0.201)		(0.228)		(0.195)		(0.213)	
	N/3	1.40	bc	1.29	ab	1.33	a	1.34	a	1.34	b
		(0.245)		(0.216)		(0.225)		(0.142)		(0.176)	

- Each mean figure from 3 replications.
- Mean separation within column by t-test ($p \leq 0.05$).
- Standard error of means in bracket.
- *1 = Leaf relative growth rate,
  *2 = Stem relative growth rate,
  *3 = Shoot relative growth rate,
  *4 = Root relative growth rate,
  *5 = Mean relative growth rate.

scion-budded trees at the end of the first season. Thus, it appears that as the trees were severely shoot pruned following budding, they responded in order to rebalance the shoot-root size equilibrium. In the rootstock trees, this phenomenon, however, appeared to have occurred earlier, *i.e.*, during the first year. The data indicate that the regulating mechanism of shoot-root balance in compound trees may be more complex than in seedlings, at least during the early years of growth.

2.3.6. Changes in Allometric Relationships

With the inclusion of leaf dry weight, there was a considerable reduction in the coefficient of determination (R^2) for shoot-root allometric relationships (k_T) (Table 2.6; 2.7). In addition, the variation with respect to the intercepts or regression coefficients was higher when leaf weights were included in the regressions. There was, however, better discrimination between the allometric values between stem and root dry weights (k_S) than the values between shoot and roots (k_T). Thus, k_S appears to be more appropriate, giving more meaningful and stronger relationship than k_T.

Results from both data are generally similar, in that the trees on rootstock 2/2 had higher k values than trees on other rootstocks, while all k(s) of trees on rootstock 1/1 were lower than unity. In the presence of leaves, k_T of trees on the same rootstock was not significantly different, except those on rootstock 3/3, for which, H/3 was greater than other cultivars (Table 2.6; Fig. 2.10). On the other hand, k_S values for rootstocks were less than, or equal to unity, and generally less than the scion-budded trees on the same rootstock, although most differences were not significant (Table 2.7; Fig. 2.11). Rootstock 3/3 had the lowest k_S value whereas N/2 trees the highest. These values were significantly different from the other combinations. The low k_S value of rootstocks, in general, reflected the greater root growth over shoot growth, which was the reverse of the situation found in the scion-budded trees. The two extreme values suggest that in N/2 tree RGR_S was approximately twice RGR_R, while RGR_S was only 0.78 of RGR_R in rootstock 3/3. The intercept of the regression line with the y-axis (ln stem dry weight) of the rootstocks was higher than that for scion-budded trees. This reflected the larger plant size during early growth. This result for k_S, was in line with preceding

results, which suggests that in the presence of scion of different genetic material, the shoot-root equilibrium was slower to develop than in seedlings.

TABLE 2.6. *Allometric relationship between shoot and root dry weight (k_T) of nashi trees over the course of second year of growth*

Time	Scion/rootstock	ln a	*1 se(ln a)	k_T		se (k_T)	R^2 (%)
February 1988 - February 1989	1/1	0.927	0.880	0.924	a	0.166	70.4
	H/1	1.478	0.858	0.810	a	0.180	69.2
	N/1	0.934	1.019	0.894	a	0.211	59.9
	2/2	-0.761	1.178	1.198	b	0.209	80.4
	H/2	-0.259	3.064	1.118	ab	0.631	23.9
	N/2	-1.694	2.784	1.402	b	0.594	74.9
	3/3	1.028	0.680	0.833	a	0.118	79.2
	H/3	-1.856	1.220	1.377	b	0.234	74.2
	N/3	-0.288	0.786	1.046	a	0.155	77.7

- k_T values from slopes of linear regressions of $\ln y = \ln a + k_T \ln x$, where y is shoot d.wt. and x is root d.wt. Each parameter estimated from 15 plants.
- Comparisons of k_T based on t-test ($p \leq 0.05$), $df_{(error)} = 26$.
- *1 = Standard error.

TABLE 2.7. *Allometric relationship between stem and root dry weight (k_S) of nashi trees over the course of second year of growth*

Time	Scion/rootstock	ln a	*1 se(ln a)	k_S		se (k_S)	R^2 (%)
February 1988- February 1989	1/1	0.834	0.649	0.909	b	0.123	80.9
	H/1	0.749	0.595	0.923	b	0.125	85.8
	N/1	0.264	0.618	0.953	bc	0.128	83.5
	2/2	0.088	0.955	1.008	bc	0.170	81.5
	H/2	-0.982	2.575	1.238	c	0.530	35.3
	N/2	-4.260	0.696	1.900	d	0.143	98.9
	3/3	1.166	0.555	0.776	a	0.097	83.2
	H/3	-1.216	0.859	1.214	c	0.165	81.9
	N/3	-0.329	0.612	1.002	bc	0.121	84.1

- K_S values from slopes of linear regressions of $\ln y = \ln a + k_S \ln x$, where y is stem d.wt. and x is root d.wt. Each parameter estimated from 15 plants.
- Comparisons of k_S based on t-test ($p \leq 0.05$), $df_{(error)} = 26$.
- *1 = Standard error.

Figure 2.10. Allometric relationship between shoot and root dry weight (k_T) of nashi trees over the course of second year of growth.

Scion/rootstock 1/1: R2 = 70.4%, y = 0.927 + 0.92 x,
H/1: R2 = 69.2%, y = 1.478 + 0.81 x,
N/1: R2 = 59.9%, y = 0.934 + 0.89 x,
2/2: R2 = 80.4%, y =-0.761 + 1.20 x.
H/2: R2 = 23.9% y =-0.259 + 1.12 x,
N/2: R2 = 74.9%, y =-1.694 + 1.40 x,
3/3: R2 = 79.2%, y = 1.028 + 0.83 x,
H/3: R2 = 74.2%, y =-1.856 + 1.38 x,
N/3: R2 = 77.7%, y =-0.288 + 1.05 x,

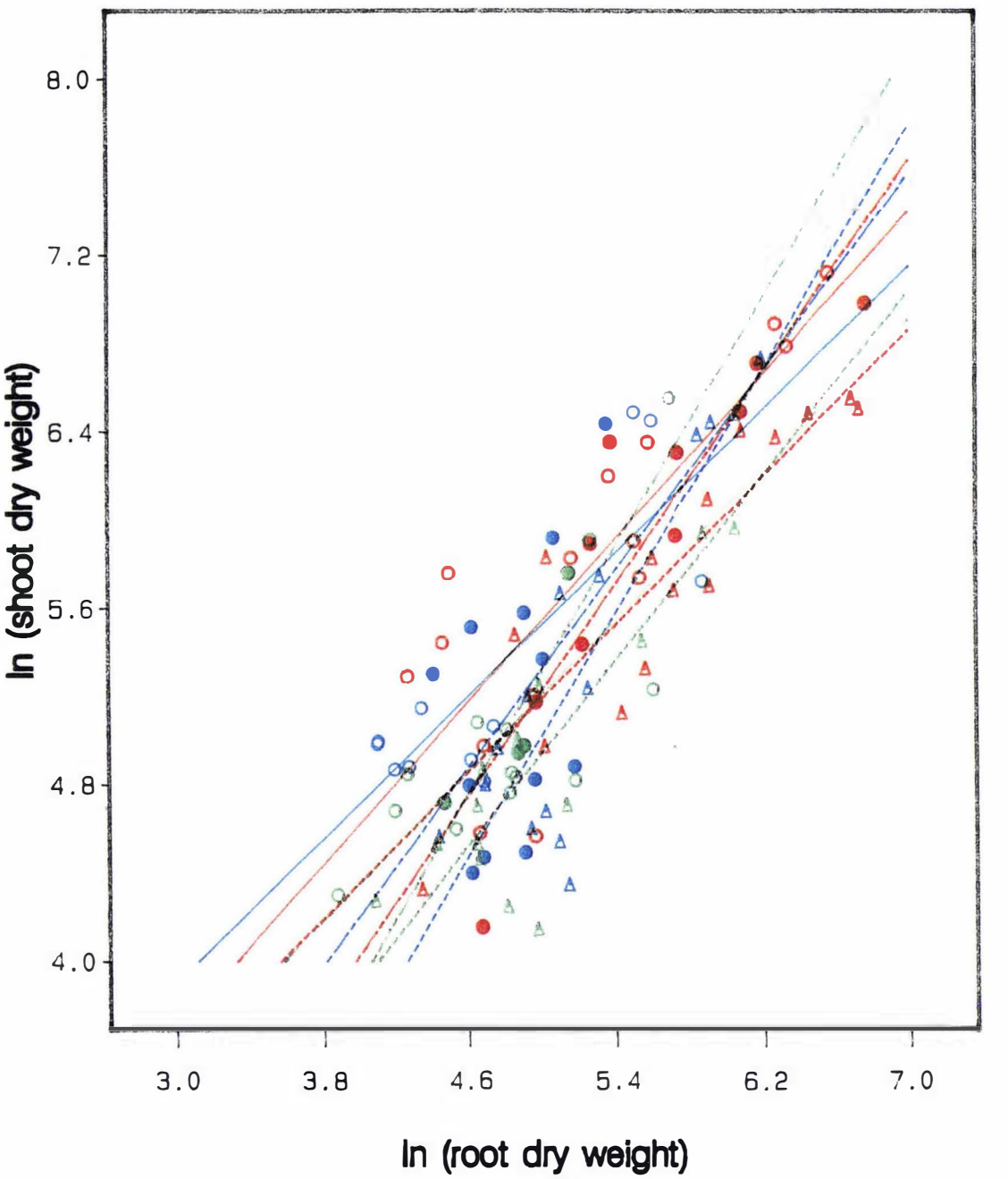
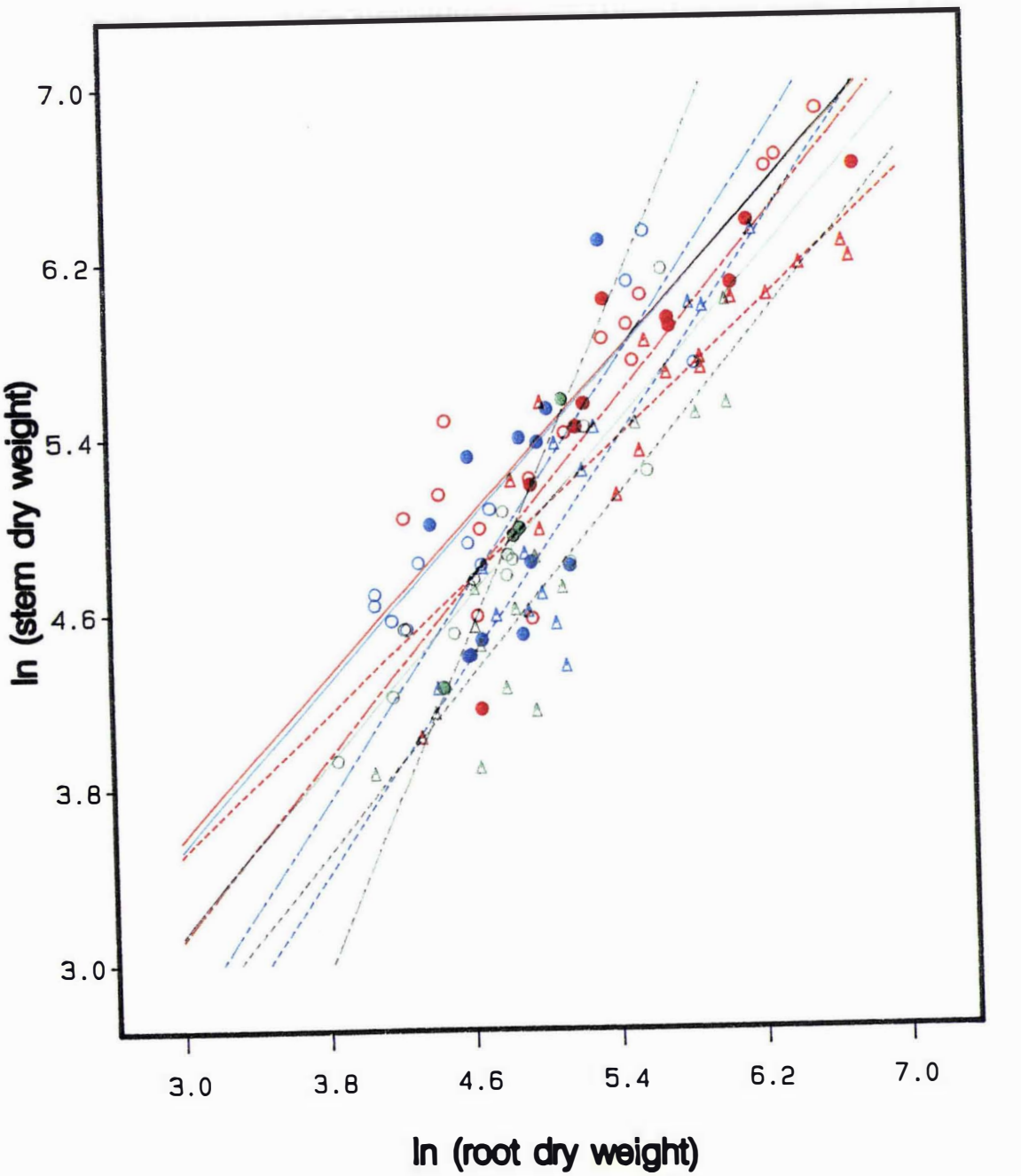

8.0
7.2
6.4
5.6
4.8
4.0
ln (shoot dry weight)
3.0
3.8
4.6
5.4
6.2
7.0
ln (root dry weight)
Treatment
1/1
H/1
N/1
2/2
H/2
N/2
3/3
H/3
N/3

Figure 2.11. Allometric relationship between stem and root dry weight (kS) of nashi trees over the course of second year of growth.

Scion/rootstock 1/1: R2 = 80.9%, y = 0.834 + 0.91 x,
H/1: R2 = 85.8%, y = 0.749 + 0.92 x,
N/1: R2 = 83.5%, y = 0.264 + 0.95 x,
2/2: R2 = 81.5%, y = 0.088 + 1.01 x.
H/2: R2 = 35.3% y =-0.982 + 1.24 x,
N/2: R2 = 98.9%, y =-4.260 + 1.90 x,
3/3: R2 = 83.2%, y = 1.166 + 0.78 x,
H/3: R2 = 81.9%, y =-1.216 + 1.21 x,
N/3: R2 = 84.1%, y =-0.329 + 1.00 x,


7.0
6.2
5.4
4.6
3.8
3.0
ln (stem dry weight)
3.0
3.8
4.6
5.4
6.2
7.0
ln (root dry weight)
Treatment
1/1
N/2
H/1
3/3
N/1
H/3
2/2
N/3
H/2

2.4. DISCUSSION

2.4.1. Growth of Nashi Trees after Budding

The size of scion-budded trees was markedly smaller than rootstock trees, irrespective of rootstock vigour, over the two year period observed. It appears, therefore, that properties of the scion initially limited growth. This phenomenon has also been reported in apples of the same age (Vyvyan 1955). Growth of trees composed of different clones was not lower than those of similar clones within the first year after budding, although this occurred in the later years. It was also noted that the growth of these trees was not substantial during this period. In contrast, for young nashi trees in this experiment, growth was many fold greater after one year of growth (Fig. 2.3 to 2.7). This difference may have been caused by both site and species differences. Growth in the second year was, however, much greater in apples than nashi trees, *i.e.*, 6 to 8 compared to 3 to 4 fold (Table 2.3). In apples, there was no apparent effect of residual root size on the growth of apple trees, in early years (Vyvyan 1955). In the second year, the size of the trees was already, more or less, in the order of rootstock. This phenomenon did not occur in nashi trees. The scion suppressed growth in the first year. When stronger growth occurred (a season later than rootstock trees) the effect of the imbalance in shoot-root ratio predominated. The size of scion-budded trees was in the expected order of scion growth potential, and not apparently related to rootstock (Table 2.3). A similar effect has also been noted by Rogers and Beakbane (1957), who recorded that scion performance over the first two to three years of age provided a sufficiently reliable indication of the long term influence of that scion. Considering that a scion bud was worked onto a well established and relatively large root system (compared to the size of scion bud), the imbalance of these two systems would persist for at least some time. This phenomenon, however, has not been observed in transplanted seedlings, which might be regarded as the opposite situation (Vyvyan 1934). This may be due to more rapid rebalancing of shoot-root ratio in transplanted seedlings. The data indicate that growth activity may be less flexible in shoots than roots.

There was no visible evidence of incompatibility. For instance, there was no breaking at the (bud)graft-union, over growth at, below or above the union,

union, unusual leaf yellowing, or growth decline at early age, *etc.* (Hartmann and Kester 1983; Garner 1988), observed during the period of the experiment. It was noted that failure of bud-take on rootstock 2/2 was high (60% of total replicates for this treatment, compared to 10-25% in other scion-budded trees, and 0-1% in rootstock trees). According to Jones (1974), the graft-union commonly impedes a reasonable fraction of growth factors ascending from the roots. There is, therefore, the possibility of a difference in the degree of completeness of graft unions, which may have impaired the performance of rootstock 2/2. The conductive union formed between like tissues is more rapid, providing greater growth substrate flows, than those formed between unlike tissues. Alternatively, Vyvyan (1955) has proposed that the slower growth of scion-budded trees is due to the mutual adjustments of their growth habits, and the commencement and cessation of growing periods.

On the other hand, there was no difference between rootstocks in terms of vigour. Vigour of all rootstocks appeared to diminish with time and final tree size was not well related to initial rootstock vigour. For example, the potentially vigorous rootstock (2/2) which had a distinctly larger root size had a correspondingly large leaf area, leading to large top size and hence a large tree compared to other treatments. This vigour potential, however, was apparent only during the first season and disappeared thereafter. This result indicates that early growth of trees on an unknown rootstock is not adequate for forecasting the overall growth potential of the mature tree. Rogers and Vyvyan (1957) also concluded that vigour potential of a tree could change at later ages. Furthermore, the evidently greater growth of the rootstocks over the scion-budded trees has been observed to diminish with age (Tubbs 1980). At five years of age, the former was smaller than the latter. Other evidence in pear also indicated a similar reversal (Tubbs 1977 a). The relative vigour of Quince C, compared to other quince rootstocks, was reversed when it was mature. For these reasons, young trees proved unsuitable for the study of allometric relationship. Consequently, caution should be expressed when comparing the response of young budded trees to external treatments, since the work on young trees would have limited value in relation to mature trees.

2.4.2. Characteristics of Scions and Rootstocks

Neither rootstock nor scion morphological characteristics appeared to be changed by the partner. Similar results were reported in two-year old apple trees (Rogers and Vyvyan 1957). Root size continued to be a function of the rootstock, while the ramification of shoots remained related to the scion characteristics. It was clear at the final harvest that root size of the scion-budded trees was clustered with respect to rootstocks (Table 2.2, 2.3 and Fig. 2.2). On the other hand, profuse branching of rootstock shoots contrasted with the shy branching of the scions (data not shown). Distinctive leaf characteristics, *e.g.* leaf size, of the scions was also unaltered by the rootstocks (Table 2.1).

Nevertheless, scion influence on the commencement of root activity, during the active period, was obvious. The presence of a cultivar bud on the rootstocks delayed the commencement of root activity in early spring (Fig 2.6). As a consequence, at this time, the rootstocks gained in total weight rapidly while the scion-budded trees showed little or no increment irrespective of rootstocks (Fig. 2.7). Although all root measures tended to indicate this effect (Table 2.2, 2.3), only root volume (Fig. 2.2) and dry weight (Fig. 2.6) showed differences with respect to rootstocks. In fact, an abundance of white roots on rootstock trees at this time was observed, reflecting the high activity of the roots. The close relation between these two attributes seems to indicate that volume is better related to root activity, probably because it combines properties of root length and root number. Tan *et al.* (1981) and Richards (1986) has also reported that root volume is well correlated to growth of plants.

2.4.3. Pattern of Growth Distribution in Young Nashi Trees with Respect to Seasonal Changes

The movement of the photoassimilates and carbohydrate reserves in relation to seasonal changes was accounted for by changes in the proportions of organs in the trees. The increment of dry weight within a young nashi tree partitioned into approximately 45% and 55% in stem and roots respectively, during the dormant period. The construction of new leaf mass caused a pronounced

reduction in the root proportion during early spring. In the presence of leaves, which comprised less than 20% of the plant, the fraction of either stem or roots was reduced to 40%. The result was in accord with the radioisotope study of Hansen and Grauslund (1973) who found that prior to leaf fall, most of the radioactive carbons fed to leaves were transferred to roots, within which the reserves were then formed. The reduction of the root fraction appeared to be positively correlated with the degree of new growth produced by the shoot (Table 2.4), being much greater in the rootstocks (Table 2.4). Root activity of the scion budded trees appeared, therefore, to have been retarded.

2.4.4. Shoot-root Ratios of Young Nashi Trees after Budding

Although the effects of severe shoot pruning was obvious in both rootstock and scion budded trees, the timing of the response of these two groups appears to be different between scion-budded and rootstock trees. The increase of shoot-root ratio due to the pruning effect remained apparent in the rootstocks only during the first year, while it persisted into the second year in scion budded trees. In other words, the shoot-root equilibrium was attained more rapidly in the rootstocks. In contrast to newly planted cuttings, the initial shoot-root ratio was low and hence, the absorption rate must also have been low, despite the fact that there was a large number of roots for each shoot unit. These results indicate that although shoot-root interactions may regulate growth in the seedling trees on their own roots, this mechanism does not operate alone in worked trees, at least during the early years after budding, as has also been noted by other works (Tubbs 1973).

2.4.5. Allometric Relationships of Young Nashi Trees after Budding

The fact that variation in shoot dry weight was inadequately explained by the coefficient of determination (R^2) of the allometric equations for scion-budded trees, combined with conclusions reached for other attributes, indicates that the residual effects due to budding in these plants most strongly influenced the pattern of growth distribution during the experimental period.

It may be premature to draw more than very tentative conclusions from the results of this investigation, which was confined to three rootstock seedlings,

and budded trees of the rootstocks and two scions for two seasons of growth. The results, taken in conjunction with those from other investigations, however, seem to indicate the unsuitability of the young fruit trees for studying of allometric relationships and shoot-root relationships. For this purpose, annual crop plant, such as tomato, may be more appropriate.

CHAPTER 3
THE ROLE OF GIBBERELLIC ACID ON GROWTH AND SHOOT-ROOT ALLOMETRY OF TOMATO SEEDLINGS

3.1. INTRODUCTION

The mechanism distributing the growth increment between two inter-dependent systems within a plant in an allometric manner has long been proposed to be regulated via hormonal signal(s) (Went 1938; Wareing 1970). Various studies have indicated that one group of such hormones might be gibberellins (GAs) (Phillips 1964; Jones and Phillips 1966; Reid *et al.* 1969; Reid and Crozier 1971; Carmi and Heuer 1981). For instance, there is evidence which indicate that root tips are potential sites of GA biosynthesis (Phillips 1964; Jones and Phillips 1966).

The use of growth regulators is based on the premise that they will be absorbed and act as chemical stimuli in a similar manner to endogenous sources of analogous hormones. If root produced hormones are mediators of root dependent shoot phenomena, it should be possible to mimic effects of intact roots with exogenously supplied growth regulators. Such responses have been demonstrated in many experiments. For instance, exogenously supplied GAs have been shown to stimulate expansion of excised-leaves (Beakbane 1965), and to restore growth of the top of plants in which root growth is limited by root inundation (Reid and Crozier 1971), or restriction (Carmi and Heuer 1981). This raises the question of whether GAs have such a role in controlling the allometric growth relationship between the shoot and the roots, and therefore, the overall plant growth via the activity of the root system. When roots are actively growing, tips are inevitably produced in abundance (Maggs 1965; Werner and Young 1982). The question therefore arises, is information relating to increased root growth communicated to the shoot by the level of GAs produced by the roots and translocated upwards?

In this study, since the shoot-root relationship was to be closely examined, an aeroponic system was used to conduct the experiments for the following reasons:

(a). Root harvest could be managed efficiently and effectively. In a conventional soil system, it has been estimated that one-third of the roots may be lost during harvest (Van Noordwijk and Floris 1979).
(b). Limitations in root environments could be eliminated. Soil physical and biological properties make it difficult to create an ideal and uniform soil medium (Letey 1985). Due to the activity of individual roots, a depletion zone may be created in soil around the roots, which results in competition between roots for nutrients. This together with limitation in water and oxygen supply, which may be limited in conventional soil or water medium systems (Hurd 1978; Nir 1980) can be eliminated. Confounding effects caused by the interaction of roots with their surroundings may also be eliminated in aeroponic systems. The dynamic interaction caused by the root properties and the soil environment which may confound the plant response have not been eliminated in many experiments in which application of external growth regulators has been performed. All such factors must be removed if the effects of treatments under scrutiny are to be identified.
(c). Growth regulators can be applied, in precise doses, directly to the root system. This enables the experimental procedure to more closely mimic an effect upon hormone synthesis in the root system and consequent export of hormone to the shoot is affected. In addition, growth regulators fed in this way are most likely to move with and become part of the natural root hormone complement.

In the first experiment described here, GA_3 was applied as sprays to roots and shoot systems to mimic the effects of endogenously synthesized gibberellins produced in those organs. It was also considered that by using the separate sites of application, differences in response due to the site of origin or due to translocation of the chemical to the alternate organ might be identified.

In the second GA experiment, treatments were changed to ensure a continuous supply of a sufficiently high level of GA_3 was maintained throughout the course of the experiment. It was proposed, that by exposing the shoot or the roots to a more-or-less constant dose of exogenous chemical over time, this would more closely mimic the natural system in a continuously and uniformly growing plant. Furthermore, such a system would be less artificially dynamic and make interpretation of responses less error prone.

3.2. MATERIALS AND METHODS

3.2.1. Experiment 1

3.2.1.1. Experimental Procedure

The experiment was conducted during a period of 9 weeks from March to May 1988 in a 3x6 m glasshouse where temperatures were kept between 15 and 25^{o}C using a heating system and fan ventilation. Tomato seeds, cultivar VF 145-21-4 P, were pre-germinated on moist blotting paper for 5 days at 100% RH. Seedlings were transplanted to 4-cm-diameter plix seedling trays, containing pumice and fine sand mixed in the ratio of 1:1 (vol/vol) with a complete complement of fertilizers. Four-week old seedlings consisting of 5-6 leaves were selected and transferred into slots made on the cover of an aeroponic tank. Individual seedlings were spaced at 20 cm within each slot with 15 cm between slots giving a total of 24 plants per tank. Each plant was supported by a string, one end of which was tied loosely to the stem base, from where it was spiralled along the stem length, and attached to an aluminium frame above the cover (Plate 3.1).

The aeroponic system consisted of nutrient solution (with or without plant growth regulator) circulating through a tube between a reservoir covered with a tight lid and coated entirely with black polyvinyl sheet, and a closed, painted and a galvanized tank (Plate 3.1). The tank, 60 X 120 X 55 cm in size, was inclined slightly towards the drain. It was covered with a slightly larger wooden cover, in which four 1 cm wide slots were made at 15 cm apart. Beneath the cover, white polyvinyl sheets were applied and cut along each slot to reduce the gap and minimize water loss while allowing the suspended to grow in the slots. Solution was pumped through tubing formed, inside the tank, into a rectangular closed loop, on which 10 jets fixed 10 cm apart (Fig 3.1) provided a continuous fine spray to all points of the tank. The main tube was connected to a pump (Tsurumi, model Family-5, output 45 watts, capacity max. 35 litres.min^{-1}), submerged in the experimental solution in a reservoir housing the pump. The run of the sprays inside the tank drained through a hole at the lowest point of the aeroponic tank

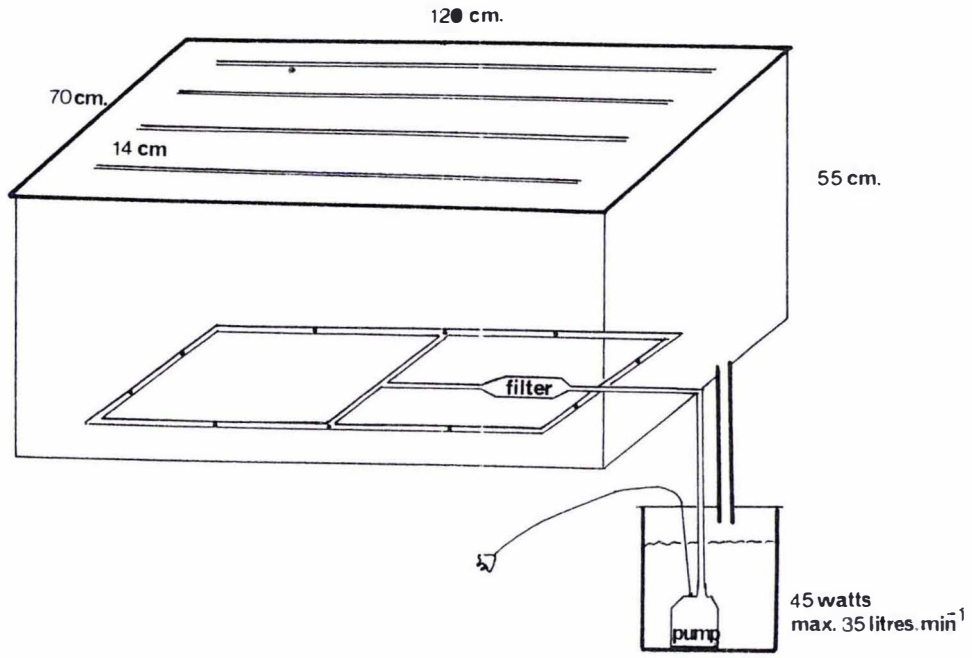


Figure 3.1. Schematic diagram of the aeroponic system.

Plate 3.1. Layout of the experiments using growth regulators.

back to the pump reservoir. Each system contained 15 litres of nutrient (and growth regulators) cycling between the tank and the reservoir. The solution, for all treatments, was replaced twice a week or when 80% depleted in any reservoir, whichever came first. Jets were checked daily and replaced if not functioning properly.

Designated treatments were applied to tomato plants following a two week period of establishment. Gibberellic acid (GA_3, MW 346.38, DBH, 90% a.i.) was dissolved in 10 ml of 90% ethanol and then diluted with distilled water to make up a stock solution containing the desired concentration. The solution was stored in a dark, cool room (5°C) until diluted and used. Two times a week, shoot treatments of aqueous GA_3, were carefully applied with hand pressurized sprayers, which gave a fine mist at the rate of 6-7 ml per plant. A cardboard shield was used to intercept drift while spraying. Plants were thoroughly wetted, without run off to contaminate the nutrient solution. Treatments with no GA_3 shoot application were sprayed with distilled water (containing the similar concentration of ethanol). To apply root treatments, the cover of each aeroponic tank was removed with plants suspended in place. Individual root systems were then sprayed in a similar manner to the shoots, except that within three minutes of GA_3 application roots were thoroughly rinsed to minimize subsequent contamination of the nutrient solution with GA_3. The plants (suspended on the cover) were then returned to the aeroponic system.

3.2.1.2. Experimental Design

Four sets of the aeroponic system were arranged along the length of a glasshouse. Four plants per treatment (plus six extra plants to be harvested prior to treatments) were randomly assigned to four individual tanks, each of which therefore represented a block. After an acclimatization period of two weeks, one plant was harvested for each treatment per block as the zero time harvest to give an initial dry weight for the calculation of relative growth rate (not used to contribute to pooled mean and its ANOVA). Three subsequent harvests were made at weekly intervals. The same number of plants were culled at each harvest, which was planned as a 2X3 factorial experiment in a RCBD, with two levels of GA3

concentration as a foliar spray (factor A) and three levels as a root spray (factor B). The application zone and concentrations, and the composition of nutrient solution used are shown in Table 3.1 and 3.2, respectively. There was no physiological basis for the selection of these concentrations, or frequencies of application, other than to ensure a plant response without visible damage to the tissues. All data were eventually pooled and considered as split-plot-in-time experiment in a RCBD, with the factorial treatments as the main plot and time as the sub-plot factor.

3.2.1.3. Collection of Data

Similar harvesting procedures and measurements to the nashi study were followed. All harvested materials were eventually dried at 70^{o}C for 48 hours and then weighed.

The parameters measured at each harvest were:

Leaf :

- Leaf area (Licor area meter model 3100)
- Leaf number
- Leaf dry weight

Stem :

- Total shoot length
- Individual internode length
- Internode number
- Total lateral length
- Branch number
- Total stem dry weight

Root :

- Root length (Comair root length scanner)
- Root number
- Root dry weight

TABLE 3.1. *Sites of application and GA_3 concentrations used in experiment 1*

GA_3 treatment	Shoot application	Root application
Control	Distilled water	NFT solution
Shoot 0, Root 1	Distilled water	NFT + 2.6×10^{-6} M GA_3
Shoot 0, Root 2	Distilled water	NFT + 2.6×10^{-5} M GA_3
Shoot 1, Root 0	2.6×10^{-5} M GA_3	NFT solution
Shoot 1, Root 1	2.6×10^{-5} M GA_3	NFT + 2.6×10^{-6} M GA_3
Shoot 1, Root 2	2.6×10^{-5} M GA_3	NFT + 2.6×10^{-5} M GA_3

TABLE 3.2. *Composition of stock and nutrient film solutions used in the aeroponic experiments (after Cooper 1979)*

Chemicals	g. per 2 litre stock soln	ml stock soln per litre of final soln	g. per 100 litre final soln
Major elements			
-KH_2PO_4	131.5	4	26.5
-KNO_3	291.5	4	58.3
-$Ca(NO_3)_2.4H_2O$	501.5	4	100.3
-$MgSO_4.7H_2O$	256.5	4	51.3
Minor elements			
-EDTA iron	158.0	1	7.9
-$MnSO_4.H_2O$	12.2 }		0.61
-H_3BO_3	3.4 }		0.17
-$CuSO_4.5H_2O$	0.78 }	1	0.039
-$(NH4)_6Mo_7O_{24}.4H_2O$	0.74 }		0.037
-$ZnSO_4.7H_2O$	0.88 }		0.044

The four major elements and iron were kept in separate two-litre bottles, while the other minor elements were stored together in another bottle. The amount of stock was taken at the rate shown in the third column to make up each litre of final solution. The pH was adjusted to 5.8-6.0 using diluted nitric acid and potassium hydroxide.

3.2.1.4. Data Analyses

Mean Analyses and Comparisons

Mean analyses and comparisons, and estimation of k-values were similar to those described in the nashi study. With only four replications at each harvest, however, regression analysis could not be performed. Thus, allometric constants (k-values) were computed only for the combined harvest. Comparisons of k-values were made by unprotected Lsd test (at $p \geq 0.5$).

Calculation of Ratios of Relative Growth Rates and their Variances

Relative growth rates were calculated as described in the previous study. The ratio of two RGR(s) was then derived directly from the calculated RGR means, *e.g.*,

$$RGR_{LR} = RGR_L / RGR_R;$$

The approximation of variance of the ratio was derived using the following equation (Gordon *et al.* 1972):

$$V_{x/y} = [x^2V_y^2 + y^2V_x^2 - 2xy\ cov(x,y)]/V_y^4,$$

where
- $V_{x/y}$ is variance of ratio x to y;
- x is expected value of x;
- y is expected value of y;
- V_x is variance of x;
- V_y is variance of y;
- cov(x,y) is covariance between attribute x and y.

3.2.2. Experiment 2

3.2.2.1. Experimental Procedure and Design

Apart from the experimental procedures which were carried out (between June and September 1988) in the same way as in the first GA_3 experiment, treatments were applied to one site per plant only since neither additive nor interactive responses between shoot and root GA_3 were considered further. Shoot spray was conducted as described previously (section 3.2.1.1), while root application was achieved by incorporating the stock solution into the nutrient system, thereby facilitating continuous application. Treatments of one shoot concentration at 2.9×10^{-5} M, two root concentrations at 5.8×10^{-5} and 2.9×10^{-4} M and a water, control treatment, were allocated at random to the tanks. The constraint of supplying one treatment to each tank prevented blocking. Each harvest, as well as pooled harvest data, was considered as lists of treatments (with internal replications only).

3.2.2.2. Collection of Data and Data Analyses

Destructive harvests commenced a week after treatment application and were made at one week intervals. Similar procedures to the previous study were used for data collection and analyses. One difference, however, was that in this experiment the supply of GA_3 solutions to roots imposed a constraint so that blocking was not possible as each individual tank could represent only one treatment. Data collected at each harvest were therefore analysed as list analyses, using analysis of variance (ANOVA) and least significance difference (Lsd) test. Pooled data for each attribute across all harvests were analysed in the same manner (with time effect extracted out). Calculation of all derived means followed the same methods described previously in section 3.2.1.2.

3.3. RESULTS

3.3.1. Experiment 1

Analysis of variance showed that there was no significant interaction between the two factors (A = shoot and B = root application), either at any harvest or in pooled data, for all attributes investigated. That is because the shoot/root GA_3 effects were not additive and are not related to shoot or root treatments, the effects of each treatment were distinctively expressed, and often, inconsistent with time (*e.g.* Table 3.3, 3.4 and 3.8). Thus, each A*B combination was treated as a single individual treatment, ignoring the factors. In addition, within the range of root application studied, GA_3 did not exhibit an unequivocal dose-response. For instance, the degree of reduction in leaf area (Table 3.3) and leaf dry weight (Table 3.4) caused by the two root concentrations fluctuated with time, as also occurred with the stimulatory effect on stem dry weight (Table 3.4) and stem weight ratio (Table 3.8). From these observations, it follows that, by and large, root treatment did not give a response at all. There appears to be two groups of responses, with respect to shoot treatments (Table 3.8). The responses to shoot treatments were, clearly, significantly different from the control in the proportions of organs to total plant dry weight, while no consistent responses were observed by the root treatments. On the other hand, at the same concentration, a shoot spray generally showed a stronger effect than root application. This may partly due to differences in effectiveness of the application procedure; water rinsing followed only root spray treatments.

3.3.1.1. Changes in Leaf Attributes

Leaf Area

Leaf area increased with time in all treatments (Table 3.3). Although differences among means were not significant, shoot treatments, in general, tended to reduce leaf area.

TABLE 3.3. *Changes in leaf attributes with time as affected by GA_3 treatments (experiment 1)*

Harvest no.	GA_3 treatment	Leaf area cm2	Leaf area ratio cm2.mg-1	Specific leaf area cm2.mg-1
		ns	ns	ns
1	Control	830	0.170	0.292
	Shoot 0, Root 1	764	0.193	0.320
	Shoot 0, Root 2	864	0.196	0.329
	Shoot 1, Root 0	721	0.213	0.357
	Shoot 1, Root 1	721	0.197	0.332
	Shoot 1, Root 2	987	0.201	0.340
	se	141	0.10	0.017
		ns	ns	ns
2	Control	1910	0.211	0.359
	Shoot 0, Root 1	1644	0.211	0.378
	Shoot 0, Root 2	2079	0.212	0.383
	Shoot 1, Root 0	1745	0.207	0.380
	Shoot 1, Root 1	2543	0.210	0.348
	Shoot 1, Root 2	2292	0.207	0.356
	se	346	0.008	0.013
		ns	ns	ns
3	Control	3760	0.179	0.299
	Shoot 0, Root 1	3278	0.186	0.307
	Shoot 0, Root 2	3147	0.185	0.307
	Shoot 1, Root 0	2756	0.153	0.275
	Shoot 1, Root 1	3866	0.166	0.292
	Shoot 1, Root 2	3343	0.159	0.281
	se	498	0.008	0.015
		ns	ns	ns
Pooled	Control	2167	0.187	0.316
	Shoot 0, Root 1	1895	0.197	0.335
	Shoot 0, Root 2	2030	0.198	0.340
	Shoot 1, Root 0	1740	0.191	0.337
	Shoot 1, Root 1	2377	0.191	0.324
	Shoot 1, Root 2	2207	0.189	0.326
	se	199	0.009	0.015

- Each mean figure from 4 replications with $df_{(error)} = 15$ at harvests, and pooled mean from 12 replications with $df_{(error)} = 36$.

Leaf Area Ratio (LAR)

There were no significant effects of GA_3 on LAR (total leaf area in relation to whole plant dry weight), although at the final harvest the means appeared to separate into two groups; *viz.* the control and root treatments, and the shoot/root treatments (Table 3.3). It seemed that LAR was not related to its leaf area, implying that the effect of GA_3 on leaf area was probably via reduced plant size, not the proportion of leaf area per plant.

Specific Leaf Area (SLA)

The general pattern of specific leaf area (the ratio of total leaf area to total leaf dry weigth) was similar to that of LAR (Table 3.3). While no significant differences were obtained at individual harvests or in the pooled mean, the latter, nevertheless, indicated a trend towards increased SLA following GA_3 application. It was also noticed that the treated plants generally exhibited slight roll of leaf edges (see later, in experiment 2).

3.3.1.2. Changes in Absolute Growth

Leaf Dry Weight

No significant effects of GA_3 on leaf growth (Table 3.4) were detected due to high variation, which was a major factor affecting the statistical outcome. It was noteworthy that leaf growth appeared to be decreased, at the first harvest only, by all GA_3 treatments, except the shoot/root spray at high concentration.

Stem Dry weight

In contrast to other attributes, stem weight consistently appeared to be affected by GA_3 treatments and differences were amplified with time (Table 3.4). Nonetheless, the results remained non-significant at all harvests. Pooled means indicated that combined shoot/root treatments appeared to increase stem growth ($p \geq 0.13$).

TABLE 3.4. *Changes in dry weight of plant organs and whole plant with time as affected by GA_3 treatments (experiment 1)*

Harvest no.	GA_3 treatment	L_w*1 g	S_w*2 g	T_w*3 g	R_w*4 g	W*5 g
		ns	ns	ns	ns	ns
1	Control	3.00	0.77	3.77	1.31	5.07
	Shoot 0, Root 1	2.41	0.66	3.07	0.90	3.97
	Shoot 0, Root 2	2.62	0.70	3.32	1.06	4.38
	Shoot 1, Root 0	2.00	0.54	2.54	0.82	3.35
	Shoot 1, Root 1	2.18	0.65	2.83	0.84	3.67
	Shoot 1, Root 2	2.92	0.94	3.85	1.10	4.95
	se	0.54	0.13	0.67	0.19	0.77
		ns	ns	ns	ns	ns
2	Control	5.29	1.60	6.89	2.12	9.01
	Shoot 0, Root 1	4.37	1.21	5.58	2.24	7.82
	Shoot 0, Root 2	5.46	1.74	7.20	2.61	9.81
	Shoot 1, Root 0	4.65	1.61	6.25	2.29	8.54
	Shoot 1, Root 1	7.38	2.22	9.60	2.59	12.19
	Shoot 1, Root 2	6.42	2.11	8.52	2.51	11.03
	se	0.96	0.33	1.28	0.42	1.64
		ns	ns	ns	ns	ns
3	Control	12.71	3.63	16.34	4.94	21.28
	Shoot 0, Root 1	10.79	3.03	13.82	3.87	17.69
	Shoot 0, Root 2	10.41	2.88	13.29	3.95	17.24
	Shoot 1, Root 0	10.07	3.90	13.96	4.15	18.12
	Shoot 1, Root 1	13.10	5.25	18.35	4.66	23.00
	Shoot 1, Root 2	11.98	4.79	16.77	4.15	20.92
	se	1.60	0.66	2.23	0.52	2.66
		ns	ns	ns	ns	ns
Pooled	Control	7.00	2.00	9.00	2.79	11.79
	Shoot 0, Root 1	5.86	1.63	7.49	2.33	9.83
	Shoot 0, Root 2	6.16	1.77	7.94	2.54	10.47
	Shoot 1, Root 0	5.57	2.01	7.58	2.42	10.00
	Shoot 1, Root 1	7.56	2.71	10.26	2.69	12.95
	Shoot 1, Root 2	7.11	2.61	9.71	2.59	12.30
	se	0.63	0.23	0.85	0.22	1.70

- Each mean figure from 4 replications with $df_{(error)} = 15$ at harvests, and pooled mean from 12 replications with $df_{(error)} = 36$.
- *1 = Leaf d.wt., *2 = Stem d.wt., *3 = Shoot d.wt., *4 = Root d.wt., *5 = Whole plant d.wt.

Shoot Dry Weight

Shoot growth response gave mixed results of both leaf and stem growth, with no significant difference between treatments detected (Table 3.4) at any harvest. In general, leaf and stem growth appeared to be increased in the shoot/root treatments at individual harvests. The pooled means also reveal this tendency.

Root Dry Weight

Root dry weight increased with time in all harvests. No significant effect of GA_3 on root growth was obtained despite very uniform reduction by GA_3 at most harvests ($p \leq 0.30 - 0.64$).

Whole Plant Dry Weight

There was no significant effect of GA_3 on plant dry weight, due to substantial variation of the plant size (Table 3.4). At the first harvest, GA_3 effect appeared to be inhibitory but this did not persist. While the overall growth of plants was not influenced by shoot or root spray of GA_3, leaf and stem growth appeared to be promoted by combined shoot/root treatments.

3.3.1.3. Changes in Relative Growth Rates

Despite quite a large range of means at each of the harvests, no significant difference were demonstrated for any RGR(s) (Table 3.5), due to considerable variation. All plants had a similar pattern of change in RGR(s) and progression in shoot RGR (RGR_T) closely followed RGR_L, indicating the strong influence of leaf growth rate over the shoot. Root RGR (RGR_R) appeared to be affected by GA_3, however, no significant difference was detected at any harvest. The control RGR_R was close to the extreme value at all harvests, in a manner that was similar to that in RGR_L.

ABLE 3.5. *Changes in relative growth rate of plant organs and whole plant with time as affected by GA_3 treatments (experiment 1)*

eek	GA_3 treatment	RGR_L *1 $g.g^{-1}.day^{-1}$	RGR_S *2 $g.g^{-1}.day^{-1}$	RGR_T *3 $g.g^{-1}.day^{-1}$	RGR_R *4 $g.g^{-1}.day^{-1}$	RGR_W *5 $g.g^{-1}.day^{-1}$
		ns	ns	ns	ns	ns
	Control	0.233	0.197	0.224	0.218	0.222
		(0.049)	(0.045)	(0.048)	(0.044)	(0.047)
	Shoot 0, Root 1	0.199	0.171	0.193	0.160	0.184
		(0.050)	(0.046)	(0.049)	(0.046)	(0.048)
	Shoot 0, Root 2	0.210	0.175	0.202	0.184	0.197
		(0.050)	(0.048)	(0.049)	(0.046)	(0.048)
	Shoot 1, Root 0	0.183	0.152	0.175	0.156	0.170
		(0.045)	(0.042)	(0.044)	(0.041)	(0.043)
	Shoot 1, Root 1	0.191	0.173	0.187	0.155	0.178
		(0.047)	(0.042)	(0.046)	(0.044)	(0.045)
	Shoot 1, Root 2	0.234	0.227	0.232	0.194	0.222
		(0.047)	(0.042)	(0.046)	(0.044)	(0.045)
		ns	ns	ns	ns	ns
	Control	0.082	0.093	0.085	0.070	0.081
		(0.029)	(0.035)	(0.030)	(0.021)	(0.027)
	Shoot 0, Root 1	0.094	0.094	0.095	0.138	0.106
		(0.025)	(0.022)	(0.024)	(0.024)	(0.023)
	Shoot 0, Root 2	0.113	0.138	0.119	0.137	0.124
		(0.027)	(0.029)	(0.027)	(0.021)	(0.025)
	Shoot 1, Root 0	0.115	0.153	0.124	0.138	0.128
		(0.019)	(0.014)	(0.017)	(0.023)	(0.018)
	Shoot 1, Root 1	0.176	0.178	0.176	0.160	0.173
		(0.020)	(0.022)	(0.020)	(0.025)	(0.020)
	Shoot 1, Root 2	0.106	0.107	0.107	0.112	0.108
		(0.026)	(0.026)	(0.026)	(0.029)	(0.026)
		ns	ns	ns	ns	ns
	Control	0.125	0.122	0.124	0.117	0.122
		(0.028)	(0.039)	(0.031)	(0.024)	(0.029)
	Shoot 0, Root 1	0.129	0.130	0.129	0.080	0.116
		(0.014)	(0.015)	(0.013)	(0.011)	(0.010)
	Shoot 0, Root 2	0.092	0.074	0.088	0.056	0.079
		(0.020)	(0.022)	(0.020)	(0.017)	(0.019)
	Shoot 1, Root 0	0.116	0.129	0.119	0.094	0.112
		(0.020)	(0.016)	(0.018)	(0.023)	(0.019)
	Shoot 1, Root 1	0.080	0.120	0.091	0.087	0.089
		(0.019)	(0.020)	(0.019)	(0.023)	(0.019)
	Shoot 1, Root 2	0.094	0.125	0.102	0.080	0.098
		(0.028)	(0.028)	(0.027)	(0.027)	(0.026)

Each mean figure from 4 replications.
Mean separation within column by t-test ($p \leq 0.05$).
Standard error of means in bracket.
*1 = Leaf relative growth rate,
*2 = Stem relative growth rate,
*3 = Shoot relative growth rate,
*4 = Root relative growth rate,
*5 = Mean relative growth rate.

3.3.1.4. Changes in Allometric Relationships Between Shoot and Root System

The coefficient of determination (R^2) for the regression was high, indicating that the allometric relationships were very strong between the shoot constituents and roots.

Leaf-root Allometry (k_L)

The allometric relationship between leaves and roots was strong. The coefficient of determination (R^2) ranging between 90.6 and 94.1% (Table 3.6). Gibberellic acid reduced the regression coefficient (k_L) significantly, making the k_L value of the control highest of all treatments. No significant difference between GA_3 treatments was detected. All k values, however, were higher than unity, except the GA_3 root treatment at higher concentration.

Stem-root Allometry (k_S)

A very strong allometric relationship was also found between stem and root (R^2 between 90.9 to 97.2%) (Table 3.6). Most of the values were greater than unity, while the k_S of the control was greatest. The significant reduction of k_S obtained at the low GA_3 root treatment (Table 3.6), however, did not fit logically with other effects and stem weight ratio (discussed later). Overall the data suggest little effect by GA_3 on k_S.

Shoot-root Allometry (k_T)

The concomitant reduction in both k_L and k_T suggests the allometric relationship between leaves and roots is the prime influence governing the overall shoot-root allometry. Results indicate the shoot-root allometric value (k_T) was reduced by all GA_3 treatments compared to the control (Table 3.6). A strong relationship (R^2 between 89.4 to 96.8%) was also found to exist between these two attributes. The differences in the allometric association between organs explain little of the data derived from the relationship between growth of organs of the

TABLE 3.6. *Changes in allometric relationships between dry weight of shoot and root organs as affected by GA_3 treatments (experiment 1)*

GA_3 treatment	ln a	*1 se (ln a)	k		se (k)	R^2 (%)
y = Leaf dry weight			*			
Control	-1.695	0.924	1.165	b	0.119	90.6
Shoot 0, Root 1	-0.242	0.693	0.980	a	0.091	92.0
Shoot 0, Root 2	-0.997	0.655	1.078	a	0.085	94.1
Shoot 1, Root 0	-1.171	0.706	1.120	a	0.093	93.6
Shoot 1, Root 1	-1.073	0.684	1.128	a	0.089	94.1
Shoot 1, Root 2	-0.858	0.793	1.103	a	0.103	92.0
y = Stem dry weight			*			
Control	0.225	0.617	1.116	b	0.079	97.2
Shoot 0, Root 1	1.357	0.736	0.971	a	0.097	90.9
Shoot 0, Root 2	0.850	0.633	1.034	b	0.082	94.0
Shoot 1, Root 0	1.155	0.453	0.996	b	0.060	96.5
Shoot 1, Root 1	1.027	0.513	1.037	b	0.067	96.0
Shoot 1, Root 2	1.181	0.686	1.015	b	0.089	92.8
y = Shoot dry weight			*			
Control	0.079	0.558	1.103	b	0.072	95.9
Shoot 0, Root 1	1.135	0.802	0.967	a	0.106	89.4
Shoot 0, Root 2	0.690	0.654	1.022	a	0.085	93.5
Shoot 1, Root 0	1.159	0.416	0.957	a	0.055	96.8
Shoot 1, Root 1	0.972	0.511	1.006	a	0.066	95.8
Shoot 1, Root 2	1.134	0.691	0.982	a	0.090	92.3

- K values from slopes of linear regressions of $\ln y = \ln a + k \ln x$, where y is either shoot, stem or leaf d.wt. and x is root d.wt. Each parameter estimated from 12 plants.
- Comparisons of k based on t-test ($p \leq 0.05$), $df_{(error)} = 20$.
- *1 = Standard error.

plants in this study.

The data gained from the experiment conclusively indicate that the shoot-root ratio was increased by GA_3 treatments. Another report (Wood and Hanover 1980) suggests that such an effect might be expected, but that if this occurred it was not via an effect on the k value. The parameter of the allometric relation which was disturbed by treatments, in a way that is consistent with other data, was the value of intercept of the regression line (on the ordinate). Treatment effects on this parameter were most marked for the stem versus root relation in which it would have had the effect of initially increasing the stem to root ratio compared to the control. This effect is also apparent in the allometric relation between shoot and roots which reflects the influence of stem weight in the overall allometric relationship.

According to Wareing (1970), a strong allometric relation between plant organs is evidence of a physiological link between the processes controlling the growth of those organs. Further, since the logarithm of the dry weight gives an estimate of the RGR (Pearsall 1927; Ledig *et al.* 1970), the ratio of the RGR(s) may reveal additional components of this relationship.

3.3.1.5. Changes in Ratios of Relative Growth Rates

Because of very high variation, the ratios of RGR(s) showed no significant difference at any harvest (Table 3.7). The ratio of leaf to root relative growth rate (RGR_{LR}) fluctuated in GA_3-treated plants, although this was not so apparent in the ratio of stem to root relative growth rate (RGR_{SR}). The ratios declined at the second week and increased in the third week. This trend was also apparent in the ratio between stem and leaf relative growth rate (RGR_{SL}). One obvious trend of the data was that GA_3 shoot application increased RGR_{SL} towards the final harvest. The changes in the ratio of shoot to root relative growth rate (RGR_{TR}) paralleled RGR_{LR} which further indicates the influence of the latter on the overall shoot and root relationship.

TABLE 3.7 *Changes in ratios of relative growth rates with time as affected by GA_3 treatments (experiment 1)*

Week	GA_3 treatment	RGR_{LR} *1	RGR_{SR} *2	RGR_{TR} *3	RGR_{SL} *4
		ns	ns	ns	ns
1	Control	1.07	0.90	1.03	0.85
		(0.315)	(0.269)	(0.297)	(0.294)
	Shoot 0, Root 1	1.25	1.07	1.20	0.86
		(0.484)	(0.417)	(0.457)	(0.353)
	Shoot 0, Root 2	1.14	0.95	1.09	0.83
		(0.397)	(0.344)	(0.375)	(0.335)
	Shoot 1, Root 0	1.17	0.97	1.13	0.83
		(0.432)	(0.366)	(0.404)	(0.350)
	Shoot 1, Root 1	1.23	1.12	1.21	0.91
		(0.475)	(0.423)	(0.450)	(0.365)
	Shoot 1, Root 2	1.21	1.17	1.20	0.97
		(0.371)	(0.340)	(0.354)	(0.300)
		ns	ns	ns	ns
2	Control	1.17	1.32	1.20	1.14
		(1.348)	(0.582)	(0.498)	(1.100)
	Shoot 0, Root 1	0.68	0.68	0.69	1.00
		(0.523)	(0.177)	(0.185)	(0.956)
	Shoot 0, Root 2	0.83	1.01	0.87	1.22
		(0.584)	(0.236)	(0.212)	(0.854)
	Shoot 1, Root 0	0.83	1.11	0.90	1.33
		(0.595)	(0.170)	(0.159)	(0.932)
	Shoot 1, Root 1	1.10	1.12	1.10	1.01
		(0.583)	(0.186)	(0.185)	(0.524)
	Shoot 1, Root 2	0.95	0.96	0.95	1.01
		(0.755)	(0.311)	(0.307)	(0.839)
		ns	ns	ns	ns
3	Control	1.07	1.05	1.06	0.98
		(0.695)	(0.393)	(0.334)	(0.765)
	Shoot 0, Root 1	1.61	1.62	1.60	1.01
		(1.127)	(0.252)	(0.235)	(0.670)
	Shoot 0, Root 2	1.63	1.32	1.56	0.81
		(1.681)	(0.521)	(0.557)	(0.871)
	Shoot 1, Root 0	1.23	1.36	1.26	1.10
		(0.893)	(0.360)	(0.355)	(0.793)
	Shoot 1, Root 1	0.93	1.38	1.05	1.49
		(0.836)	(0.413)	(0.339)	(1.341)
	Shoot 1, Root 2	1.17	1.56	1.27	1.34
		(1.066)	(0.608)	(0.530)	(1.146)

- Each mean figure from 4 replications.
- Mean separation within column by t-test ($p \leq 0.05$).
- Standard error of means in bracket.
- *1 = Ratio of leaf to root relative growth rate,
  *2 = Ratio of stem to root relative growth rate,
  *3 = Ratio of shoot to root relative growth rate,
  *4 = Ratio of stem to leaf relative growth rate.

3.3.1.6. Changes in the Distribution of Assimilates

The distribution of dry matter between the different organs of the plant is an important measure of the interacting effects of age, plant size, and the growth rates of individual organs. The previous section analysed the effects of treatments on plant dimensions and growth rates of the plant and its component parts. This section discusses how the differences between treatments came about. Weight ratios of individual organs in relation to the whole plant amplify effects of treatments which favour or disadvantage a particular organ compared to other constituents of the plant.

Leaf Weight Ratio (LWR)

Leaf weight ratio of control plants increased progressively with time whereas the LWR of GA_3 treated plants appeared to fluctuate (Table 3.8; Fig. 3.2 a). By the third harvest, treatments appeared to have segregated into two groups, those receiving shoot applications of GA_3, and the control and remaining GA3 treatments ($p \leq 0.10$).

Stem Weight Ratio (SWR)

At the final harvest, treatment means showed an obvious separation of SWR into two groups (Fig. 3.2 b), which resulted in a significant differences between the pooled means. Stem weight ratio was increased significantly in the treatments receiving shoot sprays with or without root application (Table 3.8). The fact that GA_3 treatments elicited significant effects only when applied to the shoot of the plants, suggests that the methods of application used to apply GAs to the roots were only marginally effective.

Root Weight Ratio (RWR)

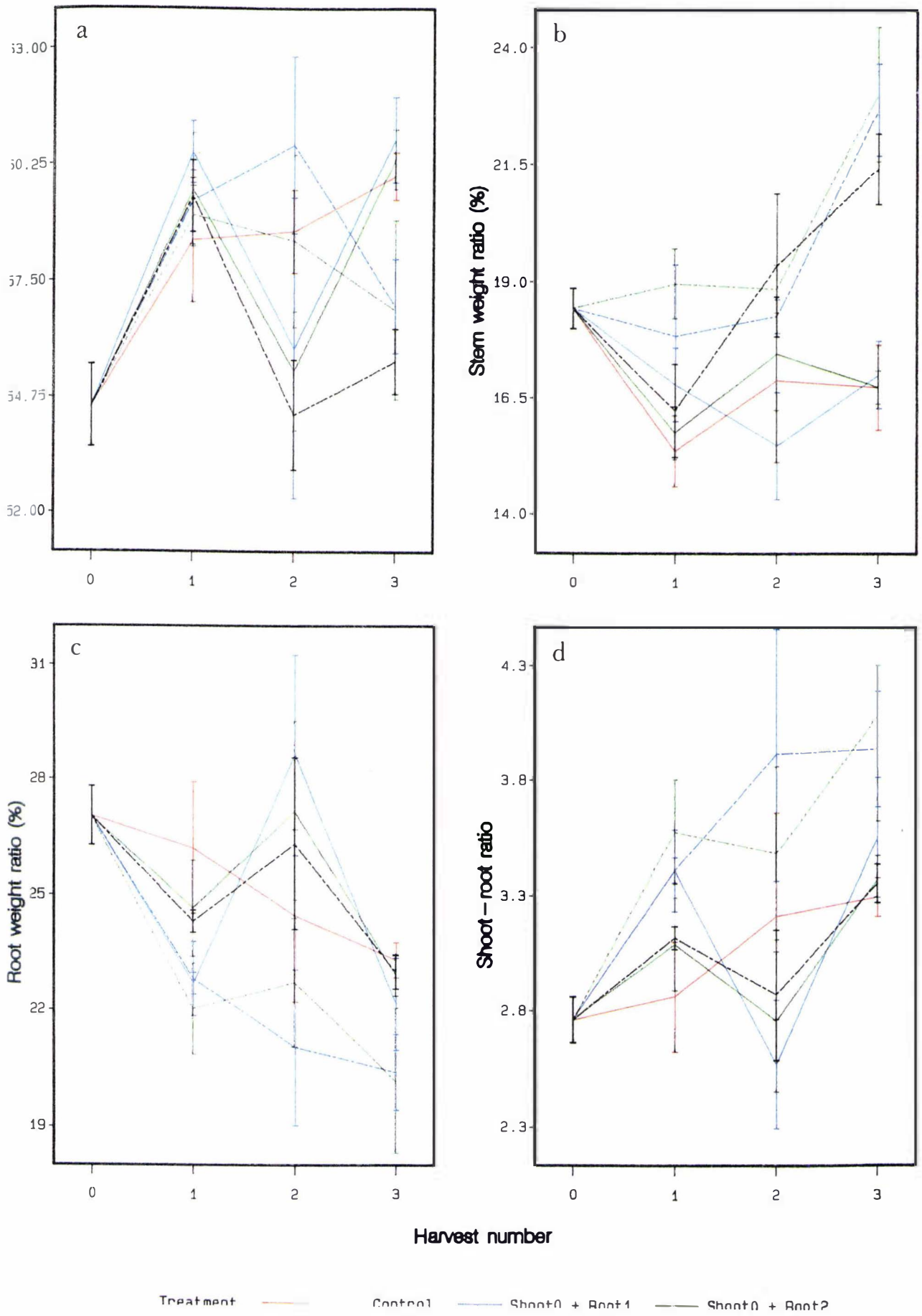
Despite the absence of any significant effect on RWR, it appeared that RWR was reduced by shoot/root applications (Table 3.8; Fig. 3.2 c). Root weight ratio also segregated into two groups; the shoot/root GA_3 treatments and the remainder.

TABLE 3.8. *Changes in dry weight distribution with time as affected by GA_3 treatments, expressed as a ratio of plant organ to total plant dry weight and shoot-root ratio (experiment 1)*

Harvest no.	GA_3 treatment	Leaf Weight ratio %	Stem Weight ratio %	Root Weight ratio %	Shoot-root ratio
		ns	ns	ns	ns
1	Control	58.4	15.3	26.2	2.86
	Shoot 0, Root 1	60.5	16.8	22.7	3.41
	Shoot 0, Root 2	59.6	15.7	24.6	3.09
	Shoot 1, Root 0	59.5	16.2	24.3	3.12
	Shoot 1, Root 1	59.4	17.8	22.8	3.41
	Shoot 1, Root 2	59.0	19.0	22.0	3.58
	se	1.1	0.9	1.1	0.20
		ns	ns	ns	ns
2	Control	58.6	16.9	24.5	3.21
	Shoot 0, Root 1	55.9	15.5	28.6	2.57
	Shoot 0, Root 2	55.3	17.5	27.2	2.76
	Shoot 1, Root 0	54.3	19.4	26.3	2.87
	Shoot 1, Root 1	60.7	18.3	21.0	3.91
	Shoot 1, Root 2	58.4	18.9	22.7	3.48
	se	2.2	1.3	2.4	0.43
		ns	**	ns	ns
3	Control	60.0	16.7 a	23.3	3.29
	Shoot 0, Root 1	60.8	17.0 a	22.2	3.55
	Shoot 0, Root 2	60.4	16.7 a	22.9	3.37
	Shoot 1, Root 0	55.6	21.4 b	23.0	3.35
	Shoot 1, Root 1	56.9	22.7 b	20.4	3.94
	Shoot 1, Root 2	56.8	23.0 b	20.2	4.08
	se	1.1	0.9	1.0	0.22
		ns	*	ns	ns
Pooled	Control	59.0	16.3 a	24.7	3.12
	Shoot 0, Root 1	59.1	16.4 a	24.5	3.18
	Shoot 0, Root 2	58.4	16.6 a	24.9	3.07
	Shoot 1, Root 0	56.5	19.0 b	24.5	3.11
	Shoot 1, Root 1	59.0	19.6 b	21.4	3.75
	Shoot 1, Root 2	58.1	20.3 b	21.6	3.71
	se	1.7	1.1	1.5	0.30

- Each mean figure from 4 replications with $df_{(error)} = 15$ at harvests, and pooled mean from 12 replications with $df_{(error)} = 36$.
- Mean separation within column by Lsd ($p \leq 0.05$).

Figure 3.2. Changes in the proportion of photoassimilates partitioned into tomato seedling organs when supplied via the roots and or the shoot with GA_3 at varying concentrations (experiment 1); (a) leaf weight ratio, (b) stem weight ratio, (c) root weight ratio and (d) shoot-root ratio. I = standard error of means.


a
b
c
d
Stem weight ratio (%)
Root weight ratio (%)
Shoot – root ratio
Harvest number
Treatment
Control
Shoot0 + Root1
Shoot0 + Root2

These results provide some statistical verification of effects that appeared to be present in other data. Having established a significant effect in one tissue or organ makes the observation of non-significant trends in others more meaningful. It is well known (Jones 1983) that GA_3 stimulates stem/internode elongation and growth. In this experiment, no stimulation in total growth was obtained, which has also been reported by others (Wood and Hanover 1980). It therefore follows that enhanced stem growth could only have occurred at the expense of other organs and this appears to have been the leaves and roots.

Shoot-root Ratio

The decline of RWR resulted in a corresponding increase in shoot-root ratio. Treatments receiving shoot/root sprays (in which RWR was low) appeared to have the highest shoot-root ratio (Table 3.8; Fig. 3.2 d).

3.3.2. Experiment 2

3.3.2.1. Morphological Changes

Leaf Attributes

Leaf Area

Despite inconsistent statistical differences at serial harvests, the pooled means indicate leaf area was suppressed significantly by GA_3 (Table 3.9). The result shows that in general the reduction of leaf area appeared to be related to GA_3 concentration. The high concentration reduced leaf area more strongly than other treatments.

Leaf Area Ratio (LAR)

In contrast to the control in which LAR fluctuated between harvests, LAR in GA_3 treatments declined progressively with time. Excepting the first harvest, GA_3 application reduced LAR significantly (Table 3.9). The pooled means showed differential effects of GA_3 due to concentrations. The high concentration applied to the roots reduced LAR more strongly than other treatments.

Specific Leaf Area (SLA)

Gibberellic acid had no significant effect on SLA (Table 3.9). Nonetheless, leaf lamina of plants fed with GA_3 appeared to be thinner and tended to have rolled edges (Plate 3.2), which persisted until the final harvest. Values of SLA appeared to decline during the first two weeks but decreased slightly towards the later harvest, except for the shoot-sprayed plants. This may suggest that during the early weeks, accumulation of dry matter was unable to keep pace with leaf area development in some treatments. This is a common phenomenon in leaf development, during which lamina thickness often continues to increase after expansion in area has ceased (Dale 1982).

TABLE 3.9. *Changes in leaf attributes with time as affected by GA_3 treatments (experiment 2)*

Harvest no.	GA_3 treatment		Leaf area cm^2	Leaf area ratio $cm^{-2}.mg^{-1}$	Specific leaf area $cm^{-2}.mg^{-1}$	Leaf number	Leaf size cm^2
			ns	ns	ns		
1	Control		246	0.216	0.397	-	-
	Shoot	$2.9X10^{-5}M$	192	0.229	0.427	-	-
	Root	$5.8X10^{-5}M$	258	0.220	0.413	-	-
	Root	$2.9X10^{-4}M$	195	0.212	0.416	-	-
	se		38	0.006	0.011	-	-
			*	**	ns		
2	Control		512 b	0.220 b	0.387	-	-
	Shoot	$2.9X10^{-5}M$	372 a	0.216 b	0.418	-	-
	Root	$5.8X10^{-5}M$	347 a	0.209 b	0.408	-	-
	Root	$2.9X10^{-4}M$	301 a	0.184 a	0.382	-	-
	se		49	0.007	0.015	-	-
			ns	*	ns		
3	Control		741	0.197 b	0.327	-	-
	Shoot	$2.9X10^{-5}M$	694	0.179ab	0.348	-	-
	Root	$5.8X10^{-5}M$	542	0.169 a	0.346	-	-
	Root	$2.9X10^{-4}M$	496	0.162 a	0.338	-	-
	se		73	0.007	0.014	-	-
			ns	**	ns	**	ns
4	Control		1440	0.229 b	0.371	9.88 b	147
	Shoot	$2.9X10^{-5}M$	1017	0.170 a	0.339	7.88 a	126
	Root	$5.8X10^{-5}M$	1065	0.177 a	0.356	7.25 a	153
	Root	$2.9X10^{-4}M$	1116	0.172 a	0.360	7.38 a	148
	se		132	0.006	0.011	0.58	13
			**	**	ns		
Pooled	Control		734 b	0.215 c	0.372	-	-
	Shoot	$2.9X10^{-5}M$	569 a	0.198 b	0.383	-	-
	Root	$5.8X10^{-5}M$	553 a	0.194 b	0.382	-	-
	Root	$2.9X10^{-4}M$	527 a	0.183 a	0.375	-	-
	se		41	0.004	0.006	-	-

- Each mean figure from 8 replications with $df_{(error)} = 28$ at harvests, and pooled mean from 32 replications with $df_{(error)} = 112$.
- Mean separation within column by Lsd ($p \leq 0.05$).

Plate 3.2. Morphological changes of tomato shoots treated with GA3. From left to right: shoot 2.9 x 10-5 M, root 5.8 x 10-5 M, control and root 2.9 x 10-4 M, respectively.

Leaf Number and Leaf Size

Leaf number which was measured only at the final harvest, revealed an important effect of GA_3 on the leaf development (Table 3.9). Leaf number was reduced to a similar degree by all GA_3 treatments. On average, there were approximately two fewer leaves on treated plants compared to the control. It was quite clear that leaf number was the major factor causing the decrease in leaf area of GA_3 treated plants. There was no significant difference in final leaf size, although this attribute was only measured at the final harvest. It should be noted, however, that there was considerable variation in individual leaf size.

Stem Attributes

Individual Internode Length

A highly significant increase was observed in most internodes at all harvests (Table 3.10); there was a two to three fold increase in internode length caused by GA_3. The enhancing effect was related to the age of the internode, rather than the GA_3 concentration applied. More highly positioned internodes were exposed to GA_3 for longer periods and consequently longer internodes resulted. The first internode did not respond to GA_3 because its growth had ceased prior to treatment. A similar result was reported by Carmi and Heuer (1981). On the other hand, the highest internode, had had insufficient time to respond to the compound by the time of harvest. Although data are not shown, the internode length of lateral shoots was also clearly increased (Plate 3.2; see also the total lateral length and lateral number).

Considering these variations in internode length with respect to time and position, the effect of different GA_3 treatments on internode length was remarkably similar throughout the experiment. As there were quantitative differences between other attributes that appeared to be related to concentration of GA_3 or the site of application, these results may indicate, that with respect to this attribute, the plant response was approaching saturation.

Harvest no.	GA_3 treatment			Int#1 *1 cm	Int#2 cm	Int#3 cm	Int#4 cm	Int#5 cm	Int#6 cm	Int#7 cm	Int#8 cm	Int#9 cm
				ns	**	**	**	**	ns			
2	Control			4.00	3.78 a	2.10 a	2.05 a	2.29 a	2.48	-	-	-
	Shoot	$2.9X10^{-5}$	M	4.31	5.31 b	4.89 b	6.18 b	6.18 b	3.46	-	-	-
	Root	$5.8X10^{-5}$	M	4.56	5.74 b	4.84 b	6.15 b	4.93 b	2.64	-	-	-
	Root	$2.9X10^{-4}$	M	3.51	5.41 b	4.85 b	5.50 b	5.21 b	4.75	-	-	-
se				0.41	0.33	0.39	0.29	0.53	0.77	-	-	-
				ns	**	**	**	**	**	ns		
3	Control			4.96	3.81 a	2.45 a	2.09 a	2.68 a	2.81 a	2.15	-	- -
	Shoot	$2.9X10^{-5}$	M	5.40	5.98 b	5.85 b	6.69 b	8.25 b	10.60 b	4.99	-	-
	Root	$5.8X10^{-5}$	M	4.40	6.15 b	5.41 b	6.80 b	8.69 b	10.10 b	3.65	-	-
	Root	$2.9X10^{-4}$	M	4.88	5.69 b	6.06 b	8.75 c	9.16 b	9.44 b	4.61	-	-
se				0.42	0.37	0.60	0.65	0.62	1.17	0.89	-	-
				ns	**	**	**	**	**	**	**	**
4	Control			4.33	3.88 a	2.41 a	2.05 a	2.80 a	2.99 a	2.81 a	3.50 a	2.31 a
	Shoot	$2.9X10^{-5}$	M	4.01	5.15 ab	4.73 b	7.06 b	8.85 b	11.06 b	12.88 c	8.98 b	6.41 b
	Root	$5.8X10^{-5}$	M	3.56	5.38 b	4.94 b	6.96 b	7.99 b	10.28 b	8.40 b	7.14 b	6.63 b
	Root	$2.9X10^{-4}$	M	4.68	5.99 b	4.96 b	7.99 b	8.78 b	9.65 b	11.50 bc	9.20 b	7.14 b
se				0.53	0.48	0.38	0.58	0.72	0.78	1.54	0.76	0.80
				ns	**	**	**	**	**	**		
Pooled	Control			4.43	3.82 a	2.32 a	2.06 a	2.59 a	2.76 a	2.48 a	-	-
	Shoot	$2.9X10^{-5}$	M	4.58	5.48 b	5.15 b	6.64 b	7.76 b	8.38 b	8.93 c	-	-
	Root	$5.8X10^{-5}$	M	4.18	5.75 b	5.06 b	6.64 b	7.20 b	7.67 b	6.03 b	-	-
	Root	$2.9X10^{-4}$	M	4.22	5.69 b	5.29 b	7.41 b	7.72 b	7.95 b	8.06 bc	-	-
se				0.46	0.40	0.47	0.53	0.63	0.93	1.26	-	-

- Each mean figure from 8 replications with $df_{(error)} = 28$ at harvests and pooled mean figure for Int#1 to Int#6 from 24 replications with $df_{(error)} = 84$.
- Mean separation within column by Lsd ($p \leq 0.05$).
- *1 = Internode Order; 1th to 9th from the shoot-root juncture upwards.

Main Shoot Length

As a consequence of enhanced internode length, the length of the main shoot was approximately double that of the control (Table 3.11). The effect was highly significant and consistent throughout (Plate 3.2).

Total Lateral Number and Length

Lateral number was reduced considerably by GA_3 treatments (Plate 3.2). There were about one and three branches on treated and control plants respectively (Table 3.11). In contrast to main shoot length, no differences in the total lateral length was detected at the final harvest (Table 3.11). It is obvious, however, that the control treatment produced more, but shorter laterals than the GA_3 treated plants (Plate 3.2). Thus, the increase in the total shoot length was due to the increased length of the main shoot only.

3.3.2.2. Changes in Absolute Growth

Leaf Dry Weight

The effect of GA_3 on inhibition of leaf growth is apparent in terms of leaf dry weight. Although the difference was significant only at the third harvest (Table 3.12), the trend towards reduction by GA_3 was apparent throughout. The pooled means reveal unequivocally that leaf dry weight was reduced by about a quarter compared to the control.

Stem Dry Weight

In contrast to leaf growth, GA_3 strongly promoted stem growth compared to the control, and this difference amplified with time. On average, GA_3 treated plants had 47 to 62% more stem weight than controls (Table 3.12). Since all three organs were competing for the same pool of photoassimilates, GA_3 diverted photoassimilates into stem, at the expense of the leaves and roots.

TABLE 3.11. *Changes in stem attributes with time as affected by GA_3 treatments (experiment 2)*

Harvest no.	GA_3 treatment		Main Shoot length cm	Total Lateral length cm	Total shoot length cm	Lateral number
			**			
2	Control		28.8 a	-	-	-
	Shoot	$2.9X10^{-5}M$	43.6 b	-	-	-
	Root	$5.8X10^{-5}M$	40.7 b	-	-	-
	Root	$2.9X10^{-4}M$	45.1 b	-	-	-
	se		1.8	-	-	-
			**			**
3	Control		33.0 a	-	-	1.50 b
	Shoot	$2.9X10^{-5}M$	64.3 b	-	-	0.88ab
	Root	$5.8X10^{-5}M$	60.6 b	-	-	0.25 a
	Root	$2.9X10^{-4}M$	63.9 b	-	-	0.25 a
	se		2.5	-	-	0.25
			**	ns	**	**
4	Control		40.3 a	30.7	71 a	4.63 b
	Shoot	$2.9X10^{-5}M$	84.9 b	30.8	116 b	1.88 a
	Root	$5.8X10^{-5}M$	79.5 b	25.1	105 b	2.13 a
	Root	$2.9X10^{-4}M$	89.1 b	31.6	121 b	1.63 a
	se		2.4	7.1	7	0.54
			**			**
Pooled	Control		34.0 a	-	-	3.06 b
	Shoot	$2.9X10^{-5}M$	63.9 c	-	-	1.38 a
	Root	$5.8X10^{-5}M$	59.7 b	-	-	1.19 a
	Root	$2.9X10^{-4}M$	66.7 c	-	-	0.94 a
	se		1.3	-	-	0.42
	$df_{(error)}$		74			54

- Each mean figure from 8 replications with $df_{(error)}$ = 28 at harvests, and pooled mean from 16 and 24 replications with $df_{(error)}$ as indicated.
- Mean separation within column by Lsd ($p \leq 0.05$).

TABLE 3.12. *Changes in dry weight of plant organs and whole plant with time as affected by GA_3 treatments (experiment 2)*

Harvest no.	GA_3 treatment	L_w*1 g	S_w*2 g	T_w*3 g	R_w*4 g	W*5 g
		ns	ns	ns	ns	ns
1	Control	0.62	0.20	0.82	0.31	1.13
	Shoot $2.9X10^{-5}M$	0.45	0.18	0.63	0.20	0.83
	Root $5.8X10^{-5}M$	0.62	0.24	0.86	0.30	1.16
	Root $2.9X10^{-4}M$	0.47	0.22	0.69	0.23	0.92
	se	0.09	0.03	0.12	0.04	0.16
		ns	ns	ns	*	ns
2	Control	1.33	0.43	1.76	0.57 b	2.33
	Shoot $2.9X10^{-5}M$	0.91	0.49	1.40	0.34 a	1.74
	Root $5.8X10^{-5}M$	0.77	0.39	1.16	0.26 a	1.52
	Root $2.9X10^{-4}M$	0.94	0.51	1.46	0.43 ab	1.89
	se	0.16	0.07	0.22	0.06	0.28
		*	*	ns	*	ns
3	Control	2.51 b	0.69 a	3.19	0.96 b	4.15
	Shoot $2.9X10^{-5}M$	2.01 ab	1.22 b	3.23	0.66 a	3.90
	Root $5.8X10^{-5}M$	1.75 a	1.06 b	2.81	0.72 a	3.54
	Root $2.9X10^{-4}M$	1.59 a	1.05 b	2.64	0.64 a	3.28
	se	0.23	0.12	0.34	0.08	0.42
		ns	**	ns	ns	ns
4	Control	3.84	1.13 a	4.97	1.34	6.33
	Shoot $2.9X10^{-5}M$	2.89	1.98 b	4.88	0.92	5.90
	Root $5.8X10^{-5}M$	2.96	1.86 b	4.82	1.17	6.05
	Root $2.9X10^{-4}M$	3.07	2.14 b	5.21	1.20	6.49
	se	0.35	0.18	0.52	0.12	0.64
		**	**	ns	**	ns
Pooled	Control	2.03 b	0.60 a	2.63	0.78 b	3.41
	Shoot $2.9X10^{-5}M$	1.57 a	0.97 b	2.54	0.53 a	3.09
	Root $5.8X10^{-5}M$	1.51 a	0.88 b	2.39	0.63 a	3.04
	Root $2.9X10^{-4}M$	1.47 a	0.95 b	2.43	0.61 a	3.06
	se	0.11	0.06	0.17	0.04	0.21

- Each mean figure from 4 replications with $df_{(error)}$ = 28 at harvests, and pooled mean from 32 replications with $df_{(error)}$ = 112.
- Mean separation within column by Lsd ($p \leq 0.05$).
- *1 = Leaf d.wt., *2 = Stem d.wt., *3 = Shoot d.wt., *4 = Root d.wt., *5 = Whole plant d.wt.

Shoot Dry Weight

Treatments of GA_3 tended to reduced total shoot weight slightly, although not significantly, as expressed in the pooled means (Table 3.12). The dual effects of increased stem and decreased leaf dry weight did not quite balance each other, with the net result that shoot dry weight was reduced slightly.

Root Dry Weight

Root dry weight increased with time and the root weight of the control was highest at all harvests. Root growth was suppressed considerably by GA_3 treatments, and at the second and third harvests the difference was significant (Table 3.12). During these periods, the GA_3-treated plants produced approximately one-third to one-forth less root dry weight than the control.

Whole Plant Dry Weight

No significant effect of GA_3 on plant dry weight was detected (Table 3.12). Nevertheless, in all but one treatment at the first and at the final harvest, the weight of the control plants appeared to be higher. The pooled results also indicate that GA_3-treated plants were smaller than the control. Since leaf and root weights were reduced significantly, by a greater amount than stem weight was increased, it seems reasonable to assume that the apparent reduction in whole plant dry weight was real.

3.3.2.3. Changes in Relative Growth Rates

Because there was no harvest prior to treatment, relative growth rates could not be determined for the first week period. Consequently, results from only the subsequent weeks are shown.

Leaf Relative Growth Rate (RGR_L)

Except during the first two weeks, the difference in RGR_L between treatments was not significant. In the control, RGR_L fell as the experiment

Figure 3.3. Changes in relative growth rate of tomato seedling organs and whole plant when supplied via the roots or the shoot with GA_3 at varying concentrations (experiment 2); (a) RGR_L, (b) RGR_S and (c) RGR_T. I = standard error of means.

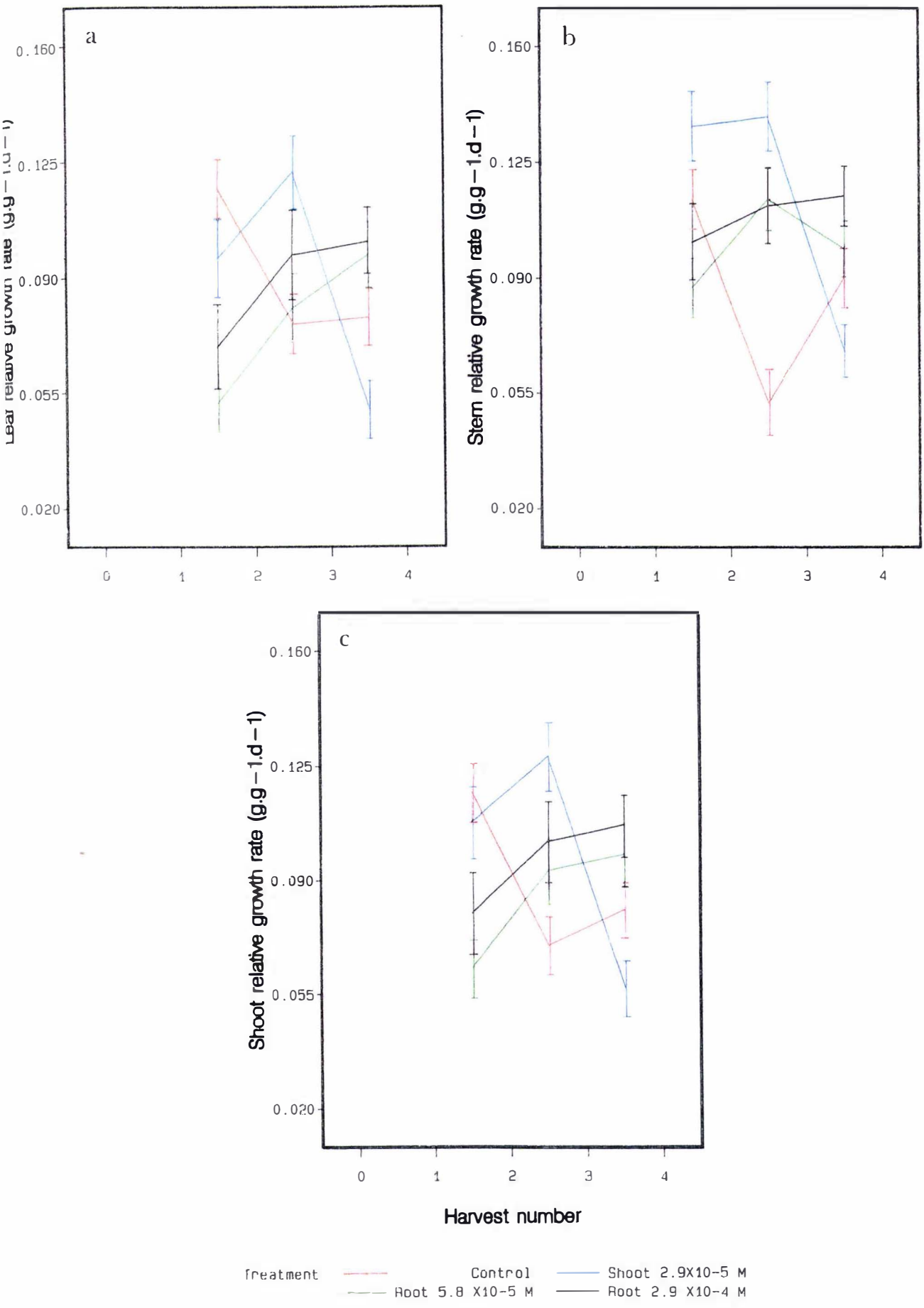
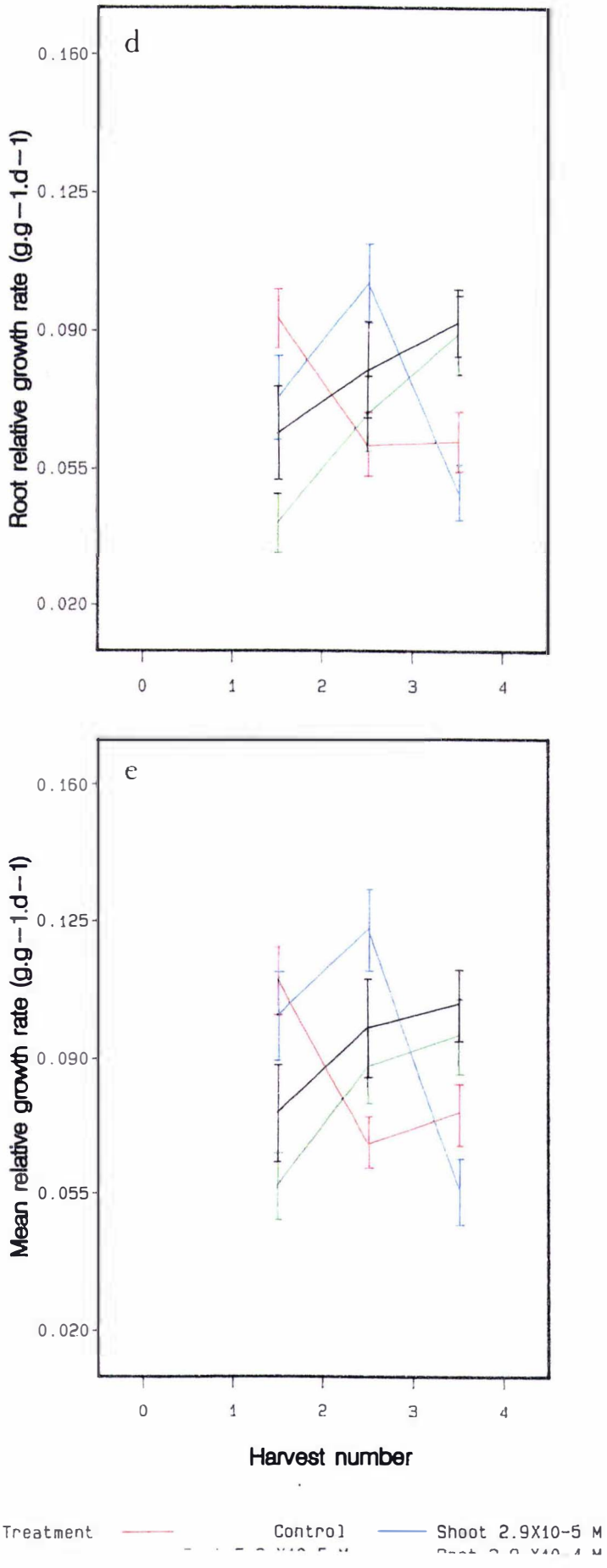

a
b
c
0.160
0.125
0.090
0.055
0.020
0
1
2
3
4
Stem relative growth rate (g.g−1.d−1)
Shoot relative growth rate (g.g−1.d−1)
Harvest number
Treatment
Control
Shoot 2.9X10-5 M
Root 5.8 X10-5 M
Root 2.9 X10-4 M

Figure 3.3.(cont.) Changes in relative growth rate of tomato seedling organs and whole plant when supplied via the roots or the shoot with GA_3 at varying concentrations (experiment 2); (d) RGR_R and (e) RGR_W. I = standard error of means.


d
0.160
0.125
0.090
0.055
0.020
Root relative growth rate (g.g−1.d−1)
0
1
2
3
4
e
0.160
0.125
0.090
0.055
0.020
Mean relative growth rate (g.g−1.d−1)
0
1
2
3
4
Harvest number
Treatment
Control
Shoot 2.9X10-5 M

progressed. In contrast, in all GA_3 treatments RGR_L was reduced following one week of exposure to GA_3, after which it appeared to increase. In the final week, the RGR_L of GA_3 root treatments continued to increase whereas that of shoot treatment dropped sharply. The fluctuation of RGR_L in the GA_3 treatments, when compared to the control, seemed to suggest that leaf development is delayed in these treatments. The developmental changes of RGR_L closely paralleled changes in whole plant RGR (RGR_W) (Fig. 3.3 a).

Stem Relative Growth Rate (RGR_S)

In general, RGR_S of GA_3 treated plants fell from the first to the second week and recovered in the following week (Fig. 3.3 b). During the sharp fall of RGR_S in the control which occurred during the second week (the time between the first and second harvest), the greatest difference between the control and GA_3 treatments was detected. The shoot GA_3 treatment showed a stronger effect on RGR_S than the root treatments. The shoot treatment increased RGR_S more rapidly and to a greater degree during the experimental period than root treatments. Although not significant, GA_3 seemed to increase RGR_S, with the exception of shoot treatment at the final harvest.

Shoot Relative Growth Rate (RGR_T)

Shoot relative growth rate was influenced by the RGR_L as strongly as whole plant relative growth rate (RGR_W) (Fig. 3.3 c). The changes in RGR(s) for each time of measurement corresponded closely, showing the strong link between growth of leaves and the shoot as a whole.

Root Relative Growth Rate (RGR_R)

Although the pattern of changes in RGR_R was not identical to RGR_L (Fig. 3.3 d), they were nevertheless quite similar. The RGR_R of treated plants was greatest after a week of exposure to GA_3, although no statistical differences could be established.

Whole Plant Relative Growth Rate (RGR_W)

Gibberellic acid altered the pattern of changes in RGR_W considerably (Fig. 3.3 e), although no significant difference was detected. During the first week of treatments, RGR_W in all GA_3 treatments was reduced, although shoot-applied GA_3 appeared to suppress RGR_W less severely than root treatments. During the following week, RGR_W of the control was lowest, reflecting the larger plant size at the early stage of this treatment. In contrast to the control, RGR_W in GA_3 treatments increased progressively during the experiment. Considering that the difference in total plant weight decreased (and perhaps was eliminated) by the final harvest, the above changes in RGR_W may suggest plants were adjusting to the exogenous growth regulator supply, after an initial suppression.

As occurred in RGR(s) of leaf, shoot and whole plant, GA_3 altered RGR(s) by reducing these during the first week. Despite subsequent recovery by GA_3 treated plants, the advantage gained by the control, caused by early difference in the size, was maintained throughout the course of the experiment. With respect to the relationship of growth rates between organs, RGR_L was correlated highly to RGR_R, whereas RGR_S was not. Consistent with the strong influence of the RGR_L on the RGR_T and RGR_W, the strong relationship between these parameters and RGR_R appeared convincing.

3.3.2.4. Changes in Allometric Relationships Between Shoot and Root Systems

Strong allometric relationships with significant differences between treatments were detected at most harvests. No useful deduction, however, could be made from allometric regression equations between leaves and roots (k_L), stem and roots (k_S) and shoot and roots (k_T) (Table 3.13, 3.14 and 3.15; and Fig. 3.4, 3.5 and 3.6, respectively) for individual harvests. It must be remembered that growth by roots and other plant parts although linked is probably not synchronous in time (Mullin 1963; Drew and Ledig 1980; Drew 1982; Chalmers 1987). Certainly, when growth is disturbed, compensatory growth occurs, during which rebalancing of root and shoot function takes place (Brouwer 1963). During such

TABLE 3.13. *Changes in allometric relationship between leaf and root dry weight (k_L) with time as affected by GA_3 treatments (experiment 2)*

Harvest no.	GA_3 treatment	ln a	*1 se(ln a)	k_L		se (k_L)	R^2 (%)
				*			
1	Control	-0.593	0.745	1.223	b	0.131	93.5
	Shoot $2.9X10^{-5}M$	0.636	0.528	1.033	a	0.101	94.6
	Root $5.8X10^{-5}M$	0.685	0.950	1.006	a	0.168	85.6
	Root $2.9X10^{-4}M$	0.743	0.661	0.993	a	0.123	91.6
				*			
2	Control	-0.024	0.356	1.136	b	0.056	98.6
	Shoot $2.9X10^{-5}M$	0.184	0.474	1.136	b	0.082	97.0
	Root $5.8X10^{-5}M$	-0.995	1.834	1.303	b	0.310	74.7
	Root $2.9X10^{-4}M$	0.474	0.652	1.047	a	0.111	93.7
				ns			
3	Control	0.290	0.618	1.097		0.092	96.0
	Shoot $2.9X10^{-5}M$	0.846	0.357	1.040		0.055	98.3
	Root $5.8X10^{-5}M$	0.847	0.349	1.005		0.054	98.3
	Root $2.9X10^{-4}M$	0.011	1.257	1.133		0.196	84.7
				*			
4	Control	0.110	0.443	0.992	a	0.062	97.7
	Shoot $2.9X10^{-5}M$	-1.996	1.256	1.457	b	0.185	91.2
	Root $5.8X10^{-5}M$	0.912	1.099	1.003	a	0.156	87.3
	Root $2.9X10^{-4}M$	0.255	1.032	1.095	a	0.146	90.3
				*			
Pooled	Control	-0.603	0.147	1.228	c	0.023	99.0
	Shoot $2.9X10^{-5}M$	-0.086	0.161	1.179	b	0.026	98.5
	Root $5.8X10^{-5}M$	0.106	0.228	1.116	a	0.036	97.0
	Root $2.9X10^{-4}M$	0.096	0.206	1.116	a	0.033	97.4

- K_L values from slopes of linear regressions of $\ln y = \ln a + k_L \ln x$, where y is leaf d.wt. and x is root d.wt. Each parameter estimated from 8 and 32 plants and comparisons of k_L values based on t-test ($p \leq 0.05$), $df_{(error)}$ = 12 and 60 at harvests and pooled analysis, respectively.
- *1 = Standard error.

Figure 3.4. Changes in allometric relationship between leaf and root dry weight (k_L) of tomato seedlings when supplied via the roots or the shoot with GA_3 at varying concentrations (experiment 2).

Control: R^2 = 99.0%, y =-0.603 + 1.23 x,
Shoot GA_3 2.9 $X10^{-5}$ M: R^2 = 98.5%, y =-0.086 + 1.18 x,
Root GA_3 5.8 $X10^{-5}$ M: R^2 = 97.0%, y = 0.106 + 1.12 x,
Root GA_3 2.9 $X10^{-4}$ M: R^2 = 97.4%, y = 0.096 + 1.12 x.

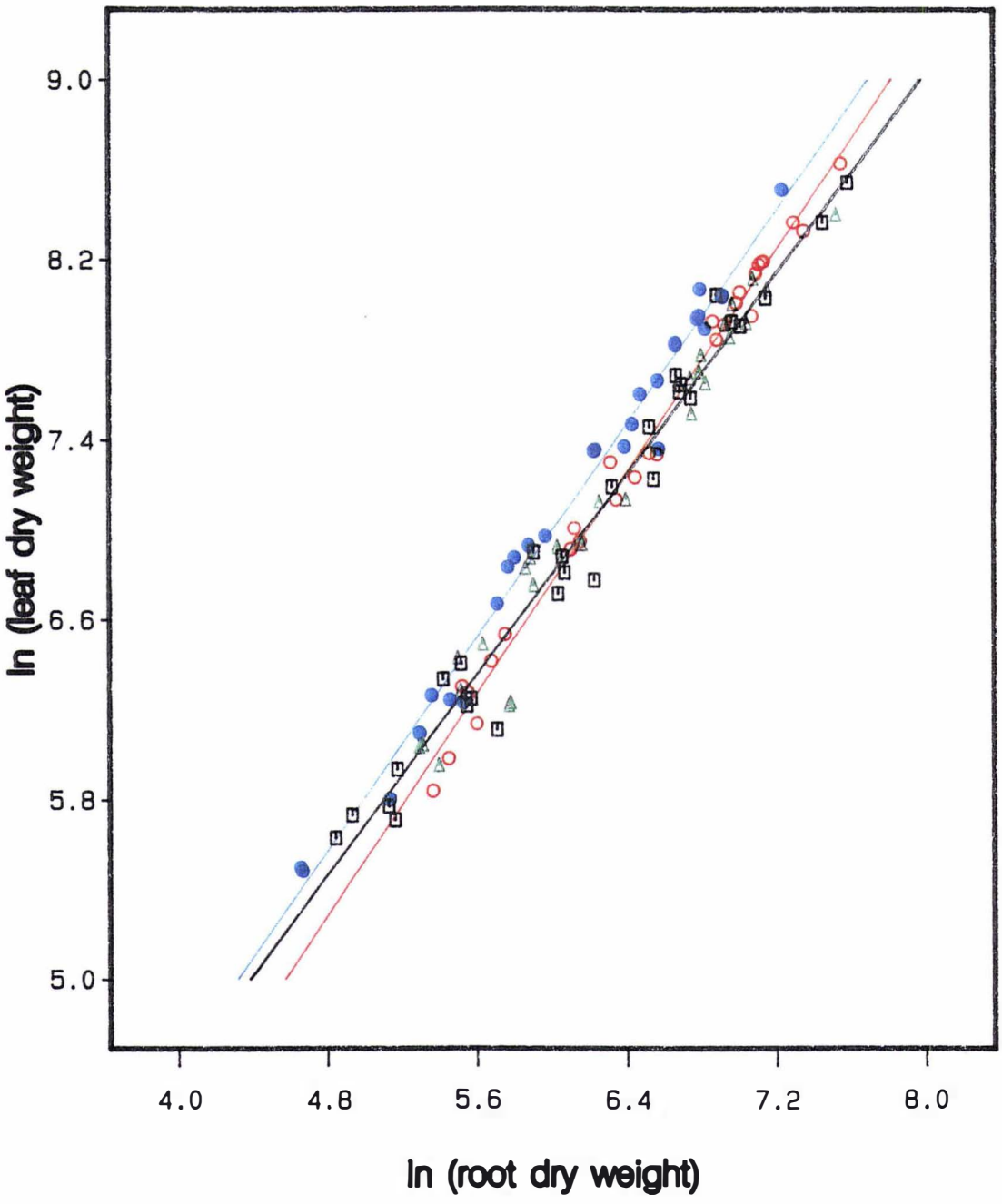

9.0
8.2
7.4
6.6
5.8
5.0
ln (leaf dry weight)
4.0
4.8
5.6
6.4
7.2
8.0
ln (root dry weight)
Treatment
Control
Shoot 2.9X10-5 M
Root 5.8 X10-5 M
Root 2.9 X10-4 M

TABLE 3.14. *Changes in allometric relationship between stem and root dry weight (k_S) with time as affected by GA_3 treatments (experiment 2)*

Harvest no.	GA_3 treatment	ln a	*1 se (ln a)	k_S	se (k_S)	R^2 (%)
				*		
1	Control	-0.917	0.622	1.082 b	0.120	94.2
	Shoot $2.9X10^{-5}M$	1.384	0.761	0.721 a	0.145	80.4
	Root $5.8X10^{-5}M$	0.037	1.104	0.952 b	0.196	79.8
	Root $2.9X10^{-4}M$	0.150	0.758	0.962 b	0.140	88.7
				*		
2	Control	-0.378	2.331	1.012 a	0.369	55.7
	Shoot $2.9X10^{-5}M$	0.037	0.615	1.057 a	0.107	94.2
	Root $5.8X10^{-5}M$	-1.982	2.110	1.351 b	0.356	70.6
	Root $2.9X10^{-4}M$	0.992	0.535	0.866 a	0.091	93.7
				*		
3	Control	-1.454	0.883	1.161 c	0.131	92.9
	Shoot $2.9X10^{-5}M$	0.865	0.357	0.961 b	0.055	98.1
	Root $5.8X10^{-5}M$	1.229	0.354	0.872 a	0.055	97.7
	Root $2.9X10^{-4}M$	-0.439	1.446	1.136 c	0.226	80.8
				*		
4	Control	-0.107	0.702	0.991 b	0.098	94.5
	Shoot $2.9X10^{-5}M$	-0.802	0.786	1.229 c	0.116	95.0
	Root $5.8X10^{-5}M$	1.474	1.196	0.858 a	0.170	80.9
	Root $2.9X10^{-4}M$	1.579	0.882	0.859 a	0.125	88.7
				*		
Pooled	Control	-1.250	0.270	1.143 a	0.041	96.2
	Shoot $2.9X10^{-5}M$	-1.871	0.325	1.377 d	0.053	95.7
	Root $5.8X10^{-5}M$	-1.918	0.430	1.337 c	0.068	92.7
	Root $2.9X10^{-4}M$	-1.264	0.321	1.253 b	0.052	95.1

- K_S values from slopes of linear regressions of $\ln y = \ln a + k_S \ln x$, where y is stem d.wt. and x is root d.wt. Each parameter estimated from 8 and 32 plants, and comparisons of k_S values based on t-test ($p \leq 0.05$), $df_{(error)}$ = 12 and 60 at harvests and pooled analysis, respectively.
- *1 = Standard error.

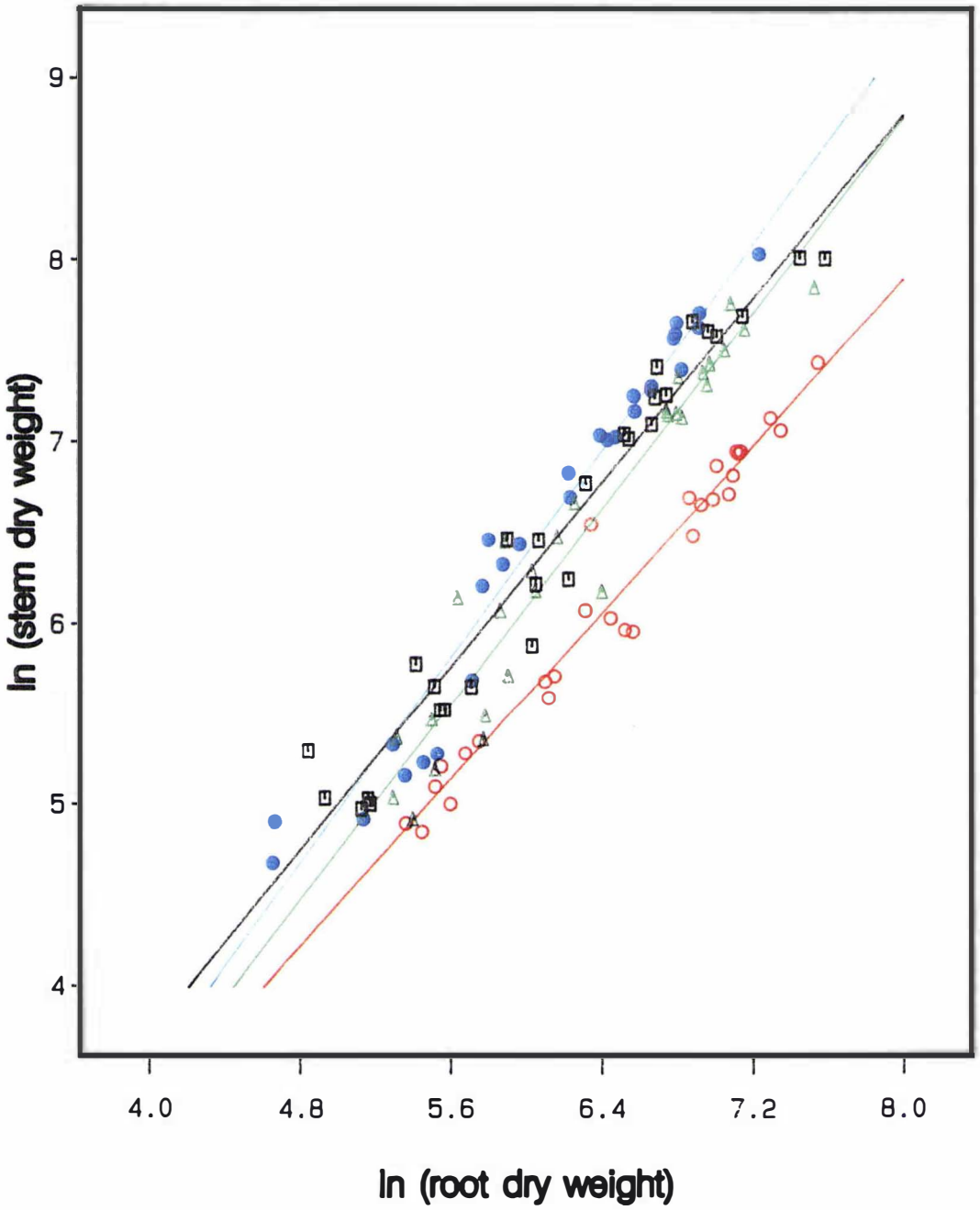

ln (stem dry weight)
9
8
7
6
5
4
4.0
4.8
5.6
6.4
7.2
8.0
ln (root dry weight)
Treatment
Control
Shoot 2.9X10-5 M
Root 5.8 X10-5 M
Root 2.9 X10-4 M

Figure 3.5. Changes in allometric relationship between stem and root dry weight (k_S) of tomato seedlings when supplied via the roots or the shoot with GA_3 at varying concentrations (experiment 2).

Control: R^2 = 96.2%, y =-1.250 + 1.14 x,
Shoot GA_3 2.9 $X10^{-5}$ M: R^2 = 95.7%, y =-1.871 + 1.38 x,
Root GA_3 5.8 $X10^{-5}$ M: R^2 = 92.7%, y =-1.918 + 1.34 x,
Root GA_3 2.9 $X10^{-4}$ M: R^2 = 95.1%, y =-1.264 + 1.25 x.

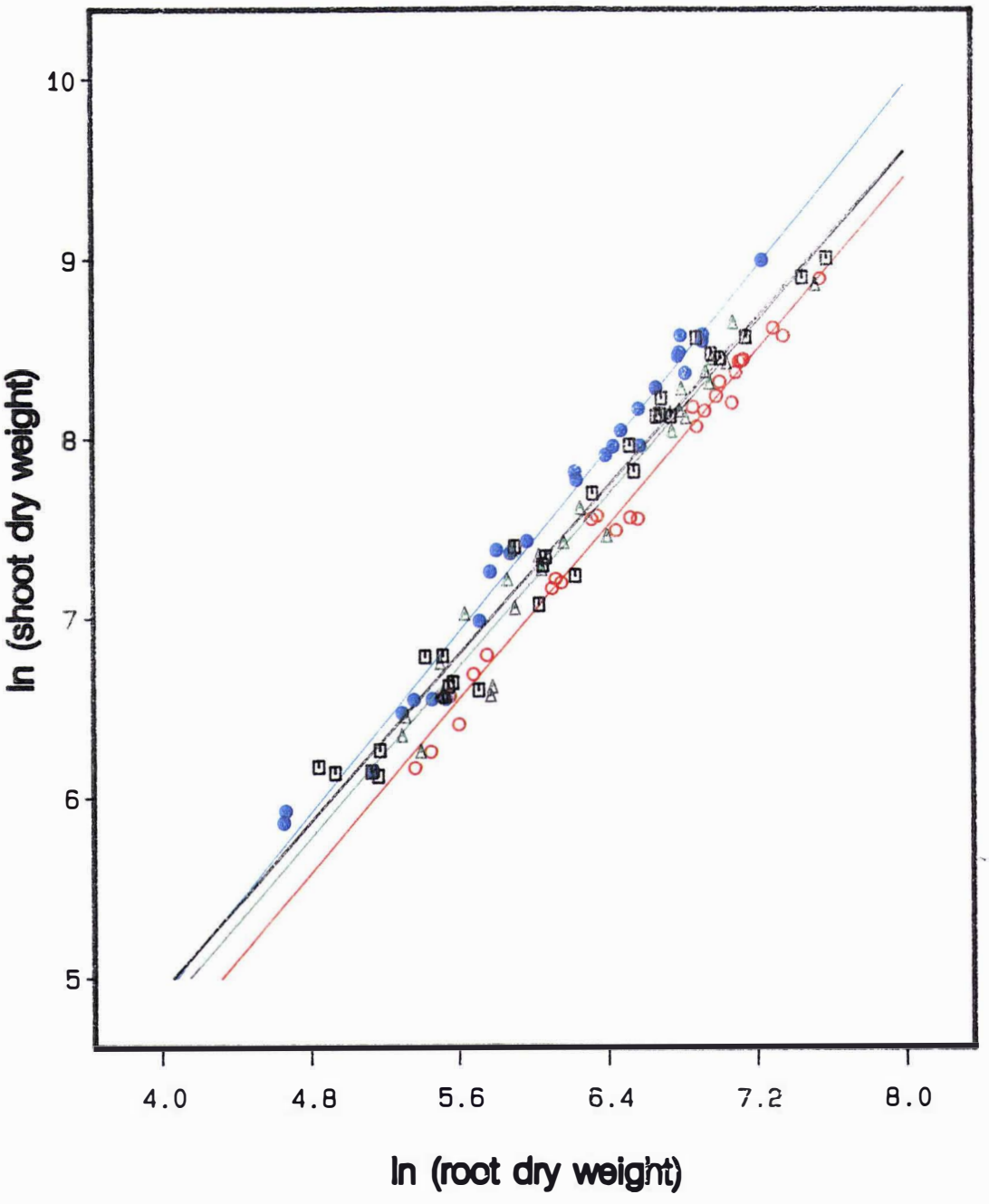
TABLE 3.15. *Changes in allometric relationship between shoot and root dry weight (k_T) with time as affected by GA_3 treatments (experiment 2)*

Harvest no.	GA_3 treatment	ln a	*1 se (ln a)	k_T		se (k_T)	R^2 (%)
					*		
1	Control	-0.110	0.682	1.188	b	0.121	94.2
	Shoot $2.9X10^{-5}M$	1.482	0.543	0.938	a	0.104	93.2
	Root $5.8X10^{-5}M$	1.113	0.932	0.988	a	0.165	85.7
	Root $2.9X10^{-4}M$	1.186	0.646	0.982	a	0.120	91.8
					*		
2	Control	0.419	0.637	1.111	b	0.101	95.3
	Shoot $2.9X10^{-5}M$	0.781	0.510	1.108	b	0.089	96.3
	Root $5.8X10^{-5}M$	-0.690	1.909	1.319	b	0.322	73.6
	Root $2.9X10^{-4}M$	1.331	0.602	0.979	a	0.103	93.8
					*		
3	Control	0.445	0.653	1.109	b	0.097	95.6
	Shoot $2.9X10^{-5}M$	1.525	0.279	1.009	b	0.043	98.9
	Root $5.8X10^{-5}M$	1.665	0.348	0.953	a	0.054	98.1
	Root $2.9X10^{-4}M$	0.497	1.284	1.135	b	0.201	84.2
					*		
4	Control	1.342	0.487	0.996	a	0.068	97.3
	Shoot $2.9X10^{-5}M$	-0.796	1.012	1.361	b	0.149	93.3
	Root $5.8X10^{-5}M$	1.779	1.033	0.951	a	0.147	87.5
	Root $2.9X10^{-4}M$	1.342	0.487	0.998	a	0.132	90.6
					*		
Pooled	Control	-0.217	0.150	1.210	a	0.023	96.2
	Shoot $2.9X10^{-5}M$	-0.096	0.190	1.256	b	0.031	98.9
	Root $5.8X10^{-5}M$	0.037	0.273	1.196	a	0.044	97.2
	Root $2.9X10^{-4}M$	0.227	0.227	1.172	a	0.037	98.2

- K_T values from slopes of linear regressions of $\ln y = \ln a + k_T \ln x$, where y is shoot d.wt. and x is root d.wt. Each parameter estimated from 8 and 32 plants, and comparisons of k_T values based on t-test ($p \leq 0.05$), $df_{(error)}$ = 12 and 60 at harvests and pooled analysis, respectively.
- *1 = Standard error.

Figure 3.6. Changes in allometric relationship between shoot and root dry weight (k_T) of tomato seedlings when supplied via the roots or the shoot with GA_3 at varying concentrations (experiment 2).

Control: R^2 = 96.2%, y =-0.217 + 1.21 x,
Shoot GA_3 2.9 $X10^{-5}$ M: R^2 = 98.9%, y =-0.096 + 1.26 x,
Root GA_3 5.8 $X10^{-5}$ M: R^2 = 97.2%, y = 0.037 + 1.20 x,
Root GA_3 2.9 $X10^{-4}$ M: R^2 = 98.2%, y = 0.227 + 1.17 x.


10
9
8
7
6
5
ln (shoot dry weight)
4.0
4.8
5.6
6.4
7.2
8.0
ln (root dry weight)
Treatment
Control
Shoot 2.9X10-5 M
Root 5.8 X10-5 M
Root 2.9 X10-4 M

periods, the allometric regression equation must change but the change applies only to the growth increment(s) required to restore balance. During this experiment there were probably temporal changes in the dynamics of growth rates of the roots and parts of the shoot. First, there would have been effects of transplanting into the tanks, and secondly, there were effects of growth regulators which may also have been transitional (see later discussion). The pooled data, however, show higher and more consistent coefficients of determination. In addition, plant weights increased six fold over the course of the experiment, and the effect of errors incurred over the narrower weight ranges at individual harvests, and any real fluctuations in k values, would be greatly reduced when the regression equation included data spanning the entire weight range of the experimental data. Thus, in the following discussion, allometric relationships obtained from the pooled data only has been used to obtain the overall k value for each treatment.

All GA_3 treatments reduced k_L but increased k_S values. By contrast, k_T was increased by shoot GA_3 treatment, while it was unaffected by root treatments. The results of k_L (Table 3.13) indicates that GA_3 reduced RGR_L when compared with RGR_R. These data also show that root GA_3 treatments had a greater influence in this regard, than the shoot treatment. On the other hand, GA_3 treatments significantly increased the k value of the allometric relation between stem and roots (Table 3.14), indicating the relative growth rate of the stem was increased compared to roots. The shoot GA_3 treatment was significantly more effective in this respect than the root treatments.

Thus, GA_3 enhanced the growth of the stem at the expense of the roots and leaves. The shoot GA_3 treatment favoured growth in the total shoot system, at the expense of the root system, to a greater extent than the root treatments (Table 3.15). These results are in close agreement with the effects of GA_3 on organ weight ratios and shoot-root ratios (see section 3.3.2.6) which suggests that GA_3 enhances assimilate partitioning towards a particular organ by enhancing the growth rate of that organ in relation to others.

3.3.2.5. Changes in Ratios of Relative Growth Rates

Although no significant differences were found in the ratios of RGR(s) (Table 3.16), the results reinforce the apparent effects reported for RGR(s), in particular, the substantial contribution of stem growth to plant growth in plants treated with GA_3. While the ratio of RGR_L to RGR_R (RGR_{LR}) of the control was constant, RGR_{LR} of treated plants declined with time, indicating that GA_3 appeared to inhibit leaf growth more strongly than root growth. It is of interest to note that the ratio of RGR_S to RGR_R (RGR_{SR}) of the control fluctuated compared to the ratios of all but shoot GA_3 treatments, which declined. Considering these together with the ratios of RGR_S to RGR_L (RGR_{SL}), it appears that in the control plants, there is a strong link between the RGR_L and RGR_R, which remains constant with time, whilst RGR_S was not well correlated with either RGR_L or RGR_R.

The RGR_S of the control fluctuated whereas it diminished with time in the GA_3 treatments. However, RGR_S may have a strong contribution to plant growth as a whole, as the ratios associated with it (RGR_{SR}, RGR_{SL} and the ratio of RGR_T to RGR_R (RGR_{TR})) exhibited similar patterns of temporal changes. Up to the third week, the RGR_{SR} appeared to be increased by GA_3 treatments, but at the final harvest this effect had disappeared. This result supports the effects of GA_3 demonstrated in other attributes and relative growth rates. It indicates that stem growth, compared to the other organs, seemed to be enhanced by GA_3 and this resulted in increased RGR_{TR}. Thus, the shoot-root ratio was expected to be raised in these treatments.

3.3.2.6. Changes in the Distribution of Assimilates

Leaf Weight Ratio (LWR)

The LWR, which indicates the leafiness of the plants, was strongly inhibited by GA_3 (Table 3.17). From the second harvest onwards, the effect of GA_3 was highly significant. The root application of GA_3 at the higher concentration showed the strongest effect followed by the lower root concentration

TABLE 3.16. *Changes in ratios of relative growth rates with time as affected by GA_3 treatments (experiment 2)*

Week	GA_3 treatment		RGR_{LR} *1	RGR_{SR} *2	RGR_{TR} *3	RGR_{SL} *4
			ns	ns	ns	ns
2	Control		1.252	1.226	1.252	0.979
			(0.262)	(0.268)	(0.262)	(0.210)
	Shoot	$2.9X10^{-5}M$	1.304	1.851	1.477	1.419
			(0.473)	(0.589)	(0.505)	(0.399)
	Root	$5.8X10^{-5}M$	1.286	2.148	1.544	1.671
			(0.606)	(0.890)	(0.682)	(0.649)
	Root	$2.9X10^{-4}M$	1.086	1.592	1.261	1.466
			(0.569)	(0.698)	(0.606)	(0.633)
			ns	ns	ns	ns
3	Control		1.250	0.849	1.148	0.679
			(0.423)	(0.376)	(0.403)	(0.293)
	Shoot	$2.9X10^{-5}M$	1.195	1.353	1.253	1.132
			(0.304)	(0.313)	(0.307)	(0.252)
	Root	$5.8X10^{-5}M$	1.167	1.645	1.339	1.409
			(0.422)	(0.502)	(0.448)	(0.411)
	Root	$2.9X10^{-4}M$	1.202	1.393	1.274	1.159
			(0.475)	(0.489)	(0.480)	(0.388)
			ns	ns	ns	ns
4	Control		1.258	1.453	1.300	1.155
			(0.383)	(0.435)	(0.394)	(0.317)
	Shoot	$2.9X10^{-5}M$	1.010	1.396	1.163	1.382
			(0.447)	(0.496)	(0.461)	(0.571)
	Root	$5.8X10^{-5}M$	1.082	1.106	1.092	1.022
			(0.313)	(0.300)	(0.307)	(0.268)
	Root	$2.9X10^{-4}M$	1.101	1.247	1.161	1.133
			(0.283)	(0.290)	(0.284)	(0.276)

- Each mean figure from 8 replications.
- Mean separation within column by t-test ($p \leq 0.05$).
- Standard error of means in bracket.
- *1 = Ratio of leaf to root relative growth rate,
  *2 = Ratio of stem to root relative growth rate,
  *3 = Ratio of shoot to root relative growth rate,
  *4 = Ratio of stem to leaf relative growth rate.

TABLE 3.17. *Changes in dry weight distribution with time as affected by GA_3 treatments, expressed as a ratio of plant organ to total plant dry weight and shoot-root ratio (experiment 2)*

Harvest no.	GA_3 treatment	Leaf weight ratio %	Stem weight ratio %	Root weight ratio %	Shoot-root ratio
		ns	**	*	*
1	Control	54.4	17.7 a	27.9 b	2.61 a
	Shoot $2.9X10^{-5}M$	53.7	22.3 bc	24.0 a	3.20 b
	Root $5.8X10^{-5}M$	53.2	20.7 b	26.1 b	2.87 ab
	Root $2.9X10^{-4}M$	51.0	23.8 c	25.2 b	2.99 b
	se	0.5	0.4	0.8	0.12
		**	**	**	**
2	Control	56.9 c	18.5 a	24.7 b	3.06 a
	Shoot $2.9X10^{-5}M$	51.9 b	28.4 c	19.8 a	4.09 b
	Root $5.8X10^{-5}M$	51.3 b	25.4 b	24.0 b	3.22 a
	Root $2.9X10^{-4}M$	48.5 a	28.4 c	23.4 b	3.32 a
	se	0.5	0.5	0.9	0.16
		**	**	**	**
3	Control	60.2 c	16.3 a	23.3 c	3.31 a
	Shoot $2.9X10^{-5}M$	51.5 b	31.5 b	17.0 a	4.88 c
	Root $5.8X10^{-5}M$	49.0 a	30.6 b	20.4 b	3.91 b
	Root $2.9X10^{-4}M$	48.1 a	31.4 b	19.6 b	4.11 b
	se	0.3	0.3	0.5	0.10
		**	**	**	**
4	Control	60.6 c	17.8 a	21.2 c	3.71 a
	Shoot $2.9X10^{-5}M$	48.5 ab	33.8 c	16.0 a	5.19 c
	Root $5.8X10^{-5}M$	48.8 b	30.9 b	19.3 b	4.16 b
	Root $2.9X10^{-4}M$	46.8 a	33.5 c	18.6 b	4.35 b
	se	0.4	0.3	0.5	0.16
		**	**	**	**
Pooled	Control	58.0 c	17.6 a	24.3 c	3.11 a
	Shoot $2.9X10^{-5}M$	51.4 b	29.0 c	19.2 a	4.33 c
	Root $5.8X10^{-5}M$	50.6 b	26.9 b	22.3 b	3.58 b
	Root $2.9X10^{-4}M$	48.6 a	29.3 c	21.9 b	3.67 b
	se	0.4	0.3	0.4	0.07

- Each mean figure from 8 replications with $df_{(error)} = 28$ harvests, pooled mean from 32 replications with $df_{(error)} = 112$.
- Mean separation within column by Lsd ($p \leq 0.05$).

and the shoot application which were not significantly different. Whereas in the control, LWR increased with time, the LWR of all GA_3 treatments decreased continuously (Fig. 3.7 a). Consequently, the difference between the two groups increased with time.

Stem Weight Ratio (SWR)

The SWR in relation to total plant size, was increased greatly by GA_3 at all harvests, and also continued to increase throughout the experiment (Fig. 3.7 b; Table 3.17). In contrast, the SWR of the control changed only slightly over the period of the experiment. By the final harvest, the SWR of GA_3 treated plants was double that of the control. The results for this attribute show that the more concentrated of the root GA_3 treatments stimulated SWR less than the shoot treatment. This effect was noted at the third and the forth harvests and also in the pooled mean. The effects on SWR were highly significant throughout.

Root Weight Ratio (RWR)

Root proportion, expressed as root weight ratio, was decreased by GA_3 at all harvests (Table 3.17). Figure 3.7 (c) showed that the root portion declined with age in all treatments. However, in the treated-plants the reduction in root proportion was intensified by GA_3. The ratio was lowest when GA_3 was applied to the shoots. When applied to roots, GA_3 also suppressed RWR, but to a lesser degree.

The GA_3 effect on RWR makes a very interesting comparison, especially with that on SWR. With respect to the latter, the effect was similar, allowing for concentration effects when applied at the roots. The greatest suppression of root growth, and therefore, RWR, however, was obtained by shoot application. This would appear to suggest that GA_3 supplied via the roots has a smaller effect on suppressing root growth than when applied directly to the shoots. This result could be explained if GA_3 enhanced the growth potential of cells in the root as well as the stem. The relative growth rates of the two competing systems could then be determined by proximity of the growth zone to the photoassimilate source.

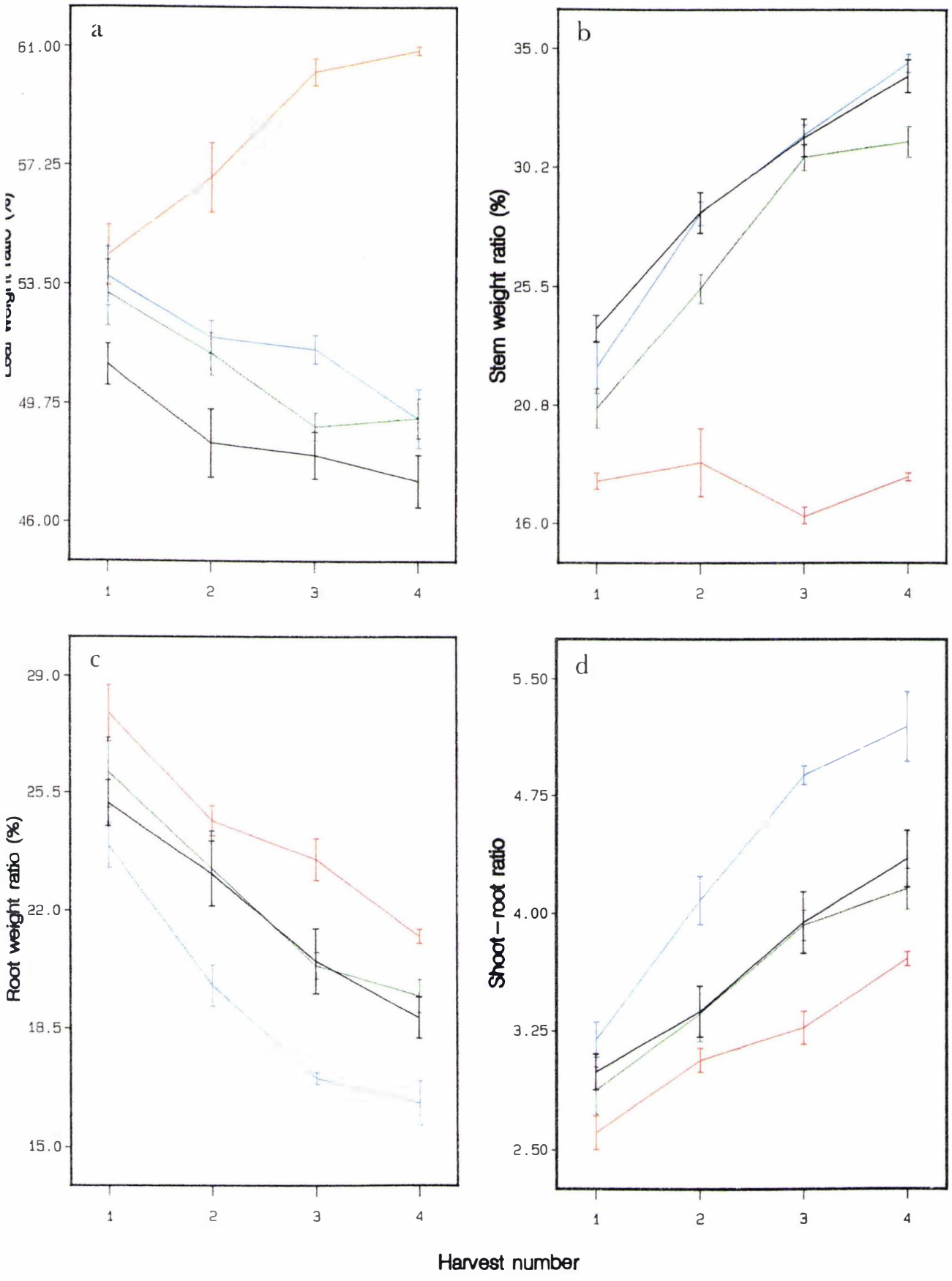

a
61.00
57.25
53.50
49.75
46.00
1
2
3
4
b
35.0
30.2
25.5
20.8
16.0
Stem weight ratio (%)
c
29.0
25.5
22.0
18.5
15.0
Root weight ratio (%)
d
5.50
4.75
4.00
3.25
2.50
Shoot-root ratio
Harvest number
Treatment
Control
Shoot 2.9 X10-5
Root 5.8 X10-5
Root 2. 9X10-4

Figure 3.7. Changes in the proportion of photoassimilates partitioned into tomato seedling organs, when supplied via the roots or the shoot with GA_3 at varying concentrations (experiment 2); (a) leaf weight ratio, (b) stem weight ratio, (c) root weight ratio and (d) shoot-root ratio. I = standard error of means.

The absolute growth data show that photoassimilate limits growth in GA_3 treated plants compared to the control.

Shoot-root Ratio

Gibberellic acid significantly increased shoot-root ratio, particularly at the later harvests (Table 3.17 and Fig. 3.7 d). In all GA_3 treatments, incremental stimulation or inhibition of growth of individual organs continued throughout the experiment, resulting in a shoot-root ratio that increased progressively with respect to the control. The imbalance between increased stem growth and reduced leaf growth by GA_3 resulted in a substantial gain in weight by the shoot. This was also accompanied by reduced root growth resulting in a significantly increased shoot-root ratio in GA_3 treated plants. Because shoot application gave the greatest effect in reducing root growth, this treatment had the greatest effect on shoot-root ratio.

3.4. DISCUSSION

3.4.1. Plant Responses in Relation to the Site of Application and Various Concentrations of GA_3

In the experiment 1, GA_3 applied at shoot or both shoot and roots tended to increase stem growth and stem weight ratio (SWR) while root sprays were ineffective. In the following experiment, however, responses of plants to GA_3 were clearer. Nevertheless, the results of the first and second GA_3 experiments were not contradictory. It can be safely assumed that root sprays did not facilitate uptake of sufficient growth regulator to give measurable effects upon growth. The following discussion, thus, will concentrate on the second experiment.

Frequent reference is made to growth regulator concentrations. The effects of concentration and site of application are often compared. The limitations of such conclusions should therefore be recognized. Differences in effectiveness of uptake of chemical, resulting from application to different organs and the use of different methods of application, make comparisons of the actual application rates quite meaningless, both within this experiment, and with other experiments, except where the mode and site of application are comparable. It is the plant response, albeit to an unknown amount of chemical that is being considered. In this respect, it is clear that the concentrations applied have been chosen well, in that similar, even overlapping responses, have been obtained. On that basis, comparisons between the sites of application are well justified. Clearly, it would have been desirable to measure rates of uptake and transport of chemical. This, however, would have been a large and complex investigation in its own right and was considered to be beyond the scope of this study.

Results from both shoot and root treatments were qualitatively similar, despite concentrations of the latter being 2 and 10 times higher. While plant height was visibly increased at all GA_3 concentrations, other effects obtained showed a range of responses from promotion to inhibition, which were, however, only detectable by precise measurement. The range of the concentrations used therefore, appeared to span the physiological range, perhaps extending at the

highest concentration to supra-optimal levels. In addition, no gross morphological changes were detected, in either experiment, at any concentration.

Generally, application of GA_3 to reciprocal organs gave qualitatively similar plant responses. Stimulation of stem growth leading to a reduction of leaf and root growth could be obtained by applying GA_3 at the either site. Other work has shown that active forms of GA are ubiquitous in plant tissues and conducting systems (Ingram *et al.* 1985; Sponsel 1985). Indeed, this fact is probably partly responsible for the difficulty that has been encountered by studies which have sought to identify tissues and /or organs from which these compounds emanate. Nevertheless, these results show that GA_3 supplied exogenously enters and reacts similarly with growth mechanisms, whether they arrive at the site of action directly, via 'artificial' pathways from the surface of shoot tissues, or, indirectly, through natural translocative pathways from the roots. This may suggest that GAs produced in either organ, control plant growth through the same pool of the endogenous hormone and act via the same mechanism. In this respect, these data resemble those obtained by Steffens and colleagues (1985) who demonstrated recovery of growth, induced by foliar application of exogenous GA, on plants fed with growth retardant (GA biosynthesis inhibitor) via aerated nutrient solution.

3.4.2. Effects of GA_3 on Plant Structures and Growth

The increased levels of GAs in leaves or roots primarily caused an promotion in stem growth and a reduction in root growth. As a consequence, LA, LAR and leaf growth were reduced. The result is in agreement with Ben-Gad *et al.* (1979) and Tognoni *et al.*(1967), who found that GA suppressed root and leaf growth and favour stem growth, which led to reduced plant growth as a whole. Nevertheless, it needs to be emphasized here that the effect of GA_3 on leaf growth was an indirect result of the direct effect of GA_3 in stimulating apical dominance. Individual leaf parameters were not affected by GA_3. The entire difference in leaf area was attributable to the reduction in leaf number due to suppression of lateral development.

On the other hand, growth of leaves of monocotyledonous plants have been shown to be stimulated by GAs. In maize and rice plants elongation of leaf

sheath and /or leaf blades was enhanced by GA application (Hayashi *et al.* 1956) as was rice coleoptile segment (Soni and Kaufman 1972). The different GA effect on these plants may be due to the fact that growth in monocots occurs mainly at the leaf base whereas internode growth is less important. Although promotion in growth was directed to alternative organs, in this case, leaves, the target tissue, expanding cells was the same. This raises the question of why cell expansion in leaves was not affected in the tomato which is an interesting question deserving further attention.

Muir and Cheng (1988) also found that GA promoted growth in fresh weight and area of isolated cotyledons in light. In this instance, however, isolated organs, perhaps responded as independent free cells, rather than as components of an organism, within which priority amongst cells, tissues and organs to receive photoassimilates would also influence the relative growth of individual organs. A similar explanation may account for discrepancies observed in work with excised roots (*e.g.* Butcher and Street 1960; Pecket 1960).

While growth of stem tissues was promoted by GA_3 in these experiments, there was no evidence that total plant growth was promoted. Indeed, although results were not significant, GA_3 treated plants tended to be smaller than control plants, and it was clear that the increase in stem weight did not match the total reduction in leaf and root weight. Considering that in this (tomato) system leaf area was reduced, it is logical to conclude that overall growth would be suppressed by GA_3. The extent to which one could interpret this to be a general principle, is not clear. Certainly in dicotyledonous plants in which stem growth was promoted, this could only occur at the expense (directly or indirectly) of the leaves. In monocotyledonous plants, where the growth zone is the leaf base, it is conceivable that absolute growth might be enhanced by GA.

While these results are obviously a good indication that GA may have a role in the regulation of leaf expansion, the reduction of leaf area in this study is the result of enhanced stem growth priority, rather than inhibition of leaf growth *per se*. In turn, reduced leaf area was the prime cause of the decline in plant growth as photosynthetic leaf area declined. Leaves have also been shown to be

less affected than internode length by growth retardant with known anti-gibberellin biosynthetic properties (Cathey 1964; Steffens *et al.* 1985). Leaf number in particular was reduced by 17% compared to a 91% reduction in shoot length.

It should also be pointed out that the results of this study do not contradict those reported for hydroponically-grown tomatoes, in which leaf area and overall growth were promoted by GA_3 as reported by Buggee and White (1984). This, however, only occurred when the solution temperature was maintained at 15°C. It did not occur at 25°C. The stimulated growth therefore, appeared to be the recovery of shoot growth of plants growing under cold stress rather than actual growth stimulation of GA *per se.* Since it is known that GA production, or export, is severely inhibited by prolonged exposure to cold temperatures (Atkin *et al.* 1973), exogenous GA would be expected to release growth of the shoot from the cold stress.

On the other hand, it also is important to note that reduced plant growth was an indirect effect of growth priorities, not growth inhibition. With the increased stem growth, plant structure was greatly modified towards a tall and less branched plant. It has been demonstrated that GA stimulates growth in certain situations, such as stimulation of young radicle elongation (Paleg 1965). The evidence that GA stimulates elongation of root sections (Butcher and Street 1960; Packet 1960) also supports this statement. Wheeler (1960) also showed that the GA level of bean leaves rises sharply at the time that light induced expansion begins. It seems that the level of GA fluctuates according to plant growth and development, and external environments (Sponsel 1985). These reports concur with this study on the possible role of GA in adaptation in response to environments, especially light intensity (Smith and Holmes 1977; Junttilla 1982; Jones 1983; Pharis and King 1985). As a further outcome, the change (from leaf and root production to stem production) will necessarily result in a reduced rate of leaf growth and a decreased overall growth rate.

On the other hand, the response to GA fed to the root system was quantitatively different in a number of important respects. Root growth was also disadvantaged by enhanced stem growth, but the effect was more pronounced

when GA was applied to the shoot of the plant. Maximum promotion of growth by the stem and suppression of growth by roots was obtained when GA was applied to shoot (see Table 3.9; 3.12; and 3.17). This difference in GA effects was highly significant, while all others were similar. This may point to a key difference in function between root and shoot derived hormone. It appears that root produced GA_3 may have less effect in suppressing root growth than stem produced GA_3. This could occur if part of the root produced GA was utilized in root growth as it was being transported into the shoot system (*e.g.* see Chalmers 1985).

This could have adaptive or selective advantages in that growth of the roots would be most severely suppressed in situations which originated from stimuli affecting gibberellic acid synthesis by the shoots. Thus, for instance, in low light situations, which frequently threaten plant survival, the maximum possible stimulation of stem growth from the available pool of growth substrates would result. If leaf function was the limiting factor in such a situation, additional growth by the root system would be wasteful until the plant had grown into an improved light regime. The corollary of this model would also have an adaptive significance. Enhanced root produced GA would result in less suppression of root growth and a partly attenuated effect on stem elongation. This, perhaps, leading to a more general increase in plant stature and size, and maintained root capability. This condition would be in accord with the desirable rhizosphere environment that give rise to it.

These effects of GA_3, which lead to enhanced apical dominance and stem elongation, are a well documented property of this hormone (growth regulator) (Brian and Hemming 1955; Woolley and Wareing 1972 a; Jones 1983). The adaptive role of the hormone, particularly to light environments is obvious (Pharis and King 1985). Nevertheless, a specific partitioning model, such as these data implicate, has not been previously proposed. These data demonstrate that GAs produced in shoots will have different effects to active GAs transported from the root system via xylem.

Gibberellins originating in the shoots favour growth of the stem at the expense of the roots, more than GAs exported from root system. Thus, for

instance, GA production by the shoot system in response (directly or indirectly) to shoot stimuli such as light (Wheeler 1960), will stimulate etiolation to a greater extent than GAs produced in the root system. Gibberellins originating from roots maintain root growth while at the same time stimulating stem growth in the shoot at the expense of leaves. In this respect, GA tends to maintain the balance of root function with shoot function whilst also promoting apical dominance as a component of the optimum plant structure (size and shape), for maximum production in a non-competitive growing environment.

The results of this study suggest that the tissue or organ in which physiologically active GAs originate may be an important component of plant response to environmental stress. In environmental conditions specifically limiting to shoot development, such as low irradiance, roots might not be expected to be sensitive. Consequently any signal to enhance plant height as a competitive growth strategy might be expected to originate in the illuminated part of the plant. Elongated features of shade-grown plants are reported to be mediated by phytochrome responding to the enriched far-red component of light that has passed through a leaf canopy (Holmes and Smith 1975). Morgan and Smith (1978) have shown that the ratio of leaf to stem dry weight in *Chenopodium album* was least in the intense shading. Jones (1983) noted that GA_3 can interact with phytochrome and blue light to control elongation of stem. Exogenous GA can also replace the light or cold requirement in long-day or cold-requiring plants to initiate flower formation (Pharis and King 1985). These effects, thus, induce a change in GA or hormonal balance, leading to an alteration of plant structures in the manner predicted by this model.

The results of these experiments strongly suggest that GAs act as natural regulators of partitioning of photoassimilates between expanding cells in the stem and other organs in tomatoes. High levels of GAs applied to roots or leaves promoted stem elongation and reduced growth of leaves and roots and productivity overall, irrespective of the site of the application. Nevertheless, the effect of GA on actual leaf growth was neither stimulatory nor inhibitory, but neutral. The reduction in leaf and root growth occurred indirectly when stem growth and apical dominance were promoted. Since numbers of leaves and shoot apices were

production of reciprocal hormones in the allometric balance would have been correspondingly reduced (Baker and Allen 1988). The reduced promotive signal from the leaves would stimulate less root growth and consequently less demand for photoassimilate for root growth.

3.4.3. Effects of GA_3 on the Allometric Relationships

The allometric value between the shoot and root system (k_T) was affected only by GA_3 shoot treatment (Table 3.15; Fig. 3.6). This was because, first, the shoot treatment gave the greatest response; but secondly, because the increase in k_S (Table 3.14; Fig. 3.5) and the decrease in k_L (Table 3.13; Fig. 3.4) tended to balance each other in k_T (Table 3.15; Fig. 3.6). The significant increase in k_S indicates that GA_3 increases the RGR_S in relation to the root system. This change accounts for the fact that the SWR increases with time and shows that GA_3 treatment established a new equilibrium ratio of RGR(s). Under continuous GA_3 supply to roots or shoot, the effects of GA_3 on growth were continuous and additive. This was reflected in the increasing difference in SWR, LWR and shoot-root ratio with time and the change in the kS, which increased, and k_L, which decreased, as a result of GA treatments. In this way, the rate of GA production would determine the degree of apical dominance and stem growth.

CHAPTER 4
THE ROLE OF CYTOKININS IN GROWTH AND SHOOT-ROOT ALLOMETRY OF TOMATO SEEDLINGS

4.1. INTRODUCTION

In a similar way to gibberellins, the concept of hormonal signal(s), produced by root tips controlling shoot growth, has also been applied to cytokinins (Wareing 1970; Skene 1975; Richards and Rowe 1977 b; Goodwin *et al.* 1978). Considerable evidence has shown that root cytokinins have a role in shoot growth and development (*e.g.* Woolley and Wareing 1972 a; b; Hewett and Wareing 1973; Skene 1975; Garrison *et al.* 1984). While this function of cytokinins is now widely accepted, evidence remains circumstantial, and the mechanism of action is unknown (Moore 1989).

It has been reported that growth of leaf tissues, in particular, is stimulated by exogenously applied cytokinins via protein synthesis and enzyme activity (Caers and Vendrig 1986; Kuiper and Staal 1987). In addition, the responses of the shoot, obtained when exogenous cytokinins are applied to the shoot or roots are similar (Badenoch-Jones *et al.* 1984), indicating that the shoot is the target for the action of root- produced cytokinins. Further, high contents of cytokinins are well correlated with vegetative growth, root growth and plant growth as a whole (Sitton *et al.* 1967; Luckwill and Whyte 1968; Hurd 1978; Donchev 1981; Tucker 1981; Richards 1986). Finally, the inhibition of plant growth induced by stresses, which is proposed to restrict cytokinin production within roots, can be overcome by applying exogenous cytokinins to the shoot (Richards and Rowe 1977 b; Carmi and Heuer 1981).

Since treatments of BA (Benzylaminopurine) in this experiment were to applied via the root system, factors relating to such treatments need also to be considered here.

Root uptake of cytokinins is reported to be rapid, only within the first hour after application, and declines progressively with time (Volgelmann *et al.* 1984;

Van der Krieken *et al.* 1988). The uptake mechanism remains a controversial, although it is believed to be, at least, partially passive (Fantelli *et al.* 1982; Lampugnani *et al.* 1981). Nevertheless, the uptake rate was much reduced at low temperature (5^{o}C) (Volgelmann *et al.* 1984) and appears likely to be related to transpiration (Forsyth and Van Staden 1987 b).

Uptake seemed to be limited in intact (tomato) seedlings (Van Staden and Mallett 1988). Nevertheless, the amount taken up depends to a large extent on the concentration applied (Minocha and Nissen 1982; Forsyth and Van Staden 1987; Van Staden and Mallett 1988; Bayley *et al.* 1989). In intact tree seedlings, the maximum internal concentration was found to be one-third of the external concentration (Volgelmann *et al.* 1984). The uptake across the root surfaces is limited and most of the substance supplied, ranging between 50 to 99%, remained at the site of application (Mozes and Altman 1977; Gordon *et al.* 1974), indicating strictly stelar transport within the plants (Jameson *et al.* 1987). The presence of BA in the root bathing solution was necessary only during the first two days and equilibrium between BA and its metabolites within the tissues was obtained four days after the chemical was first applied, irrespectively of BA concentration or the plant response (Volgelmann *et al.* 1984). Williams and Stahley (1968) found that one application of cytokinins yielded no response, and proposed that plant responses can not be induced unless the threshold concentration of cytokinin was reached. Nevertheless, continual supply of the chemical may not be essential for optimum response, since maximum increases in fresh weight was obtained after a pulse treatment of one hour (Longo *et al.* 1979). On the other hand, these results are difficult to interpret, since in the former, coordination between organs on intact plants was being studied, while the latter system consisted of detached watermelon cotyledons. In all instances, however, the level of metabolites was proportional to the concentration of BA applied (Van der Krieken *et al.* 1988).

Metabolism within the roots is rapid and the labelled compounds are transported to the major receivers, the leaves and shoot laterals (Davey and Van Staden 1981; Jameson *et al.* 1987), even during fruit bearing stages of development (Nooden and Letham 1984). The exogenous cytokinins used were generally nitrogen bases, which are believed to be converted to ribosides and ribotides (Van

nitrogen bases, which are believed to be converted to ribosides and ribotides (Van Staden and Davey 1979; Letham and Palni 1983; Bayley *et al.* 1989). The level of metabolites obtained in the tissues receiving exogenous cytokinins, also correlated well with external concentration of the chemical (Van der Krieken *et al.* 1988).

Different tissues differed in capacity to metabolizing cytokinins (Forsyth and Van Staden 1987; Jameson *et al.* 1987). Of the organ segments tested, leaf tissues were the most effective at BA metabolism followed by the stem, while root tissues were least active, despite the fact that there were more varieties of metabolites in roots than in other organs (Bayley *et al.* 1989). In their reviews, Letham and Palni (1983) and Zhang *et al.* (1987 a) reported that plant tissues converted exogenous cytokinin bases (including BA) into a great variety of metabolites, but that the action of most derivatives appeared to be less effective than the base itself. Because the activity of endogenous cytokinins has been found to peak just prior to significant periods of shoot development; such as breaking dormancy or bud burst (Luckwill and Whyte 1968; Hewett and Wareing 1973; Young 1989; Qamaruddin *et al.* 1990), it appears that the process of cytokinin metabolism produces the plant responses.

Although there have been many studies on the application of exogenous cytokinins, most have been related to growth restoration in stressed plants. It would be of great value, however, to investigate to what extent shoot growth may be altered or controlled by hormones from the roots in normal situations of plant growth. Application of cytokinins has not succeeded in stimulating plant growth *per se*. Tognoni *et al.* (1967), Wittwer and Dedolph (1963), and Richards (1980) concluded that cytokinins reduced plant growth because they attracted metabolites, towards the site of application, at the expense of overall growth, and frequently, shoot or root morphology was altered, indicating phytotoxic effects (Busch and Sievers 1990). Consequently, in this experiment the effects of external cytokinin (BA) have been studied. The concentrations of the chemical used were sufficiently low to avoid phytotoxic effects, and shoot treatments, which may confound interpretation, were excluded.

4.2. MATERIALS AND METHODS

4.2.1. Experimental Procedure and Design

Under the same greenhouse conditions, a similar experiment was conducted from March to June, 1989, with the same seed lot of the tomato cultivar described earlier (Chapter 3). The procedure for this experiment was the same as for the second gibberellic acid experiment, except that a synthetic cytokinin (BA) was used. The external replications were also arranged by duplicating the number of the tanks. The tanks were arranged along the length of the glasshouse. Uniform four week-old seedlings were carefully selected and transplanted onto the aeroponic tanks. After one week of establishment, treatments of 6-Benzylaminopurine (N^6-benzyladenine, MW 225.6, $C_{12}H_{11}N_5$, SERVA, Heidelberg, BA) were applied. The chemical was first dissolved in 10 ml of 90% ethanol, and then diluted by the nutrient solution, to make up the designated concentrations. The BA used during each experiment was freshly made as a stock solution and stored in a dark, cool, room (5^oC) when not in use.

The serial harvest was planned as a split-plot design with two blocks, each consisting of four tanks, each of which represented a treatment. There were four different BA concentrations (factor A); 2.22×10^{-8} M, 2.2×10^{-7} M, 2.2×10^{-6} M and control (water + ethanol), arranged in whole units with four harvest times, at weekly intervals (factor B or subunits). The BA treatments were assigned at random to the tanks and plants were collected at random at each time of harvests. With this arrangement, each harvest could also be considered as a common RCBD experiment on its own.

4.2.2. Collection of Data and Data Analyses

Destructive harvests commenced before the treatments were applied and were made at seven day intervals thereafter. Two plants were sampled from each tank for initial measurement at harvest zero, and four plants were collected from each tank at each subsequent harvest. Branches and inflorescences were measured when they were present. Similar procedures to the previous study (Chapter 2 and

3) were employed for data collection and analyses. At each harvest, data were analysed in a RCBD, using ANOVA and Lsd test. Pooled data from each attribute across all harvests were analysed using a split-plot RCBD design. Calculation of all derived means followed the methods described earlier.

The parameters measured were the same as for the second gibberellic acid experiment, except that parameters of inflorescences and root were also measured. The root measurements followed the methods described in Chapter 2.

The analyses and comparisons of means and other statistical analyses involved in the experiment followed the procedures described in Chapters 2 and 3. In this experiment, the allometric values between leaf and root parameters, which have not been determined in the previous studies, were determined using simple linear regression. Statistical tests of apparent linearity and comparisons of allometric values were carried out in the similar procedures as described for allometric equations derived from dry weights (in Chapter 2).

4.3. RESULTS

4.3.1. Morphological Changes due to BA Application

4.3.1.1. Leaf Attributes

Leaf Area

At all stages of the experiment, the effect of BA at all concentrations on leaf area was significantly different (Table 4.1). Benzylaminopurine, at low concentration, promoted leaf area production due to reduced apical dominance throughout the experimental period, although this was not initially significant. The mid-concentration appeared to suppress leaf area slightly (although not significantly), whereas the high concentration had a strongly suppressive effect (Fig. 4.1 a). These effects were consistent and thus, the general effects of BA expressed in pooled means show similar results. Plants from the low concentration treatment had 20% more leaf area than the control. Plants in the mid concentration treatment had a similar leaf area to the control, while plants treated with the high concentration had 35% less.

This result is a very important outcome because it indicates that with respect to this plant attribute the control, which received no exogenous synthetic cytokinin, was intermediate to treatments receiving synthetic growth regulators. This suggests that the exogenous compound entered, formed part of, and supplemented the pool of endogenous cytokinins, thereby eliciting a physiological response by the plant that was indistinguishable from the endogenous hormone. The low concentration thus gave a clearly physiological effect, exceeding that of the control, whereas the higher concentrations exhibited supra-optimal, and perhaps,'non-physiological' effects.

Leaf Area Ratio (LAR)

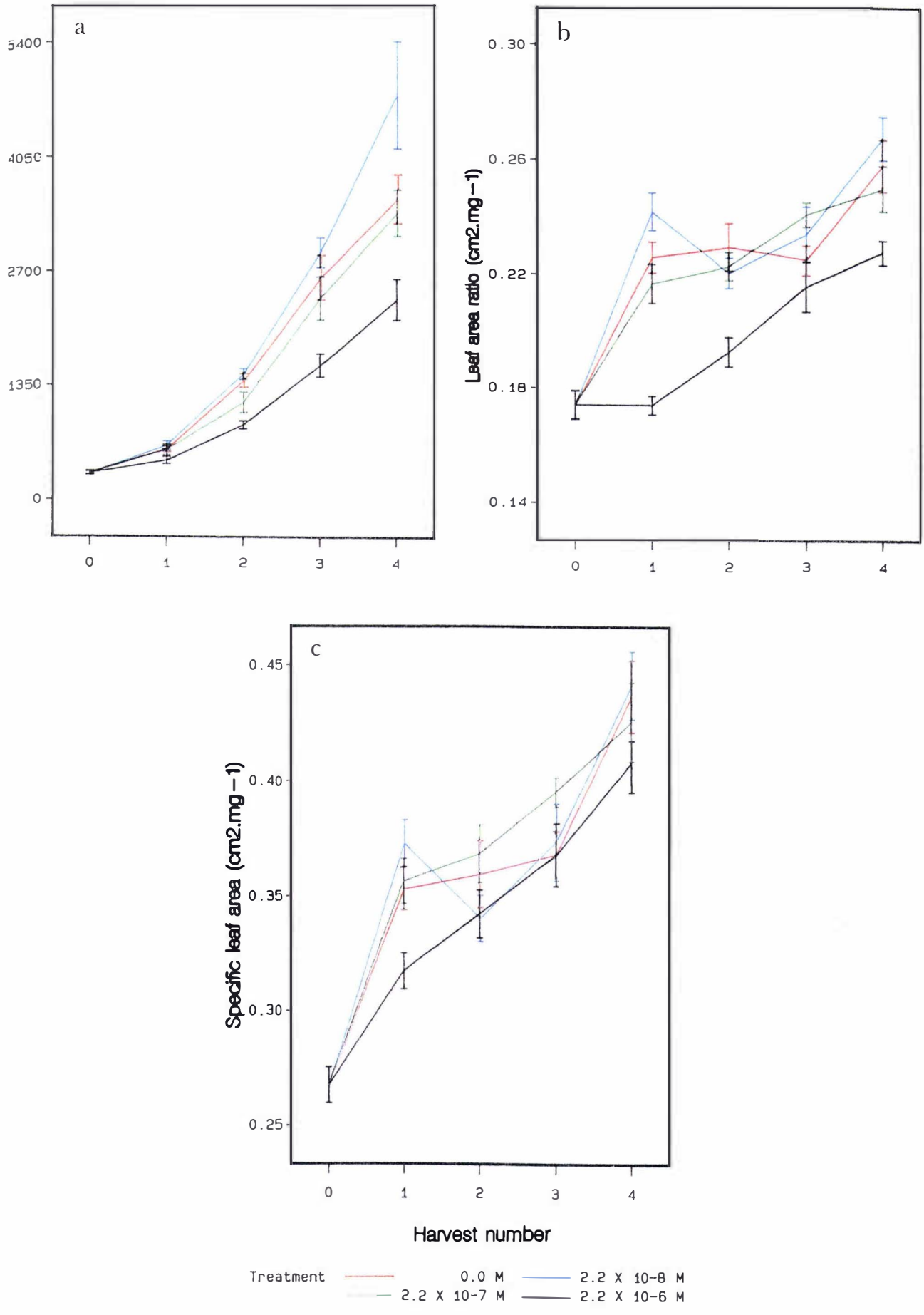
The pooled means of LAR revealed that BA reduced LAR, but only at the high concentration (Table 4.1). In fact, the LAR of the low BA treatment

LE 4.1. *Changes in leaf attributes with time as affected by root application of 6-N-benzylaminopurine*

'est	BA treatment	Leaf area cm2	Leaf area ratio cm-2.mg-1	Specific leaf area cm-2.mg-1	Leaf number	Leaf size cm2
		*	**	*	ns	ns
	Control	599 a	0.226 b	0.353 a	9.3	64.8
	$2.2X10^{-8}M$	641 a	0.242 b	0.373 a	10.0	65.8
	$2.2X10^{-7}M$	589 ab	0.217 b	0.357 a	9.1	64.6
	$2.2X10^{-6}M$	464 b	0.174 a	0.317 b	8.6	53.6
	se	44	0.005	0.009	0.6	4.3
		**	**	ns	ns	ns
	Control	1410 c	0.230 b	0.360	13.3	109.1 b
	$2.2X10^{-8}M$	1487 c	0.220 b	0.340	13.0	113.1 b
	$2.2X10^{-7}M$	1147 b	0.223 b	0.368	11.5	98.4 b
	$2.2X10^{-6}M$	882 a	0.193 a	0.342	11.0	80.3 a
	se	87	0.006	0.013	0.5	5.8
		*	ns	ns	ns	ns
	Control	2634 b	0.225	0.373	27.6	96.4
	$2.2X10^{-8}M$	2929 b	0.234	0.378	37.5	82.9
	$2.2X10^{-7}M$	2386 b	0.241	0.395	30.5	87.3
	$2.2X10^{-6}M$	1594 a	0.216	0.372	25.9	71.4
	se	211	0.008	0.013	4.7	6.5
		**	**	ns	ns	*
	Control	3566 b	0.258 b	0.437	32.9	115.8 b
	$2.2X10^{-8}M$	4782 c	0.268 b	0.442	41.0	119.0 b
	$2.2X10^{-7}M$	3396 ab	0.250 b	0.426	30.4	113.2 b
	$2.2X10^{-6}M$	2371 a	0.228 a	0.406	30.4	80.5 a
	se	397	0.004	0.014	4.5	6.8
		*	*	ns	*	**
led	Control	2052 b	0.235 b	0.379	20.7 a	96.5 b
	$2.2X10^{-8}M$	2460 c	0.241 b	0.382	25.4 b	95.2 b
	$2.2X10^{-7}M$	1880 b	0.233 b	0.386	20.4 a	90.9 b
	$2.2X10^{-6}M$	1328 a	0.203 a	0.360	19.0 a	71.4 a
	se	114	0.004	0.006	1.6	3.0

ıch mean figure from 8 replications with $df_{(error)}$ = 27 at harvests, and pooled mean from 32 replications with $df_{(error)}$ = 108.
ɜan separation within column by Lsd ($p \leq 0.05$).

Figure 4.1. Changes in leaf attributes of tomato seedlings when supplied via the roots with 6-N-benzylaminopurine at varying concentrations; (a) leaf area, (b) leaf area ratio and (c) specific leaf area. I = standard error of means.


a
5400
4050
2700
1350
0
0
1
2
3
4
b
0.30
0.26
0.22
0.18
0.14
Leaf area ratio (cm2.mg-1)
0
1
2
3
4
c
0.45
0.40
0.35
0.30
0.25
Specific leaf area (cm2.mg-1)
0
1
2
3
4
Harvest number
Treatment
0.0 M
2.2 X 10-8 M
2.2 X 10-7 M
2.2 X 10-6 M

reverse effect which was significant at the high concentration (Fig. 4.1 b). Despite LAR falling during the period between harvest one to three, LAR of the control and the low BA concentration remained higher than other treatments due to their larger plant size rather than area of individual leaves. These results add weight to the conclusion that the highest BA concentration gave 'non-physiological effects'.

Specific Leaf Area (SLA)

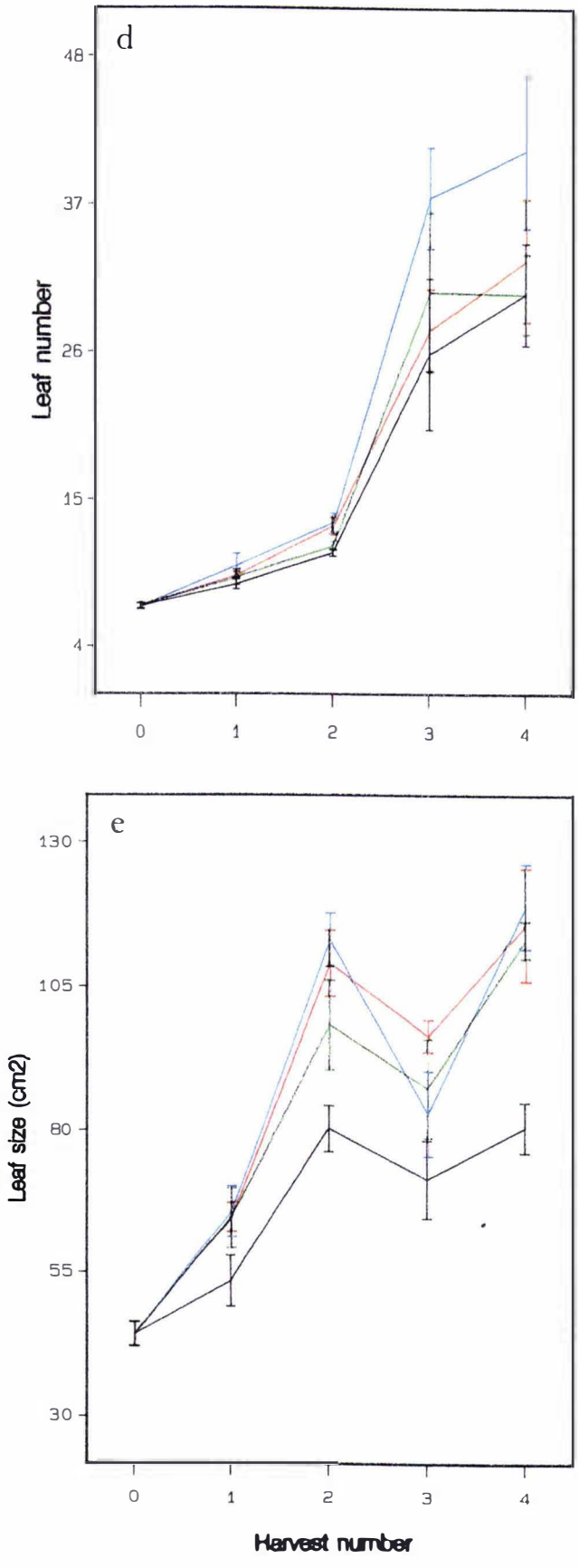
Although the high BA concentration significantly inhibited SLA at the first harvest, this effect did not persist (Table 4.1). At the second harvest, the SLA of the low concentration treatment decreased considerably (Fig. 4.1 c). This occurred against increasing SLA for all other treatments, and despite the fact that the dry weight and leaf area of the low BA treatment still exceeded those of the remaining treatments. This SLA decrease suggests that there was a lower rate of expansion in relation to dry matter accumulation at the time between the first two harvests than during other experimental periods. A comparison between the mean SLA(s) of the first and second harvests was made using t-test, the decrease, however, was not significant.

This result together with the effect on leaf area indicates that leaf expansion during the first week is an important factor causing superior plant size in the low BA treatment.

Leaf Number

Leaf number was significantly increased by low concentration of BA (Table 4.1). Leaf numbers, determined by leaves on the main stem, were not different at the two early harvests (Fig. 4.1 d). A burst of leaves produced on the side branches, commencing in the week between the second and the third harvests, was responsible for the increase in leaf number and consequently leaf area during that period. The larger production of leaves on side branches due to low BA concentration, caused the curve for this treatment to diverge rapidly from the other three treatments at the third harvest. By the time of the final harvest there were 41.0 $\pm$ 4.5 leaves on the low BA concentration compared with 30.4 to 32.9 ($\pm$ 4.5)

Figure 4.1.(cont.) Changes in leaf attributes of tomato seedlinc when supplied via the roots with 6-N-benzylaminopurine at varyir concentrations; (d) leaf number and (e) leaf size. I = standar error of means.


d
48
37
26
15
4
Leaf number
0
1
2
3
4
e
130
105
80
55
30
Leaf size (cm2)
0
1
2
3
4
Harvest number
Treatment
0.0 M
2.2 X 10-8 M
2.2 X 10-7 M
2.2 X 10-6 M

leaves on plants from the remaining treatments including the control. On average, the increase in leaf number due to the low BA treatment was five leaves, which was 23%, more than the control. The leaf area increased at the highest rate between harvests two and four (Fig.4.1 a), because there was a greater number of leaves on plants in all treatments (Table 4.1 d) after the second harvest. The increase in leaf number in the low BA treatment accounted for the substantial increase in leaf area over other treatments.

Leaf Size

The size of leaves increased progressively with time (Fig. 4.1 e), only reducing when there was a flush of new leaves at the third harvest. This apparent decrease in leaf size was greatest on the low BA treatment, reflecting the greatest increase in leaf number on that treatment. This temporary reduction was caused by the production of new leaves on side shoots. The data serve to verify the earlier conclusions (in leaf area section) with respect to this event. Average leaf size, however, was reduced by the high concentration of BA. On the other hand, this attribute was not affected by the other two BA concentrations at any time. The average leaf size of plants treated with the highest concentration of BA was 26% smaller than control. Since leaf size was not affected by the low BA treatment, while leaf number accounted for the entire difference in leaf area, it can be concluded that the effect of this treatment was on the rate of leaf initiation on the main stem and lateral shoots.

4.3.1.2. Stem Attributes

Individual Internode Length

Although all internodes were measured at all harvests, variation in the number of internodes present at each harvest prevented all internodes being used in statistical analyses. Consequently, only internodes up to the ninth were used in single and pooled analyses of internode length. Internodes one to three were not affected by the treatments because these internodes had completed growth before the first harvest (Table 4.2). Elongation of the upper internodes was rapid,

TABLE 4.2. Changes in internode length with time as affected by root application of 6-N-benzylaminopurine

Harvest no.	BA treatment	*1 Int#1 cm	Int#2 cm	Int#3 cm	Int#4 cm	Int#5 cm	Int#6 cm	Int#7 cm	Int#8 cm	Int#9 cm	*2 Total number
		ns	ns	ns	ns	ns	**	**	ns	ns	ns
1	Control	1.82	1.67	2.90	3.11	4.27	4.22 b	3.10 b	2.15	1.37	9.75
	$2.2X10^{-8}$ M	2.22	1.74	3.35	3.62	4.95	4.49 b	3.84 b	2.34	1.37	9.12
	$2.2X10^{-7}$ M	1.81	2.17	3.07	3.31	4.17	4.06 b	3.14 b	1.85	1.21	9.37
	$2.2X10^{-6}$ M	2.10	2.42	3.17	2.92	2.91	2.70 a	1.91 a	1.35	0.75	9.25
	se	0.07	0.13	0.11	0.12	0.11	0.12	0.14	0.12	0.12	0.14
		ns	ns	ns	ns	ns	ns	ns	*	ns	ns
2	Control	1.67	1.75	2.46	2.77	3.95	5.34	5.42	5.40 b	6.04	12.12
	$2.2X10^{-8}$ M	1.59	1.85	2.44	2.84	3.94	4.81	4.55	5.40 b	4.76	12.87
	$2.2X10^{-7}$ M	1.71	1.72	3.19	2.97	4.72	6.11	5.82	6.05 b	4.96	11.25
	$2.2X10^{-6}$ M	1.84	2.00	3.04	2.79	3.40	3.75	3.99	3.69 a	3.37	10.87
	se	0.08	0.09	0.12	0.15	0.19	0.19	0.17	0.23	0.23	0.24
		ns	ns	ns	ns	ns	**	ns	ns	ns	ns
3	Control	2.01	2.24	2.86	3.66	5.67	6.59 b	6.70	8.14	8.29	13.29
	$2.2X10^{-8}$ M	2.09	2.14	3.06	3.32	4.54	5.39 b	5.69	6.22	7.42	14.62
	$2.2X10^{-7}$ M	2.01	2.11	3.10	3.62	4.77	5.51 b	6.36	7.02	7.27	13.62
	$2.2X10^{-6}$ M	1.65	1.92	3.00	2.72	3.41	4.09 a	4.50	5.35	6.34	13.25
	se	0.09	0.09	0.12	0.13	0.16	0.18	0.21	0.23	0.22	0.17

(continued)

TABLE 4.2 (continued)

Harvest no.	BA treatment	Int#1 *1 cm	Int#2 cm	Int#3 cm	Int#4 cm	Int#5 cm	Int#6 cm	Int#7 cm	Int#8 cm	Int#9 cm	Total*2 number
		ns	ns	ns	ns	**	**	**	ns	ns	ns
4	Control	1.89	2.69	3.00	3.80	5.11 b	5.74 b	6.72 b	7.60	9.09	14.75
	$2.2X10^{-8}$ M	2.01	2.35	2.85	3.41	5.29 b	6.55 b	6.62 b	7.09	8.40	15.37
	$2.2X10^{-7}$ M	1.77	2.45	2.71	3.49	5.66 b	6.46 b	6.86 b	8.26	8.84	14.75
	$2.2X10^{-6}$ M	2.14	1.90	2.77	2.90	3.39 a	3.74 a	4.19 a	6.12	7.69	14.00
	se	0.08	0.12	0.10	0.11	0.17	0.17	0.28	0.28	0.31	0.19
		ns	ns	ns	**	**	**	**	**	**	ns
Pooled	Control	1.85	2.08	2.80	3.33 b	4.72 b	5.44 b	5.45 b	5.75 b	6.13 b	12.45
	$2.2X10^{-8}$ M	1.98	2.02	2.92	3.30 b	4.68 b	5.31 b	5.17 b	5.26 b	5.49 b	13.00
	$2.2X10^{-7}$ M	1.83	2.12	3.02	3.35 b	4.83 b	5.54 b	5.55 b	5.80 b	5.57 b	12.25
	$2.2X10^{-6}$ M	1.93	2.06	3.00	2.83 a	3.28 a	3.57 a	3.65 a	4.13 a	4.54 a	11.84
	se	0.08	0.11	0.12	0.13	0.16	0.17	0.20	0.22	0.05	0.19

- Each mean figure from 8 replications with $df_{(error)} = 24$ at harvests, pooled mean from 32 replications with $df_{(error)} = 108$.
- Mean separation within column by Lsd ($p \leq 0.05$).
- *1 = Internode order; 1th to 9th from the shoot-root juncture upwards.
- *2 = Total Internode Number

especially during the period between the first and the second harvests. It is of interest, that at any time other than the first harvest, each internode was longer than the one beneath. Benzylaminopurine at the high concentration shortened internode length by 30% compared with the control, but there was no effect at other concentrations.

Total Internode Number

Table 4.2 shows there was no significant difference in total number of internodes at any single harvest. The increase in number was relatively uniform over all treatments. This result, however, refers only to internodes on the main axis of each plant. There were clearly additional internodes on the laterals of plants treated with the low BA concentration (although data are not shown). Increases in both total leaf number, and total lateral length demonstrated this. As discussed earlier, the number of leaves on laterals was markedly increased by this treatment, if these leaves had been included the difference between the control and the low BA treatment would have been more marked.

Main Shoot Length

Main shoot length increased linearly with plant age during the course of the experiment, although, apparently, at different rates for different treatments (see later discussion). Table 4.3 indicates that the high concentration of BA reduced main shoot length severely while the lower concentrations had no significant effect on this attribute. The plants were relatively uniform with respect to main shoot length as reflected in the small standard error of the means. The reduction in main shoot length by the high BA treatment was cumulative and differed significantly from the other three treatments throughout, resulting in plants that were consistently one third shorter than the control.

Total Lateral Length

Measurement of the branching system was conducted from the second harvest onwards. Data of the first measurement showed a most marked difference

TABLE 4.3. *Changes in stem attributes with time as affected by root application of 6-N-benzylaminopurine*

Harvest no.	BA treatment	Main Shoot length cm	Total Lateral length cm	Total shoot length cm	Lateral number
		*			
1	Control	25.0 b	-	-	-
	$2.2X10^{-8}M$	28.5 b	-	-	-
	$2.2X10^{-7}M$	26.0 b	-	-	-
	$2.2X10^{-6}M$	20.5 a	-	-	-
	se	1.3	-	-	-
		**	*	**	*
2	Control	45.0 b	20.1 ab	65.1 b	4.00 bc
	$2.2X10^{-8}M$	43.3 b	23.9 b	67.2 b	4.25 c
	$2.2X10^{-7}M$	42.3 b	3.1 a	45.4 a	1.37 a
	$2.2X10^{-6}M$	31.2 a	4.0 a	35.2 a	2.00 ab
	se	1.8	6.0	6.3	0.75
		**	ns	*	ns
3	Control	67.5 b	46.2	113.7 b	5.25
	$2.2X10^{-8}M$	60.9 b	69.7	130.7 b	6.62
	$2.2X10^{-7}M$	62.3 b	39.3	101.6 ab	4.88
	$2.2X10^{-6}M$	46.6 a	24.5	71.1 a	4.38
	se	2.6	12.4	12.4	1.09
		**	ns	*	ns
4	Control	82.6 b	68.5	151.1 ab	5.63
	$2.2X10^{-8}M$	90.2 b	97.1	187.3 b	8.25
	$2.2X10^{-7}M$	80.2 b	54.1	134.3 a	5.25
	$2.2X10^{-6}M$	62.8 a	44.0	106.4 a	6.25
	se	3.1	20.7	19.2	1.00
		**	ns	**	ns
Pooled	Control	55.0 b	44.9	109.9 b	4.96
	$2.2X10^{-8}M$	55.7 b	63.6	128.4 c	6.37
	$2.2X10^{-7}M$	52.7 b	32.2	93.8 b	3.83
	$2.2X10^{-6}M$	40.3 a	24.2	71.0 a	4.21
	se	1.2	8.1	7.8	0.55
	$df_{(error)}$	108	80	80	80

Each mean figure from 8 replications with $df_{(error)} = 24$ at harvests, and pooled mean from 24 or 32 replications with $df_{(error)} = 80$ or 108 as indicated.
Mean separation within column by Lsd ($p \leq 0.05$).

between the two groups; *viz.* The control and the low BA treatment versus the other treatments (Table 4.3). As the experiment progressed, this difference was maintained, but did not increase. Although not significantly different at any other harvest or in the pooled means, due to variability of branching (length and number) within groups of plants, it is notable that plants at the low BA concentration appeared to have more and longer laterals than the remaining treatments throughout the experiment.

Total Shoot Length

The pattern of changes in total shoot length due to different BA concentrations over time, parallels that of leaf area (Fig. 4.1 a). The divergence of the low BA curve began at the second harvest. Considering total shoot length, leaf area and leaf number, all three attributes appear to confirm that the branching effect of low BA application is one of the initial effects of BA, contributing to the increase of leaf area and plant size.

When the data of main shoot and lateral length was aggregated the mean difference in response to BA was clearer than when each set of the data was considered alone. The pooled means of total shoot length (Table 4.3) show BA at low concentration promoted overall growth while there was no effect of the mid concentration and an opposite effect by the high concentration. This conclusion is supported by a similar trend at all harvests after the second harvest. The mean shoot length of the promoted treatment was almost double that of the inhibited treatment.

Lateral Number

Benzylaminopurine had no significant effect on the final number of laterals produced by the tomato plants in this experiment. Nevertheless, BA at low concentration appeared to increase the rate of production of laterals while at higher concentrations branching rate was inhibited. Given the overall growth promoting effect of BA, it seems reasonable to conclude that the number of laterals made a partial contribution to the total lateral length, particularly in the low BA treatment.

4.3.1.3. Flower Production

Onset of flowering was uneven, caused by large variation in flower number. Consequently no significant difference between flower numbers and dry weights among BA treatments was found (Table 4.4). In fact, on some plants fruit set had occurred whereas only a few flowers emerged on treatment counterparts. Precocity was assessed by determining the first node upon which the first flower truss formed. There was no effect of treatment on the location of the first flower truss. In general, flowering occurred at the 9^{th} or 10^{th} internodes.

4.3.1.4. Root Attributes

Root Length

Benzylaminopurine at low concentration had no effect on root length but both higher concentrations appeared to decrease root extension. In all treatments, root length increased with time, except for the control at the final harvest (Fig. 4.2 a). At the second and the third harvests, root length appeared to be reduced by BA treatments, amongst which the low concentration was least effective (Table 4.5). By the fourth harvest, however, this difference had disappeared and the effect of BA was reversed. Despite the large number of replications used in the experiment for a four week period, no significant effect of BA on root length was demonstrated. Root morphology, however, was obviously altered on the plants treated with the highest BA concentration (Plate 4.1), being more compact and shortened (see also results of root number per unit root length and root dry weight per unit root length).

Root Number

Benzylaminopurine had no significant effect on root number. The general pattern of temporal changes due to BA, however, was similar to root length (Fig. 4.2 b). At the second and third harvests, treatments appeared to separate into two different groups; the low BA treatment and control in one group and the other

LE 4.4. *Effects of 6-N-benzylaminopurine on inflorescences and development of flower truss of tomato seedlings*

est	BA treatment	Number of inflorescences	Dry Weight g	Position*1
		ns		
	Control	1.13	-	-
	$2.2X10^{-8}M$	1.25	-	-
	$2.2X10^{-7}M$	0.38	-	-
	$2.2X10^{-6}M$	0.50	-	-
	se	0.04	-	-
		ns		ns
	Control	6.00	-	9.50
	$2.2X10^{-8}M$	4.38	-	9.83
	$2.2X10^{-7}M$	5.00	-	9.71
	$2.2X10^{-6}M$	3.00	-	9.14
	se	0.95	-	0.25
		ns	ns	ns
	Control	4.38	0.019	9.25
	$2.2X10^{-8}M$	7.25	0.066	9.38
	$2.2X10^{-7}M$	5.13	0.029	8.75
	$2.2X10^{-6}M$	3.75	0.022	9.75
	se	1.39	0.017	0.30
		ns	-	ns
led	Control	3.83	-	9.37
	$2.2X10^{-8}M$	4.29	-	9.65
	$2.2X10^{-7}M$	3.50	-	9.25
	$2.2X10^{-6}M$	2.42	-	9.43
	se	0.56	-	0.17
	$df_{(error)}$	80	-	48

ach mean figure from 8 replications with $df_{(error)} = 24$ at harvests, and
ooled mean from 16 or 24 replications with $df_{(error)} = 48$ or 80 as indicated.
lean separation within column by Lsd ($p \leq 0.05$).
1 = Internode where first truss appeared.

LE 4.5. *Changes in root attributes with time as affected by root application of 6-N-benzylaminopurine*

Harvest no.	BA treatment	Root length m	Root number ($\times 10^{-3}$)	Root number per unit length m^{-1}	Root d.w.t per unit length $mg.m^{-1}$
		ns	ns	**	**
1	Control	66.3	4.73	69.9 b	7.39 b
	$2.2X10^{-8}M$	68.7	4.40	63.6 ab	6.07 a
	$2.2X10^{-7}M$	79.2	4.50	55.8 a	7.42 b
	$2.2X10^{-6}M$	60.7	3.99	64.0 b	11.85 c
	se	0.8	0.64	2.8	0.36
		ns	ns	*	**
2	Control	156.9	9.28	60.5 c	5.89 a
	$2.2X10^{-8}M$	150.0	8.83	58.6 bc	6.28 a
	$2.2X10^{-7}M$	114.9	6.22	52.7 ab	8.02 b
	$2.2X10^{-6}M$	131.9	6.99	51.8 a	9.21 c
	se	11.8	0.77	2.1	0.39
		ns	ns	*	**
3	Control	285.4	15.28	52.7 a	5.25 a
	$2.2X10^{-8}M$	281.8	14.99	52.6 a	5.45 b
	$2.2X10^{-7}M$	231.0	11.79	50.4 a	6.51 bc
	$2.2X10^{-6}M$	210.5	12.75	59.7 b	7.82 c
	se	27.4	1.74	2.2	0.41
		ns	ns	ns	*
4	Control	263.8	12.52	51.5	6.33 a
	$2.2X10^{-8}M$	325.2	18.76	56.6	6.20 a
	$2.2X10^{-7}M$	287.4	15.29	53.2	6.86 ab
	$2.2X10^{-6}M$	293.5	17.57	58.4	7.51 b
	se	37.1	2.93	2.2	0.32
		ns	ns	ns	**
Pooled	Control	193.1	10.49	58.9	6.21 a
	$2.2X10^{-8}M$	206.4	11.71	57.9	6.00 a
	$2.2X10^{-7}M$	178.1	9.47	53.0	7.21 b
	$2.2X10^{-6}M$	174.1	10.33	58.5	9.10 c
	se	12.2	0.86	1.1	0.20

ach mean figure from 8 replications with $df_{(error)} = 24$ and pooled mean from
2 replications with $df_{(error)} = 108$.
ean separation within column by Lsd ($p \leq 0.05$).

Figure 4.2. Changes in root attributes of tomato seedlings when supplied via the roots with 6-N-benzylaminopurine at varying concentrations; (a) root length, (b) root number, (c) root number per unit length and (d) root dry weight per unit length. I = standard error of means.

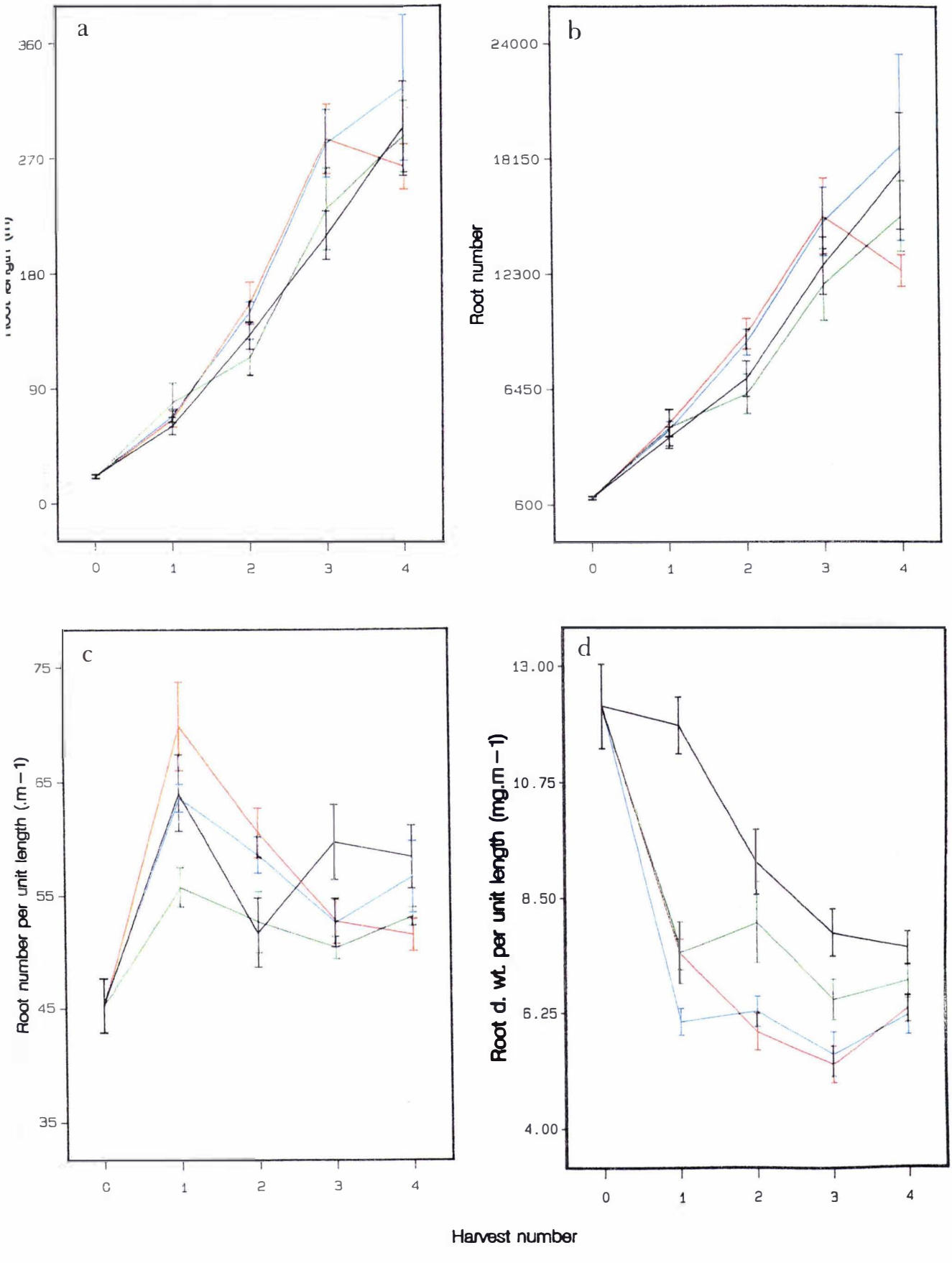

a
b
c
d
Root number
Root number per unit length (.m−1)
Root d. wt. per unit length (mg.m−1)
Harvest number
Treatment
0.0 M
2.2 X 10-8 M
2.2 X 10-7 M
2.2 X 10-6 M

Plate 4.1. Abnormal morphology of tomato root systems when roots were exposed to continual application of BA at 2.2 x 10-6 M for 8 weeks (right), compared to the control (left). No apparent abnormality in plants treated at lower concentrations.

two treatments in the other group. This may have been a segregation between 'normal' and 'phytotoxic' or 'supra-optimal' or 'non-physiological' levels. At the final harvest, however, the number of roots in the control treatment dropped to be lower than that of highest BA concentration. Variability was quite low as the general means ranged between 9473.1 (± 856.0) to 11704.8 (± 856.0). This range of about 1,000 roots, is quite small in relation to the means.

The separate measurements of root length and root number provided no information in relation to the abnormality in root morphology of the highest concentration of BA. The data derived from both attributes, may give some indication of this effect.

Root Number per Unit Root Length

The ratio of root number per unit length of root was used to measure the intensity of lateral roots produced. There was no significant difference between the pooled means of this attribute because of the irregular pattern of individual means, over the course of the experiment (Table 4.5). Nonetheless, there was a significantly lower intensity of root laterals in the plants exposed to high concentration of BA during the early harvests. A similar trend also occurred in the other BA treatments (Fig. 4.2 c). These results suggest that with the additional cytokinin supplies the production of root number per unit root length, and therefore, the synthesis the endogenous cytokinins may have been lower than in normal plants.

The disappearance of the statistical difference in this and other data suggests that the effects of BA may be transient only, disappearing in the later weeks of exposure to BA.

Root Dry Weight per Unit Root Length

The dry weight per unit length of roots measures the root thickness provided that there is no difference in the specific density of root tissues. Effects of the low BA concentration upon this attribute were significant, but did not

persist. This treatment appeared to be similar to the control from the second harvest onwards (Fig 4.2 d). At the first harvest, however, root dry weight per unit length was reduced significantly compared to the control and other cytokinin treatments. In later harvests, this treatment was very similar to the control while it was significantly greater in the higher BA treatments. Since in the pooled mean, the control gave an intermediate response between stimulation and inhibition of root dry weight per unit length (Table 4.5), this result is further evidence that the exogenous BA became part of, and supplemented the endogenous pool of cytokinins. Consequently, these data add further credence to the hypothesis that synthetic cytokinins did, at these concentrations, and by this mechanism, form part of the endogenous pool and elicit responses that are typical physiological responses to endogenously synthesized cytokinins.

Benzylaminopurine at the higher concentrations increased the thickness of lateral roots in proportion to the concentration of BA applied.

4.3.2. Changes in Absolute Growth

4.3.2.1. Leaf Dry Weight

Benzylaminopurine at the low concentration significantly increased leaf growth whereas at high concentration the effect was reversed (Table 4.6). The mid concentration, although not significantly different from the control, appeared to be slightly inhibitory. Figure 4.3 (a) shows that there was a consistent trend towards reduced leaf growth at the mid concentration, except during the final week. Reduced leaf growth by the control prior to the final harvest, in relation to the BA treatments, offset the difference between the two treatments, without affecting the other treatments. Thus, with this plant attribute the control treatment also gave an intermediate response between the low and higher BA concentrations.

4.3.2.2. Stem Dry Weight

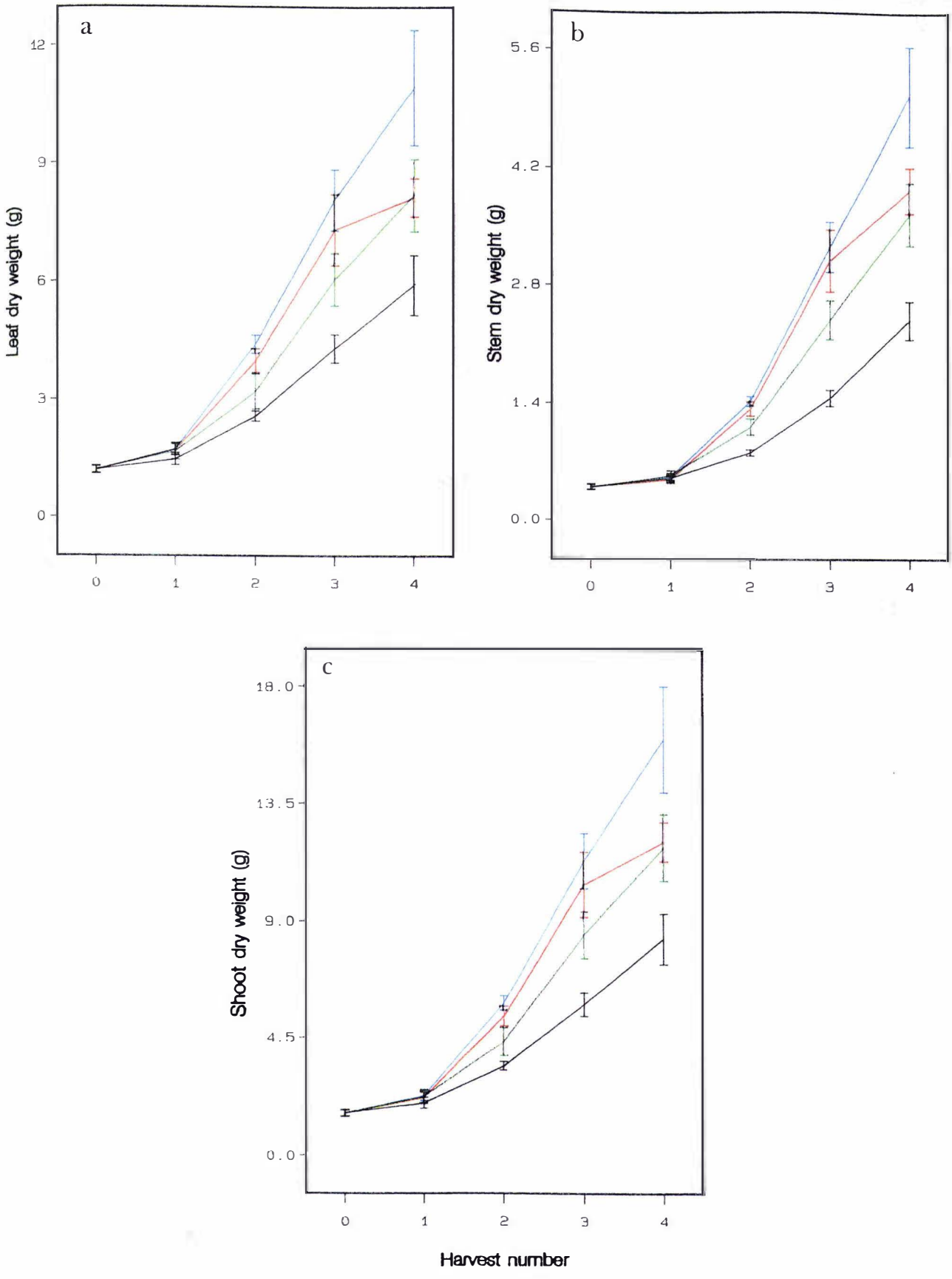
The effect of BA on stem growth appears to be similar to the effect on leaf growth, although less pronounced (Table 4.6; Fig. 4.3 b). Despite the significant

TABLE 4.6. *Changes in dry weight of plant organs and whole plant with time as affected by root application of 6-N-benzylaminopurine*

Time	BA treatment	L_w*1 g	S_w*2 g	T_w*3 g	R_w*4 g	W*5 g
		ns	ns	ns	*	ns
1	Control	1.72	0.48	2.18	0.48 a	2.66
	2.2×10^{-8}M	1.74	0.52	2.25	0.42 a	2.67
	2.2×10^{-7}M	2.68	0.53	2.20	0.54 a	2.74
	2.2×10^{-6}M	1.48	0.50	1.98	0.71 b	2.69
	se	0.16	0.05	0.21	0.05	0.26
		**	**	**	*	**
2	Control	3.98 bc	1.34 b	5.33 bc	0.89 a	6.22 bc
	2.2×10^{-8}M	4.40 c	1.44 b	5.84 c	0.94 a	6.77 c
	2.2×10^{-7}M	3.20 ab	1.12 b	4.32 ab	0.89 a	5.22 ab
	2.2×10^{-6}M	2.58 a	0.81 a	3.40 a	1.17 b	4.57 a
	se	0.32	0.08	0.39	0.07	0.46
		*	**	**	ns	**
3	Control	7.31 bc	3.10 b	10.41 bc	1.48	11.89 b
	2.2×10^{-8}M	8.06 c	3.26 b	11.32 c	1.49	12.81 b
	2.2×10^{-7}M	6.06 ab	2.40 b	8.46 ab	1.43	9.90 ab
	2.2×10^{-6}M	4.30 a	1.48 a	5.78 a	1.63	7.41 a
	se	0.68	0.25	0.93	0.14	1.06
		*	**	**	ns	*
4	Control	8.12 ab	3.95 b	12.07 ab	1.65	13.72 ab
	2.2×10^{-8}M	10.93 b	5.06 b	15.99 b	1.96	17.95 b
	2.2×10^{-7}M	8.18 ab	3.66 b	11.84 a	1.97	13.81 ab
	2.2×10^{-6}M	5.93 a	2.39 a	8.32 a	2.17	10.49 a
	se	0.99	0.40	1.38	0.22	1.5
		*	ns	ns	**	ns
Pooled	Control	5.28 b	2.28	7.67	1.13 a	8.82
	2.2×10^{-8}M	6.28 c	2.57	8.85	1.20 a	10.05
	2.2×10^{-7}M	4.78 b	1.93	6.71	1.21 a	7.92
	2.2×10^{-6}M	3.57 a	1.30	4.87	1.42 b	6.39
	se	0.31	0.12	0.43	0.07	0.49

- Each mean figure from 8 replications with $df_{(error)} = 24$ at harvests, and pooled mean from 32 replications with $df_{(error)} = 108$.
- Mean separation within column by Lsd ($P \leq 0.05$).

Figure 4.3. Changes in dry weight of tomato seedling organs and whole plant when supplied via the roots with 6-N-benzylaminopurine at varying concentrations; (a) leaf d. wt., (b) stem d. wt. and (c) shoot d. wt. I = standard error of means.


a
Leaf dry weight (g)
12
9
6
3
0
0
1
2
3
4
b
Stem dry weight (g)
5.6
4.2
2.8
1.4
0.0
0
1
2
3
4
c
Shoot dry weight (g)
18.0
13.5
9.0
4.5
0.0
0
1
2
3
4
Harvest number
Treatment
0.0 M
2.2 X 10-8 M
2.2 X 10-7 M
2.2 X 10-6 M

difference at most individual harvests, there was no significant difference in general means in the pooled analysis, although it was almost so ($p < 0.075$). In contrast to leaf dry weight, however, stem dry weight was not significantly increased at the low BA concentration at any stage of the experiment. Similar factors may account for the growth pattern of the stem as for the leaves, since the changes with time are similar, particularly at the final harvest. The same general trend, as leaf weight, can also be seen in the pooled harvest analysis, with a promotory effect of BA at low concentration and an inhibitory effect at the mid and high concentrations.

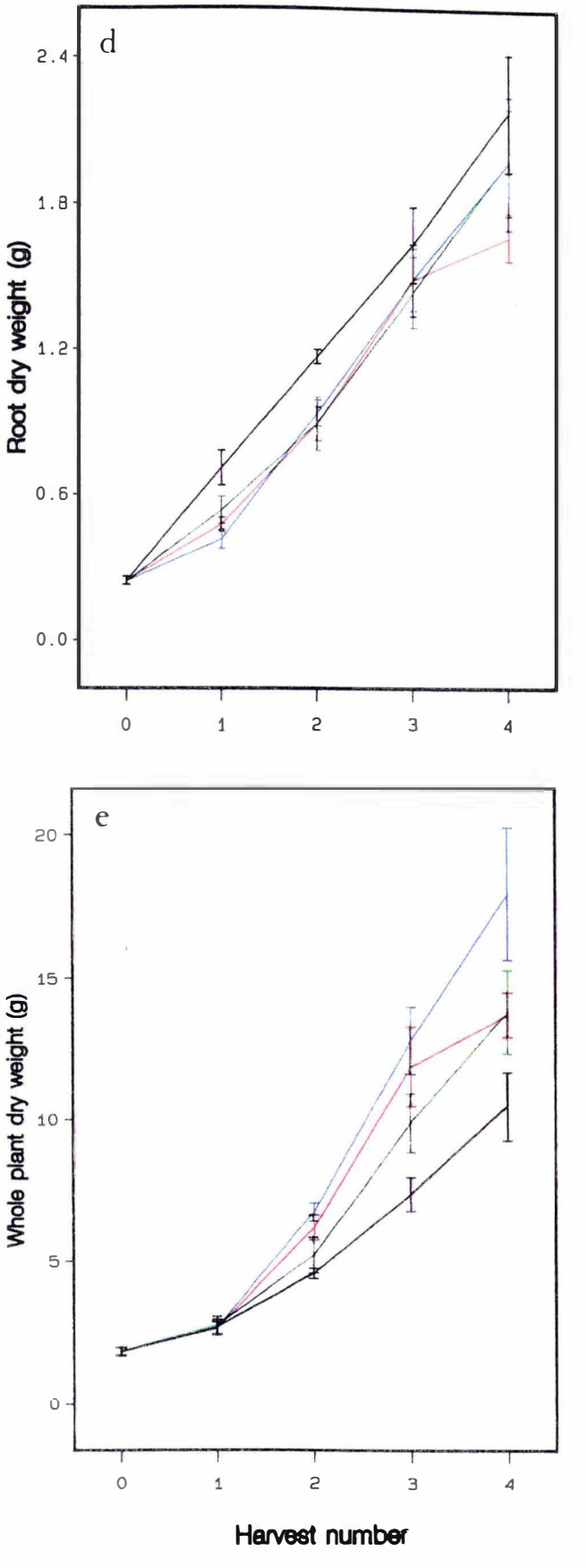
4.3.2.3. Shoot Dry Weight

Since the pattern of change in shoot dry weight with time is the sum of leaf and stem dry weight (Fig. 4.3 c), the same trends appear in shoot growth due to BA. The data (Table 4.6) show that the effects of BA treatments were greatest on the dry weight of leaves and consequently the effect on shoots statistically and qualitatively is intermediate between that on leaves and stem.

4.3.2.4. Root Dry Weight

During the first week root weight increased at quite a high rate in all treatments. Root dry weight had doubled at the second harvest, but later declined gradually with time (Table 4.6). This marked increase of root dry weight in the early harvests may be, partly, accounted for by compensatory growth which was a residual effect of transplanting into the aeroponic tanks, which initially caused root loss. Benzylaminopurine enhanced root dry weight markedly, but only at the highest concentration, while other treatments had no effect (Fig. 4.3 d). In fact, the increase in root dry weight resulting from this treatment was observed after the first week of BA application. Thereafter, there was no further stimulation of root dry weight by the high BA concentration but the difference established in week one was maintained. As noted with root number and root length, there was a decline in the rate of increase in root dry weight by the control at the final harvest.

Figure 4.3.(cont.) Changes in dry weight of tomato seedling organs and whole plant when supplied via the roots with 6-N-benzylaminopurine at varying concentrations; (d) root d. wt. and (e) whole plant d. wt. I = standard error of means.


d
Root dry weight (g)
2.4
1.8
1.2
0.6
0.0
0
1
2
3
4
e
Whole plant dry weight (g)
20
15
10
5
0
0
1
2
3
4
Harvest number
Treatment
0.0 M
2.2 X 10-8 M
2.2 X 10-7 M
2.2 X 10-6 M

4.3.2.5. Whole Plant Dry Weight

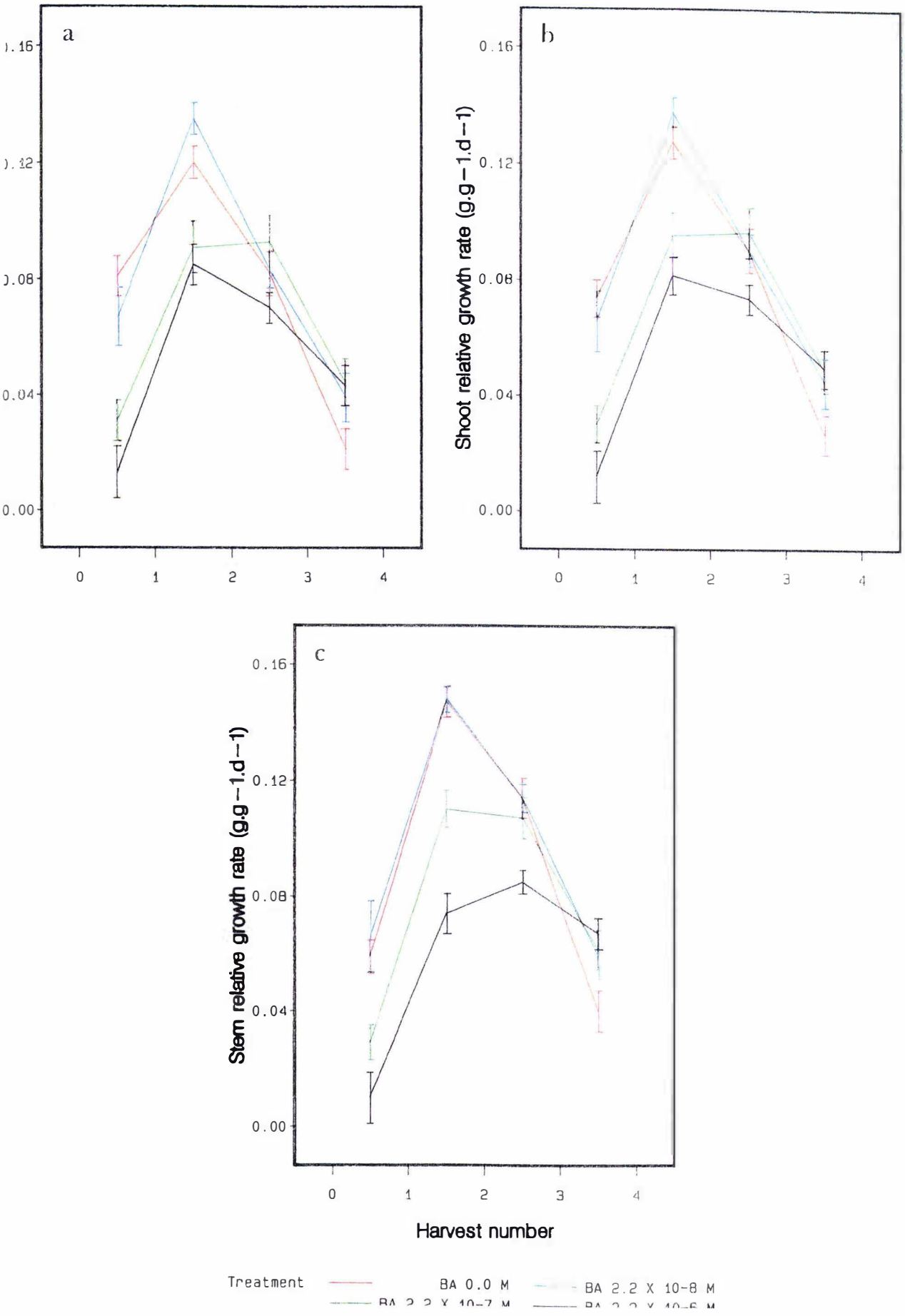
There was a significant difference between the low and high BA treatments only at certain harvests (Table 4.6). The apparent difference between the control and other treatment means became progressively larger with time. Although at the final harvest, growth was still continuing, the growth rate of the control declined before the final harvest partially offsetting the early difference between the control and the mid BA treatment (Fig. 4.3 e). The mean of low BA concentration was higher than control throughout the experiment, although not significantly, while the means of the two higher BA treatments produced consistently less dry matter than the control.

Whilst these results could only show statistical significance at the 0.06% level, taken overall the data strongly indicate that the low level of BA increased the total plant dry weight of plants growing in this system. First, the total plant dry weight of the low BA treatment was higher than the control or any other treatments at all but the initial harvest, including the pooled mean. Secondly, on each of these occasions the significance level was greater than 0.007. Thirdly, the dry weight of the leaves from the low BA treatment was significantly greater in the pooled mean and exceeded 0.02 significance level in all, but the first harvest. Considering that the weight of stems of this treatment was actually, if not significantly greater than all other treatments, and the weight of roots was greater than the control in all but the first harvest, it follows that overall, growth was very probably stimulated. Subsequent studies of the effect of BA at the low concentrations support this important conclusion (Andrews, Chalmers and Thuantavee unpublished data).

4.3.3. Changes in Relative Growth Rates

The pattern of changes in leaf relative growth rate (RGR_L) (Fig. 4.4 a) and shoot relative growth rate (RGR_T) (Fig. 4.4 c) parallel those of whole plant relative growth rate (RGR_W), indicating the overriding importance of leaves in determining the growth rate of the shoot and plant as a whole. This is because leaves were the greatest proportion by weight of the whole plants. The pattern of

Figure 4.4. Changes in relative growth rate of tomato seedling organs and whole plant when supplied via the roots with 6-N-benzylaminopurine at varying concentrations; (a) RGR_L, (b) RGR_S and (c) RGR_T. I = standard error of means.


a
b
c
0.16
0.12
0.08
0.04
0.00
0
1
2
3
4
Shoot relative growth rate (g.g−1.d−1)
Stem relative growth rate (g.g−1.d−1)
Harvest number
Treatment
BA 0.0 M
BA 2.2 X 10-8 M

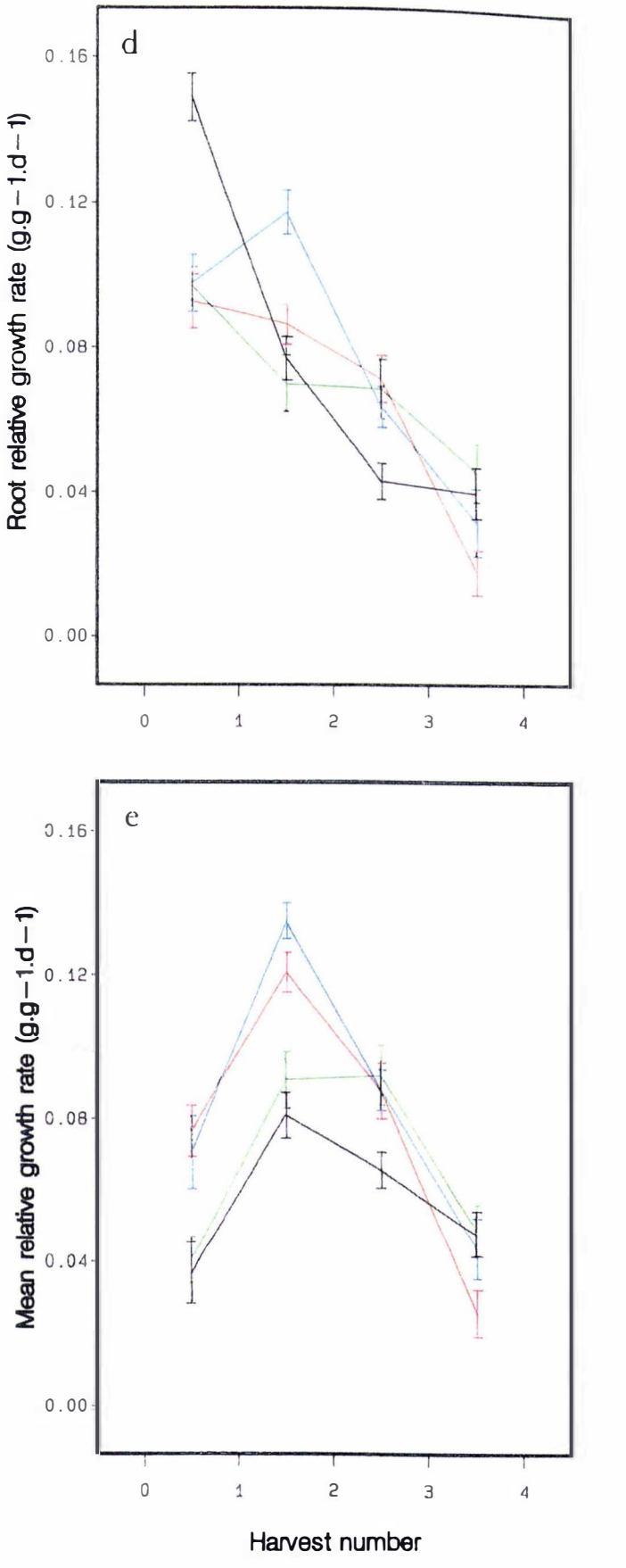
changes in relative growth rate of stem (RGR_S) Fig. 4.4 b) and root (RGR_R) (Fig. 4.4 d) differ to that of RGR_L. The RGR_S of the low BA and control were very similar throughout the experiment, except at the final harvest, suggesting that the low BA treatment was not affecting this attribute, at least, during the initial growth period. The difference between the mid and the high concentration was greatest at the second harvest and then reduced to be negligible at the final harvest. The RGR_R decreased progressively with time. At high BA concentration, RGR_R was increased significantly at the first harvest which resulted in the initial increment in root weights, but thereafter no significant effects upon this attribute persisted. The high rate of RGR_R during the first two weeks may have also been, partly, related to the residual effects of root weight loss due to transplanting into the tanks. It is of interest that in the low BA treatment, RGR_R appeared to increase during the week between the first and second harvest whereas it declined in other treatments.

During early weeks of the experiment, RGR_T, or rather RGR_L, continued to increase, while RGR_R steadily declined. The increase of leaf growth during the week between the first and second harvest may have caused the corresponding increased growth in roots at that period. In this sense, the initial effects of the low BA treatment on leaves led to the enhanced overall growth of plants.

In all treatments an increase in whole plant relative growth rate (RGR_W) occurred during the first half of the experiment, when there appeared to be two separate groups of treatments. One group consisted of the low BA and control treatments, and the other, the remainders. Thereafter, the RGR_W of the control and the low BA treatment declined sharply, while the RGR_W of the mid and the high BA treatments gradually declined. The RGR_W of the low BA treatment appeared to be higher than the control from the second harvest onwards. No significant effect of BA was revealed in the pooled means of RGR_W, because fluctuations over the course of the experiment cancelled the difference between treatments (Fig. 4.4 e). The response of control was also intermediate for this attribute.

The RGR of plant parts and the entire plant in response to cytokinin application was completely different to the response of RGR to GA. Although the

Figure 4.4.(cont.) Changes in relative growth rate of tomato seedling organs and whole plant when supplied via the roots with 6-N-benzylaminopurine at varying concentrations; (d) RGR_R and (e) RGR_W. I = standard error of means.


d
Root relative growth rate (g.g−1.d−1)
0.16
0.12
0.08
0.04
0.00
0
1
2
3
4
e
Mean relative growth rate (g.g−1.d−1)
0.16
0.12
0.08
0.04
0.00
0
1
2
3
4
Harvest number
Treatment
BA 0.0 M
BA 2.2 X 10-8 M
BA 2.2 X 10-7 M
BA 2.2 X 10-6 M

initial RGR measurement was approximately one week later in the GA experiment, the pattern of RGR change of the control treatment was similar to the cytokinin control. Following GA treatment, however, RGR(s) trended upwards while controls and cytokinin treatments trended downwards after an initial increase.

4.3.4. Changes in Allometric Relationships Between Shoot and Root System

For similar reasons as those discussed earlier (in Chapter 3), the regression of logarithmic values of dry weights of eight plants at each harvest did not yield a consistent regression coefficient or a strong coefficient of determination (R^2). They were, therefore, considered to be unsuitable for interpretation in the context of this experiment. In the sense that the RGRs of the paired organs fluctuated and may be alternately predominant as in many plants when growth is rapid (Mullin 1963; Drew and Ledig 1980; Drew 1982), the resultant k of such short intervals, especially when the plant is small, also fluctuates, but gives little or no information which is useful for the overall analysis of growth and development. When all data were included, the allometric relationship between shoot and roots (k_T) was very strong with coefficients of determination between 95 to 97% (Table 4.7). When stem dry weight is not included in the regression, the allometric relationship was even stronger, resulting in a coefficient of determination of between 96 to 98% for the allometric relationship between leaves and roots (k_L) (Fig. 4.5). The k_T (Fig. 4.7) and k_L, expressed as the slope of the regression coefficient, was unaffected by BA, although that of stem and roots, k_S (Fig. 4.6), appears to be reduced. All k values were greater than unity, which is in agreement with RGR results, in that root growth rate was generally lower than the growth rate of the shoot. In all instances, the variation between the intercepts of the regression lines is far much greater than any variation in the slopes (Table 4.7).

These results suggest one of two possible conclusions :

(a) Treatment with BA did not affect the ratio of the relative growth rates. That is, the effects of BA on shoot-root ratio were the result of moderation of the overall growth rate. Environmental and/or ontogenetic changes that result in a lower

E 4.7. *Changes in allometric relationships between dry weight of shoot and root organs as affected by root application of 6-N-benzylaminopurine*

BA treatment	ln a	*1 se(ln a)	k		se (k)	R^2 (%)
y = Leaf d.wt.						
			ns			
Control	0.032	0.317	1.211		0.046	95.88
$2.2X10^{-8}M$	0.624	0.224	1.141		0.032	97.65
$2.2X10^{-7}M$	0.053	0.308	1.181		0.044	95.98
$2.2X10^{-6}M$	-0.495	0.321	1.191		0.045	95.92
y = Stem d.wt.						
			*			
Control	-3.225	0.558	1.541	b	0.080	92.69
$2.2X10^{-8}M$	-1.735	0.473	1.339	a	0.068	92.76
$2.2X10^{-7}M$	-1.799	0.530	1.309	a	0.076	90.80
$2.2X10^{-6}M$	-2.105	0.522	1.270	a	0.073	91.03
y = Shoot d.wt.						
			ns			
Control	-0.284	0.380	1.303		0.055	95.12
$2.2X10^{-8}M$	0.577	0.282	1.194		0.041	96.63
$2.2X10^{-7}M$	0.136	0.354	1.216		0.051	95.02
$2.2X10^{-6}M$	-0.344	0.354	1.213		0.049	95.25

lues from slopes of linear regressions of ln y = ln a + k ln x, where y is either leaf d.wt., m d.wt. or shoot d.wt. and x is root d.wt. Each k estimated from 32 replications.
ıparisons of k values based on t-test ($p \leq 0.05$), $df_{(error)} = 60$.
Standard error.

Figure 4.5. Changes in allometric relationship between leaf and root dry weight (k_L) of tomato seedlings when supplied via the roots with 6-N-benzylaminopurine at varying concentrations.

Control: R^2 = 95.9%, y = 0.032 + 1.21 x,
BA 2.2 X10^{-8} M: R^2 = 97.7%, y = 0.624 + 1.14 x,
BA 2.2 X10^{-7} M: R^2 = 96.0%, y = 0.053 + 1.18 x,
BA 2.2 X10^{-6} M: R^2 = 95.9%, y =-0.495 + 1.19 x.

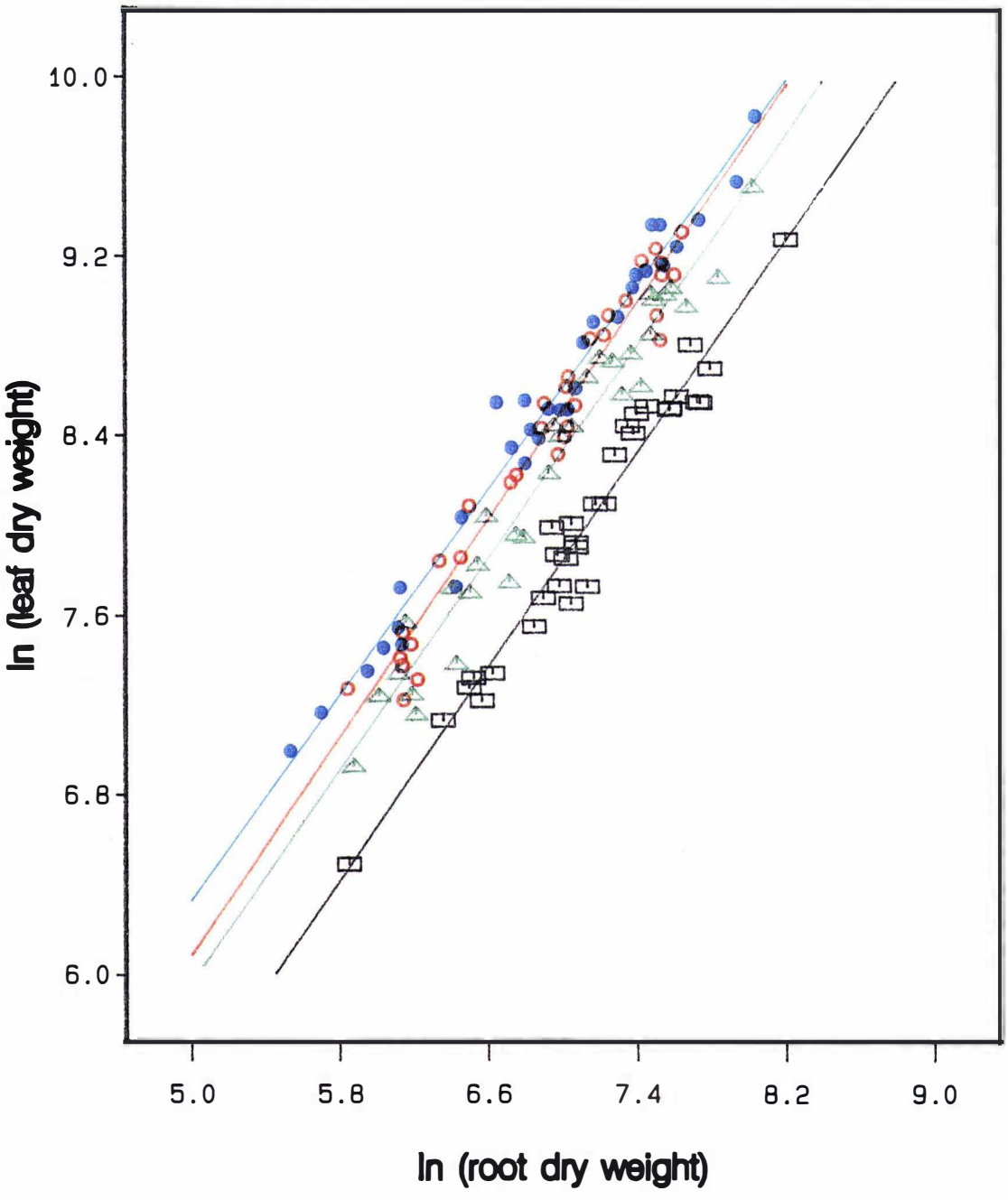

10.0
9.2
8.4
7.6
6.8
6.0
ln (leaf dry weight)
5.0
5.8
6.6
7.4
8.2
9.0
ln (root dry weight)
Treatment
0.0 M
2.2 X 10-8 M
2.2 X 10-7 M
2.2 X 10-6 M

Figure 4.6. Changes in allometric relationship (k_S) between ste and root dry weight (k_S) of tomato seedlings when supplied via th roots with 6-N-benzylaminopurine at varying concentrations.

Control: R^2 = 92.7%, y =-3.23 + 1.54 x,
BA 2.2 X10^{-8} M: R^2 = 97.8%, y =-1.74 + 1.34 x,
BA 2.2 X10^{-7} M: R^2 = 90.8%, y =-1.80 + 1.31 x,
BA 2.2 X10^{-6} M: R^2 = 91.0%, y =-2.11 + 1.27 x.

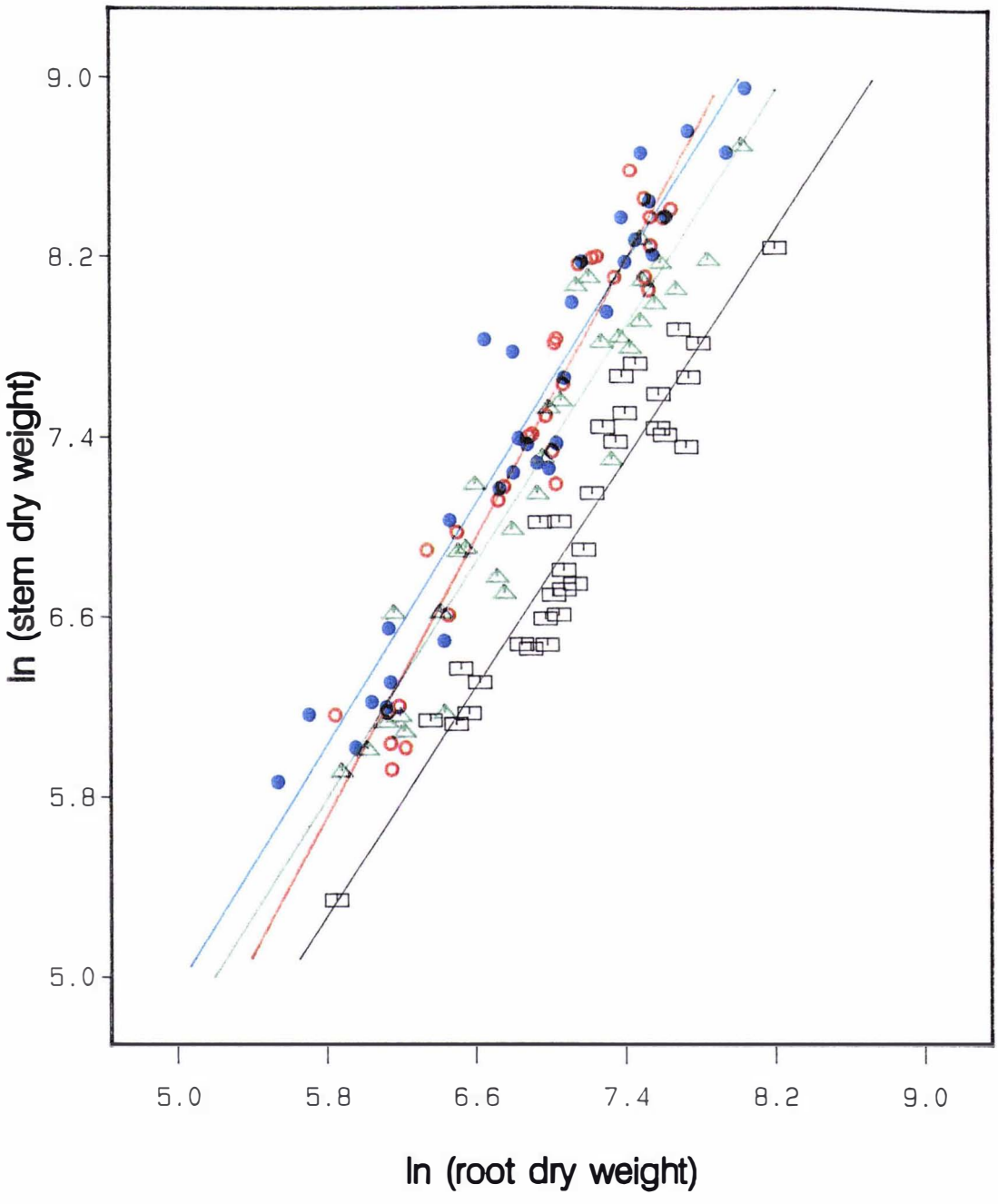
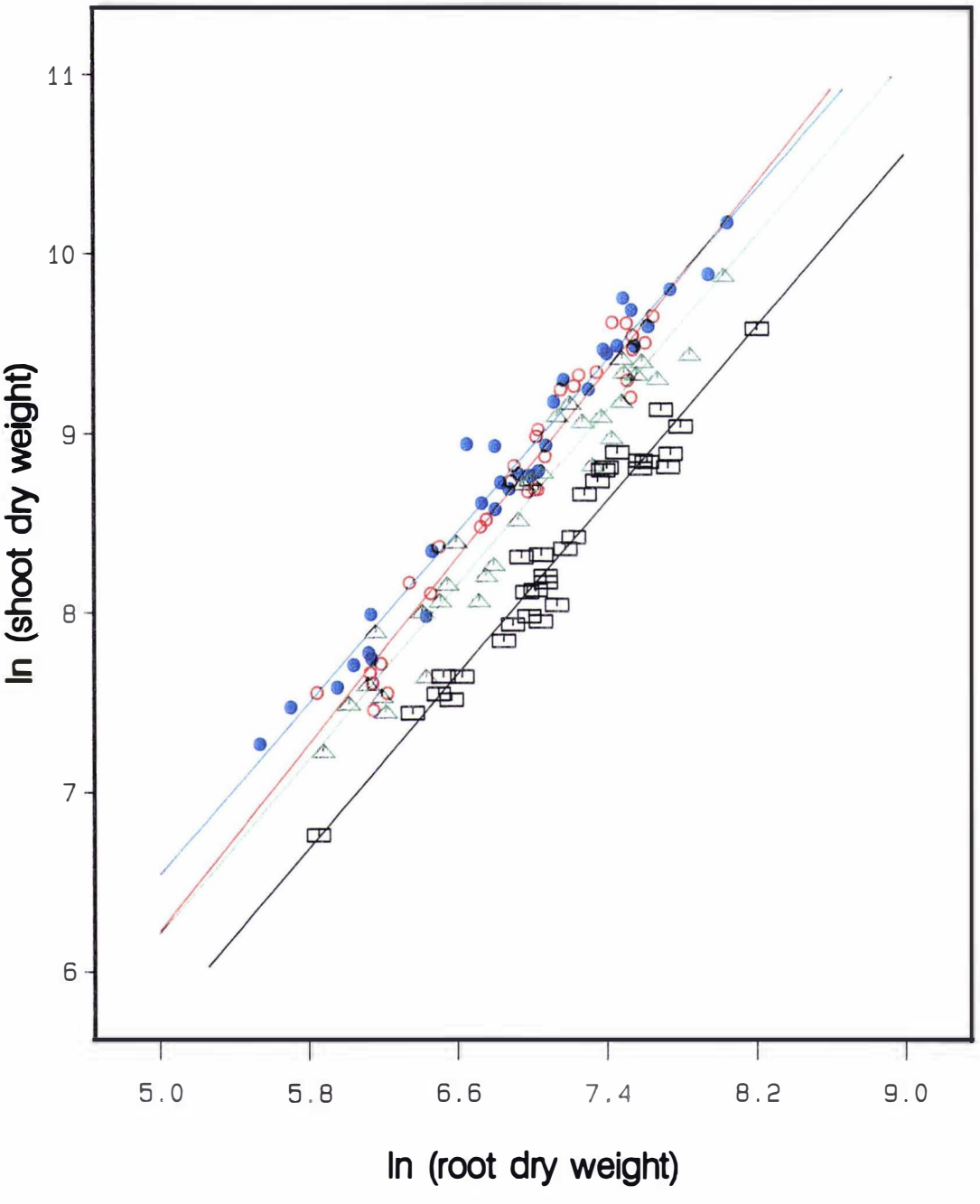

9.0
8.2
7.4
6.6
5.8
5.0
ln (stem dry weight)
5.0
5.8
6.6
7.4
8.2
9.0
ln (root dry weight)
Treatment
0.0 M
2.2 X 10-8 M
2.2 X 10-7 M
2.2 X 10-6 M

Figure 4.7. Changes in allometric relationship between shoot and root dry weight (k_T) of tomato seedlings when supplied via the roots with 6-N-benzylaminopurine at varying concentrations.

Control: R^2 = 95.1%, y =-0.284 + 1.30 x,
BA 2.2 X10^{-8} M: R^2 = 96.6%, y = 0.577 + 1.19 x,
BA 2.2 X10^{-7} M: R^2 = 95.0%, y = 0.136 + 1.22 x,
BA 2.2 X10^{-6} M: R^2 = 95.3%, y =-0.344 + 1.21 x.


ln (shoot dry weight)
11
10
9
8
7
6
5.0
5.8
6.6
7.4
8.2
9.0
ln (root dry weight)
Treatment
0.0 M
2.2 X 10-8 M
2.2 X 10-7 M
2.2 X 10-6 M

overall growth rate may lead to a higher proportion of the available photo-assimilates being channeled into root growth. This could arise if reduced cytokinin output by the root system resulted in fewer or less active metabolite sinks in the shoot of the plant.

(b) Treatments with BA changed the k value initially only, and that the homeostatic mechanism regulating shoot and root growth immediately rebalanced growth. In this model, the increased dry matter production of BA treated plants would have been due to the initial advantage in plant size, resulting from the low BA treatment.

If the latter hypothesis were correct allometry alone would be unsuitable for detecting changes brought about by BA because time is eliminated as a variable. Thus, if BA changed the relationship only briefly at the start of the experiment, after which the original relationship was restored. Changes due to BA treatment would not have accumulated over time, and the value of k would not have been altered in the long term. To further investigate this possibility, the ratio of shoot and root relative growth rate were examined more closely for individual harvests.

4.3.5. Changes in Ratios of Relative Growth Rates

During the first week only, there was a significant difference in the ratio of leaf relative growth rate to root relative growth rate (RGR_{LR}) between the BA at mid concentration and the other treatments (Table 4.8). In fact, during this period the growth rate of roots of all treatments exceeded all other organs, indicating that root production to compensate for the loss during transplanting may have been still taking place. No effect of BA on the RGR ratio at other harvests was detected. The high level of variation inherent in measurements of RGR undoubtedly contributed to the failure to measure statistical defferences in ratios of RGR(s).

Nevertheless, the measured increases in leaf area and mass strongly indicate a stimulatory effect of BA at the low concentration, which must be satisfactorily explained.

LE 4.8. *Changes in ratios of relative growth rates with time as affected by root application of 6-N-benzylaminopurine*

k	BA treatment	RGR_{LR} *1		RGR_{SR} *2	RGR_{TR} *3	RGR_{SL} *4
		*		ns	ns	ns
	Control	0.871	b	0.635	0.800	0.729
		(0.269)		(0.040)	(0.047)	(0.030)
	$2.2X10^{-8}M$	0.681	ab	0.674	0.677	0.989
		(0.030)		(0.051)	(0.047)	(0.070)
	$2.2X10^{-7}M$	0.315	a	0.299	0.312	0.949
		(0.019)		(0.028)	(0.030)	(0.088)
	$2.2X10^{-6}M$	0.087	a	0.068	0.082	0.769
		(0.018)		(0.019)	(0.019)	(0.021)
		ns		ns	ns	ns
	Control	1.372		1.687	1.464	1.229
		(0.026)		(0.029)	(0.027)	(0.016)
	$2.2X10^{-8}M$	1.147		1.259	1.173	1.098
		(0.019)		(0.018)	(0.018)	(0.012)
	$2.2X10^{-7}M$	1.297		1.571	1.368	1.211
		(0.053)		(0.054)	(0.053)	(0.036)
	$2.2X10^{-6}M$	1.102		0.965	1.069	0.876
		(0.032)		(0.030)	(0.031)	(0.026)
		ns		ns	ns	ns
	Control	1.145		1.594	1.267	1.391
		(0.042)		(0.049)	(0.044)	(0.044)
	$2.2X10^{-8}M$	1.304		1.781	1.432	1.365
		(0.041)		(0.049)	(0.043)	(0.032)
	$2.2X10^{-7}M$	1.346		1.551	1.400	1.152
		(0.060)		(0.061)	(0.060)	(0.038)
	$2.2X10^{-6}M$	1.637		1.980	1.720	1.210
		(0.064)		(0.070)	(0.065)	(0.030)
		ns		ns	ns	ns
	Control	1.147		2.155	1.465	1.878
		(0.146)		(0.217)	(0.166)	(0.199)
	$2.2X10^{-8}M$	1.204		1.832	1.398	1.522
		(0.124)		(0.165)	(0.135)	(0.112)
	$2.2X10^{-7}M$	0.962		1.334	1.078	1.386
		(0.068)		(0.078)	(0.071)	(0.084)
	$2.2X10^{-6}M$	1.086		1.671	1.246	1.539
		(0.074)		(0.092)	(0.078)	(0.079)

- Each figure from 8 replications.
- Standard error of means in bracket.
- Mean separation within column by t-test ($p \leq 0.05$).
- *1 = Ratio of leaf to root relative growth rate,
  *2 = Ratio of stem to root relative growth rate,
  *3 = Ratio of shoot to root relative growth rate,
  *4 = Ratio of stem to leaf relative growth rate.

4.3.6. Changes in Linear Relationships Between Leaf and Root Attributes

The linear relationship between leaf area and root number was moderately strong (Table 4.9) as expressed by the coefficient of determination (R^2), with the exception of the control in which R^2 was somewhat lower. Benzylaminopurine at low and mid concentrations tended to increase the regression coefficient and also the value of y-intercept. The low BA treatment, thus, had a greater leaf area per root number than the control at all times. On the other hand, during the early period, the mid concentration had a smaller leaf area per root number while the opposite was true for the high concentration treatment. These results may indicate that with BA, at the low and the mid concentration, supplementing the endogenous cytokinins, expansion of leaves was less dependent on cytokinins produced from roots (Fig. 4.8).

The relationship between leaf area and root length (Fig.4.9) could relate more closely to the surface area of the root and shoot systems, and perhaps, therefore, also leaf and root function (Table 4.9). Consequently, examination of this relation may reveal whether the rate limiting function between roots and shoots relates to the capacity to absorb and transpire water. The coefficient of determination for the linear relationship between leaf area and root length was slightly stronger than those between leaf area and root number (Table 4.9) (values ranged between 76 and 93%). While this could indicate that the root absorbing surfaces related more closely to leaf surface area than root number, no statistical difference between the regression coefficients was observed. The result predicted that, with the exception of BA at high concentration, leaf area per unit root length for BA treatments was greater than the control. This was not so, however, at the early stage of growth since the y-intercept of the control was higher than the low and mid BA treatments (Table 4.9).

By contrast, there was a relatively weak relationship between leaf number and root number (Table 4.9; Fig. 4.10) or root length (Fig. 4.11) (R^2 ranged between 59.4 and 72.4%, for root number and 58.4 and 72.4%, for root length). Nevertheless, the trends in both regression constants (a and b) (Fig. 4.10 and 4.11)

_E 4.9. *Changes in linear relationships between leaf and root attributes as affected by root application of 6-N-benzylaminopurine*

BA treatment	ln a	*1 se(ln a)	b		se (b)	R2 (%)
eaf area, x = Root Number			*			
Control	62.1	227.4	0.177	b	0.024	65.7
$2.2X10^{-8}M$	171.1	233.9	0.189	b	0.017	81.7
$2.2X10^{-7}M$	-5.4	140.9	0.197	b	0.013	88.8
$2.2X10^{-6}M$	191.4	94.4	0.110	a	0.008	87.5
.eaf area, x = Root Length			ns			
Control	-45.6	240.7	10.9		1.11	76.3
$2.2X10^{-8}M$	-128.9	230.2	12.5		0.94	85.6
$2.2X10^{-7}M$	-88.6	126.3	11.1		0.61	91.6
$2.2X10^{-6}M$	13.7	79.9	7.5		0.39	92.5
.eaf number, x = Root Number x 10^{3}			ns			
Control	2.03	2.16	1.61		0.19	72.4
$2.2X10^{-8}M$	5.70	2.98	1.65		0.21	67.6
$2.2X10^{-7}M$	1.98	2.77	1.95		0.25	66.7
$2.2X10^{-6}M$	4.09	2.71	1.44		0.22	59.4
.eaf number, x = Root length			ns			
Control	0.68	2.59	0.104		0.012	71.6
$2.2X10^{-8}M$	3.50	3.00	0.106		0.012	71.5
$2.2X10^{-7}M$	1.00	2.53	0.109		0.012	72.5
$2.2X10^{-6}M$	2.37	2.98	0.095		0.015	58.4

efficients b from slopes of linear regressions of $\ln y = \ln a + b \ln x$, where y is either af area or leaf number and x is either root number or root length. Each parameter stimated from 32 plants.
mparisons of b based on t-test ($p \leq 0.05$), $df_{(error)} = 60$.
= Standard error.

Figure 4.8. Changes in linear relationship between leaf area and root number of tomato seedlings when supplied via the roots with 6-N-benzylaminopurine at varying concentrations.

Control: R^2 = 65.7%, y = 62.1 + 0.177 x,
BA 2.2 X10^{-8} M: R^2 = 81.7%, y = 171.1 + 0.189 x,
BA 2.2 X10^{-7} M: R^2 = 88.8%, y = -5.4 + 0.197 x,
BA 2.2 X10^{-6} M: R^2 = 87.5%, y = 191.4 + 0.119 x.

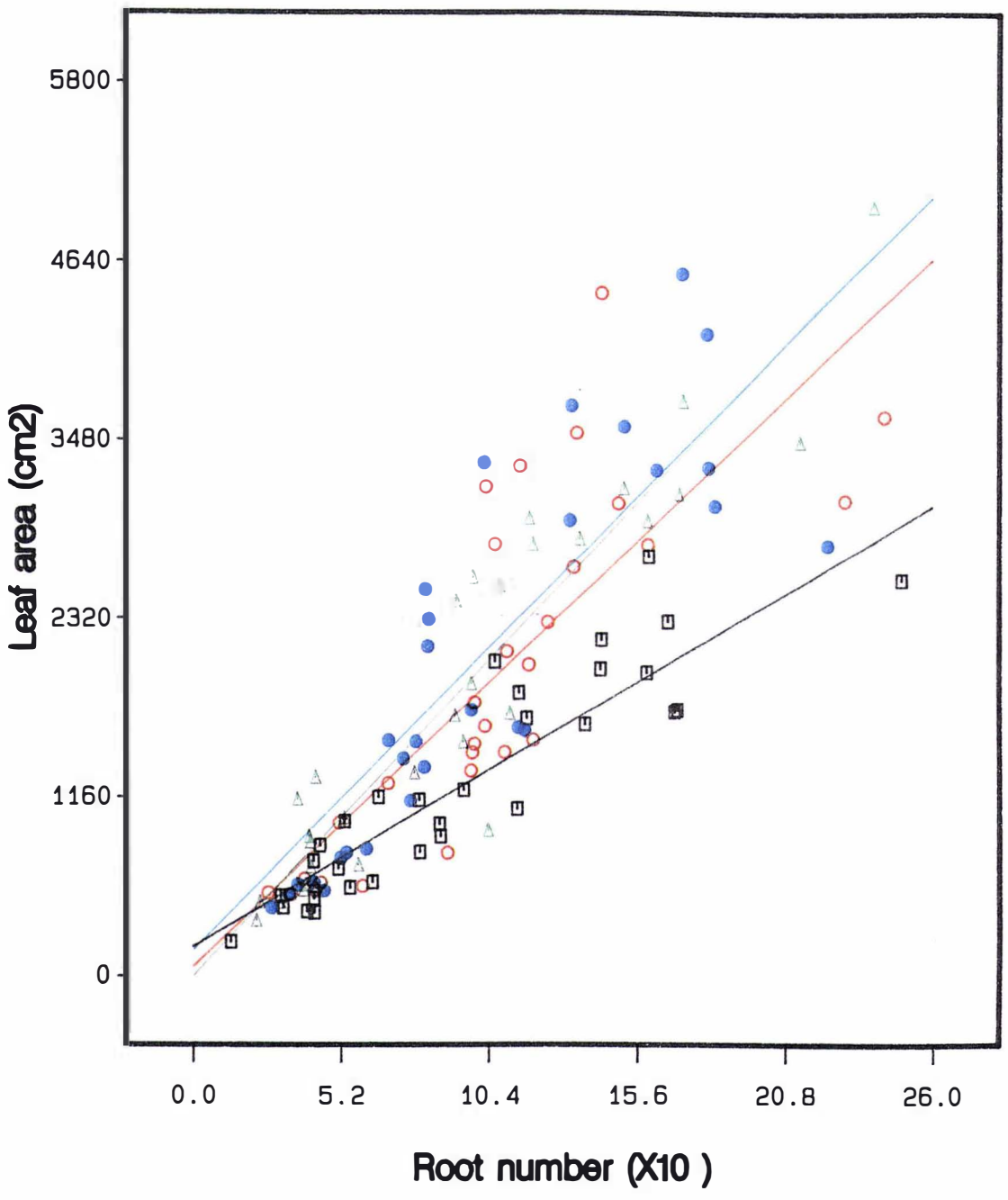
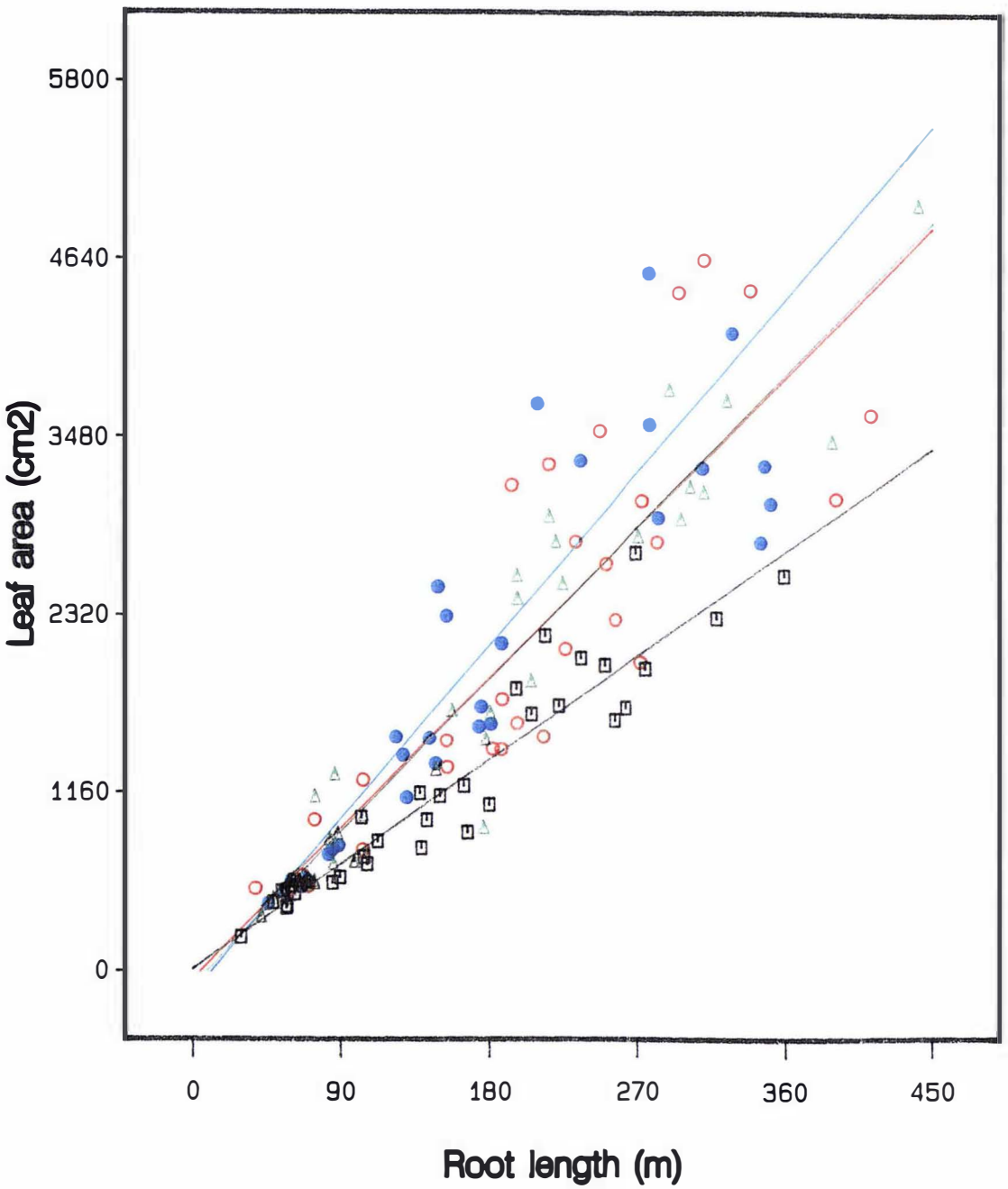

5800
4640
3480
2320
1160
0
Leaf area (cm2)
0.0
5.2
10.4
15.6
20.8
26.0
Root number (X10)
Treatment
BA 0.0 M
BA 2.2 X 10-8 M
BA 2.2 X 10-7 M
BA 2.2 X 10-6 M

Figure 4.9. Changes in linear relationship between leaf area and root length of tomato seedlings when supplied via the roots with 6-N-benzylaminopurine at varying concentrations.

Control: R^2 = 76.3%, y = -45.6 + 10.9 x,
BA 2.2 $X10^{-8}$ M: R^2 = 85.6%, y = -128.9 + 12.5 x,
BA 2.2 $X10^{-7}$ M: R^2 = 91.6%, y = -88.6 + 11.1 x,
BA 2.2 $X10^{-6}$ M: R^2 = 92.5%, y = 13.7 + 7.5 x.


5800
4640
3480
2320
1160
0
Leaf area (cm2)
0
90
180
270
360
450
Root length (m)
Treatment
BA 0.0 M
BA 2.2 X 10-8 M
BA 2.2 X 10-7 M
BA 2.2 X 10-6 M

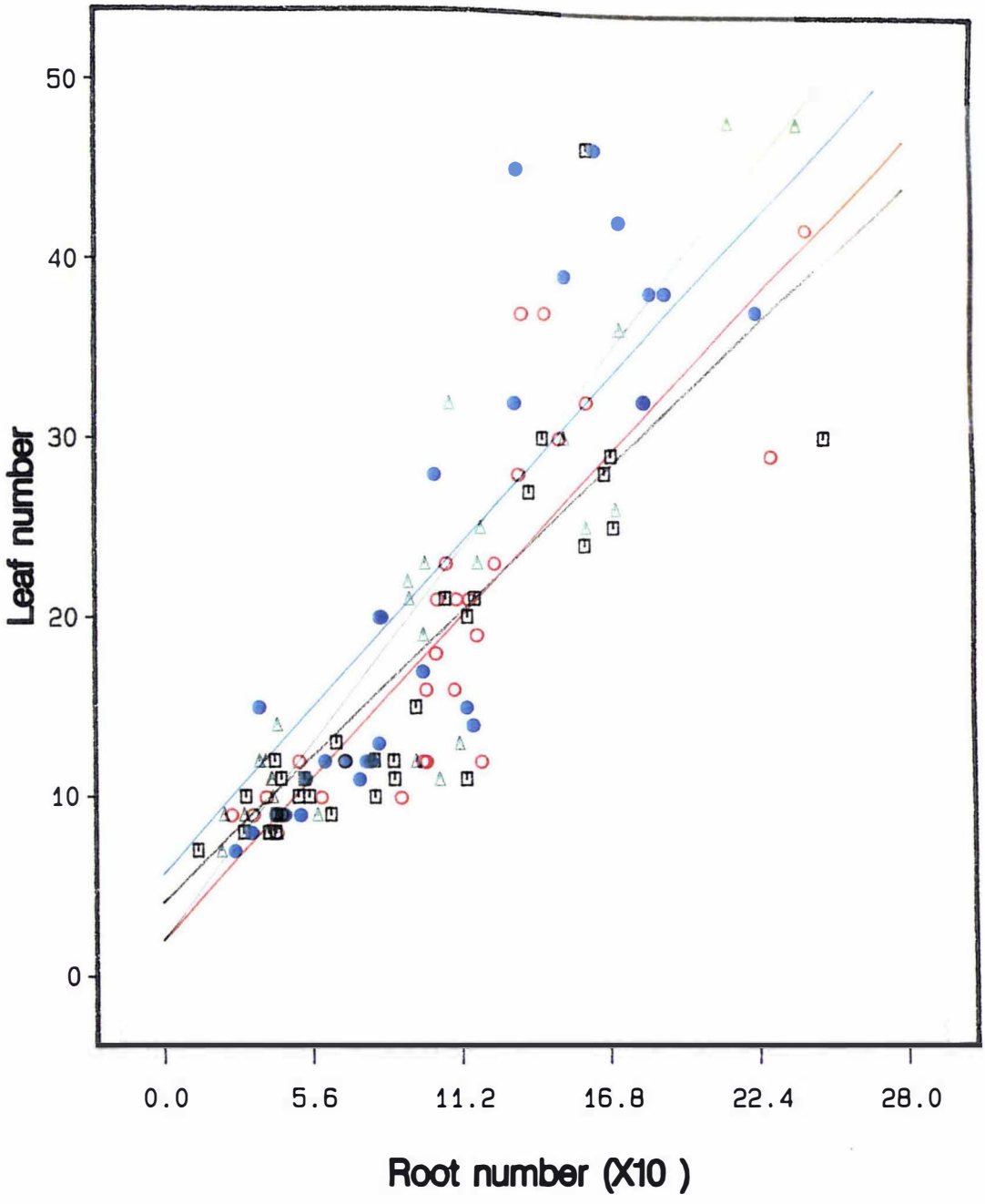

50
40
30
20
10
0
Leaf number
0.0
5.6
11.2
16.8
22.4
28.0
Root number (X10)
Treatment
BA 0.0 M
BA 2.2 X 10-8 M
BA 2.2 X 10-7 M
BA 2.2 X 10-6 M

Figure 4.10. Changes in linear relationship between leaf number and root number of tomato seedlings when supplied via the roots with 6-N-benzylaminopurine at varying concentrations.

Control: $R^2 = 72.4\%$, $y = 2.03 + 1.61 \times 10^{-3} x$,
BA 2.2×10^{-8} M: $R^2 = 67.6\%$, $y = 5.70 + 1.65 \times 10^{-3} x$,
BA 2.2×10^{-7} M: $R^2 = 66.7\%$, $y = 1.98 + 1.95 \times 10^{-3} x$,
BA 2.2×10^{-6} M: $R^2 = 59.4\%$, $y = 4.09 + 1.44 \times 10^{-3} x$.

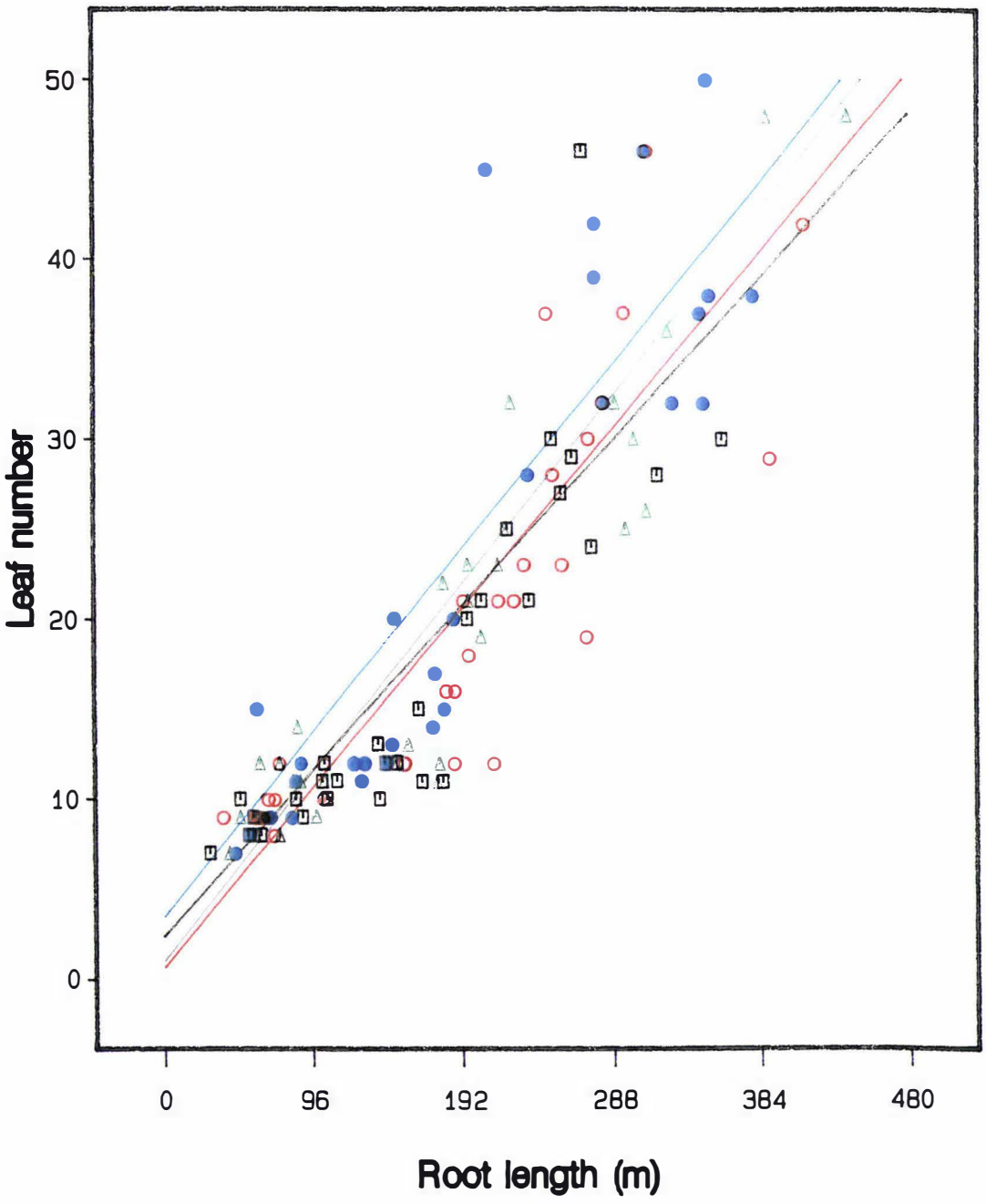

Leaf number
50
40
30
20
10
0
0
96
192
288
384
480
Root length (m)
Treatment
BA 0.0 M
BA 2.2 X 10-8 M
BA 2.2 X 10-7 M
BA 2.2 X 10-6 M

Figure 4.11. Changes in linear relationship between leaf number and root length of tomato seedlings when supplied via the roots with 6-N-benzylaminopurine at varying concentrations.

Control: R^2 = 71.6%, y = 0.68 + 0.104 x,
BA 2.2 $X10^{-8}$ M: R^2 = 71.5%, y = 3.50 + 0.106 x,
BA 2.2 $X10^{-7}$ M: R^2 = 72.5%, y = 1.00 + 0.109 x,
BA 2.2 $X10^{-6}$ M: R^2 = 58.4%, y = 2.37 + 0.095 x.

were similar to those of leaf area and root number, and leaf area and root length, respectively.

The results show that the relationships between these attributes of roots and leaves are not as strong as that established between their log dry weights, in which R^2 values were always greater than 90%. Although it has been demonstrated that, without exogenous cytokinins supplied, there is a strong relationship between leaf number and root number (Chung *et al.* 1982), leaf area and root number (Richards 1981), and leaf area and root length. These relationships, particularly in the control treatment, were substantially lower than those reported by these workers. In plants treated with cytokinins, the relation between root number and leaf number (Richards and Rowe 1977 b) accounted for an unacceptably low proportion of the variation (R^2 only 60.8%). Although higher R^2 values than those reported by Richards and Rowe (1977 b) were obtained for cytokinin treatments in this experiment, the conspicuously low R^2 of the control treatment provided convincing evidence that the linear relationships between leaf and root attributes are not as reliable as those derived from log dry weights.

4.3.7. Changes in the Distribution of Photoassimilates

4.3.7.1. Leaf Weight Ratio (LWR)

Figure 4.12 (a) reveals that the proportion of the photoassimilates supply directed towards leaves did not remain constant for each treatment during this study. Leaf weight ratio ranged between 55 to 65% (Table 4.10). Furthermore, the differences in LWR were greatest after a week of exposure to treatments. The low BA concentration produced a consistently greater leaf weight than the control throughout the experiment. In contrast, the two higher BA concentrations had a consistently lower LWR than the control, except, perhaps at the final two harvests. At the highest BA concentration the LWR increased with successive harvests, whereas in other treatments, the ratio remained constant for the second week, after which it declined. This phase, however, was limited and consequently plants produced a decreasing proportion of leaf dry weight for the remainder of the

.E 4.10. *Changes in dry weight distribution with time as affected by root application of 6-N-benzylaminopurine, expressed as a ratio of plant organ to total plant dry weight and shoot-root ratio*

:st	BA treatment	Leaf weight ratio %	Stem weight ratio %	Root weight ratio %	Shoot-root ratio
		**	ns	**	**
	Control	63.7 c	18.1	18.2 b	4.57 c
	$2.2X10^{-8}M$	64.9 d	19.5	15.6 a	5.45 d
	$2.2X10^{-7}M$	60.8 b	19.3	19.9 c	4.08 b
	$2.2X10^{-6}M$	54.9 a	18.7	26.5 d	2.79 a
	se	0.4	0.5	0.5	0.14
		**	**	**	**
	Control	64.0 c	21.8 b	14.3 a	6.04 c
	$2.2X10^{-8}M$	64.9 c	21.4 b	13.8 a	6.27 c
	$2.2X10^{-7}M$	60.7 b	22.1 b	17.2 b	4.89 b
	$2.2X10^{-6}M$	56.5 a	17.8 a	25.8 c	2.90 a
	se	0.7	0.6	0.4	0.12
		**	**	**	**
	Control	61.2 b	26.1 b	12.7 a	6.92 c
	$2.2X10^{-8}M$	62.8 c	25.6 b	11.7 a	7.62 d
	$2.2X10^{-7}M$	61.0 b	24.5 b	14.5 b	5.90 b
	$2.2X10^{-6}M$	57.9 a	20.3 a	21.9 c	3.60 a
	se	0.5	0.4	0.4	0.18
		**	**	**	**
	Control	59.1 b	28.7 c	12.2 a	7.40 c
	$2.2X10^{-8}M$	60.7 b	28.5 c	10.8 a	8.36 d
	$2.2X10^{-7}M$	59.9 b	26.8 b	14.3 b	6.11 b
	$2.2X10^{-6}M$	56.1 a	23.1 a	20.7 c	3.86 a
	se	0.5	0.5	0.5	0.25
		**	**	**	**
:d	Control	62.0 c	23.5 b	14.3 b	6.25 c
	$2.2X10^{-8}M$	63.3 d	23.7 b	13.0 a	6.93 d
	$2.2X10^{-7}M$	60.4 b	23.2 b	16.5 c	5.25 b
	$2.2X10^{-6}M$	56.3 a	20.0 a	23.7 d	3.29 a
	se	0.3	0.4	0.8	0.10

:h mean figure from 8 replications with $df_{(error)} = 24$ at harvests, and pooled mean from 32 replications with $df_{(error)} = 108$.
an separation within column by Lsd ($p \leq 0.05$).

Figure 4.12. Changes in the proportion of photoassimilates partitioned into tomato seedling organs when supplied via the roots with 6-N-benzylaminopurine at varying concentrations; (a) leaf weight ratio, (b) stem weight ratio, (c) root weight ratio and (d) shoot-root ratio. I = standard error of means.

experimental period. The tendency for LWR to fall, established that the proportion of dry matter going to new leaves steadily declines wi h increasing plant size and, or age.

4.3.7.2. Stem Weight Ratio (SWR)

In general, the SWR increased with plant age (Table 4.10; Fig. 4.12 b), reflecting the accumulation of dry weight in the stem over time. The mean SWR(s) increased from 18.1 to 19.5% following the first week pe iod to 23.1 to 28.7% at the final harvest. The increase in the proportion of stem was compensated for by the decline in the proportion of leaves (cf. Fig. 4.12 a), and roots (cf. Fig. 4.12 c). The proportion of stem and leaves were more or less equal at the first harvest. After a week of application, the ratio was not changed significantly by BA. Thereafter the low BA treatment contained the same proportion of stem as the control. The mid concentration produced less stem than the control in later weeks and the high concentration markedly less throughout the course of the experiment than the control.

4.3.7.3. Root Weight Ratio (RWR)

The low BA concentration reduced the root weight ratio whereas both higher concentrations promoted the production of roots in relation to plant size. Taking all the three ratios into account, it seems clear, that where RWR was increased, the decreasing proportion of photoassimilates used for the growth of stem was diverted into the roots as the change in the RWR was in the opposite direction to that of the stem (Table 4.10; Fig. 4.12 c). These effects, however, did not range in order of concentration, but in the opposite order to plant size. The decline in RWR was more regular than the corresponding progressions of stem and leaf, and differences between treatments were highly significant throughout.

4.3.7.4. Shoot-root Ratio

It is apparent hat heeffe cts of BA on shoot-root ratios closely parallel those on the preceding organ ratios (Table 4.10). At all stages of the experiment,

BA at low concentration had the highest shoot-root ratio because it had a higher leaf weight ratio and lower root weight ratio than all other treatments. The converse situation was obtained with the higher BA treatments. In detail, the high concentration suppressed both leaf and stem weight ratio more strongly than the mid concentration. Although plant size did not significantly differ between the low BA treatment and the control, the proportion of leaf appeared to be in the order of plant size, while the proportion of roots was in the reverse order.

The shoot-root ratios are the most definitive of the organ weight ratios (Table 4.10). The differences between treatments was established at the first harvest, and persisted throughout, while in other ratios, it became less clear with time. These highly significant differences, apparent at the first harvest, were the outcome of the initial growth stimulation of leaves by the low BA treatment, which was opposite to the other BA treatments. In contrast to GA effects, these differences did not increase with time (Fig. 4.12 d).

The preceding sections established, with respect to photoassimilate distribution, that the response of the control was intermediate compared to the high and low BA treatments. These results show that shoot-root ratio was affected in the same way as other attributes. The low concentration of BA increased, while the mid and the high concentrations reduced shoot-root ratio in proportion to concentration. Indeed, these results are the most important outcome of the effects of varying BA concentration, revealed by this study. Of the values considered, the shoot-root ratio was the most sensitive to BA, because effects on other individual tissues and organs were compounded in the shoot-root ratio.

Table 4.10 shows that the effects of the low BA treatment on the organ weight ratios and shoot-root ratio were statistically stronger than all other effects (*e.g.* increases in leaf area and other leaf attributes in Table 4.1). These data indicate that the effect of cytokinins on partitioning towards the leaves, is the primary mode of action. This effect appears to be precise and powerful, judging by the extremely low variation recorded (Table 4.10). As discussed above, effects of BA appear to have occurred prior to the first harvest, as the differences between the proportions of all plant parts remain constant, for each treatment, after the first

harvest. In contrast, the stem proportion was significantly different only between the high BA concentration and the remainder treatments. This difference was probably caused by phytotoxicity and therefore, may not be pertinent to the role of BA in growth regulation.

4.4. DISCUSSION

4.4.1. The Responses of Plants to BA Within the Range of the Concentrations Used

Under this experimental system, physical factors, water and nutrient limitations to root growth and function have been minimized compared to most conceivable natural rhizospheres. Nevertheless, total plant dry matter production was increased by supplementing the level of endogenous cytokinins produced by natural activities, very marginally, via the root system. This suggests that in a plant in which all constraints to root growth and function have been removed, growth and overall production remain a function of the root cytokinin production.

This response has not been demonstrated in similar studies by other workers (Wittwer and Dedolph 1963; Tognoni *et al.* 1967; Richards 1980). Kuiper and Staal (1988) found that addition of BA at 10^{-8} M into nutrient solution, upon which *Plantago major* was growing, was effective, at least initially, in inhibiting the reduction of growth rate induced by nutrient deficiency. In other works, however, total plant growth was reduced but root weight ratio increased by exogenously applied-cytokinins. This effect was rationalized as typical of the capability of these compounds to draw photoassimilates towards the site of the application which subsequently became growth zones (Richards 1980). In those studies, root growth rate, compared to that of the shoot, was increased, while growth in the other parts and, in particular, plant growth as a whole was reduced. In contrast, in this experiment the stimulatory effects of the very low concentration of BA was accompanied by a decreased root weight ratio (RWR) and increased shoot-root ratios which is the normal plant response to improved growing conditions and higher plant growth rate, such as occurs with fertilization (Troughton 1977) and enhanced rhizosphere condition in general (Rogers and Vyvyan 1934; Brouwer 1963; 1981; Davidson 1969 a; b; Richards and Rowe 1977 b; Ruff *et al.* 1987). On the other hand, as with earlier studies this work also found that higher levels of BA suppressed overall growth and dry matter production while decreasing shoot-root ratio and increasing RWR. At the highest concentration this treatment was clearly phytotoxic (see Plate 4.1). This and other

related results clearly indicate that increased RWR and decreased shoot-root ratio in those studies are an effect of supra-optimal cytokinin level rather than enhancement the natural promotive response. The range of concentrations used in those studies was much higher than used in this study. Furthermore, the effect was probably exacerbated by the mode and frequency of application. Tomato roots were submerged in culture solution using kinetin at 10^{-7} to 10^{-5} M (Wittwer and Dedolph 1963), or BA at 3 $X10^{-7}$ to 10^{-6} M (Tognoni *et al.* 1967), or applied via vermiculite with BA at 4.4 $X10^{-5}$ M (Richards 1980). Not surprisingly, the plant responses reported were identical to (or even greater than) the inhibitory results of BA at the high concentration, 2.2 X 10^{-6} M, obtained in this study. At the highest concentration in this and in other studies, the malformation of root systems was observed in the form of profuse production of short, stubby laterals, resulting in very compact root systems. In addition, the tips of the lateral roots pointed abnormally upwards (Plate 4.1). This response may be associated with the failure of gravitropism, which was microscopically examined by Busch and Sievers (1990) in roots supplied with very high concentrations of cytokinin and gibberellic acid.

In my preliminary experiment, 2.2 X 10^{-5} M (5 $mg.l^{-1}$) BA was phytotoxic and induced growth of 'pseudonodules' as reported by others (*e.g.* Wittwer and Dedolph 1963). Roots were severely shortened and only a few laterals, particularly of the secondary form, were produced. The so-called pseudonodules were callus-like, and all the roots were covered with a mucous-like slime. In my preliminary trials, the higher BA concentration killed the plants within a few days.

There also appeared to be differences in the cultural system which may have affected the response in these experiments. The optimum BA concentration for hydroponically grown plants could also be lower than for plants in an aeroponic system, since the roots of the former are surrounded by the solution at positive hydrostatic pressure compared to the latter system in which roots are coated with a film of solution. This conclusion is supported by subsequent observations in this laboratory in which concentrations of 10^{-9} M BA gave the promotive response in an hydroponic system (Andrews, pers. comm.), compared to 2.2 $X10^{-8}$ M (20

times higher) in this experiment. Therefore, even concentrations in the range from 10^{-7} to 10^{-5} M used by Tognoni *et al.*(1967) were probably much too high to induce the positive responses observed here.

Plants receiving non-toxic application of cytokinins responded distinctively is another important aspect, compared to other reports. The control treatment showed an intermediate response compared to the enhanced overall growth response of the low BA treatment and the non-physiological or supra-optimal responses of the mid concentration and the high concentration. In addition to overall growth, the control treatment gave an intermediate response with respect to all parameters measured. This is the first experiment in which this effect has been explicitly and unequivocally demonstrated. Importantly, these results strongly suggest, that at the low concentration, exogenous cytokinin supplemented the endogenous pool and took part of the normal suite of responses generated by cytokinin hormone(s) emanating from the roots.

4.4.2. Mode of Action of Exogenously-applied Root Cytokinins and Implications for Natural Shoot-root Interactions

Increased levels of cytokinins affected shoot-root ratio most strongly of all responses measured. Measurements of this attribute resulted in the first and greatest number of significant outcomes and the highest levels of significance ($p \leq 0.0001$). Furthermore, shoot-root ratio data were the resultant of significant, separate effects, upon leaf weight ratio and root weight ratio. Also, the effect of BA on shoot-root ratio remained consistent while it became weaker in other organ weight ratios as time progressed. Consequently we can assume that the growth responses observed were due to reciprocal changes in leaf and root fractions, and the shoot-root ratio combined coincidental effects of root supplied BA. This implies that the mode of action of the compound is via a mechanism involving the partitioning between leaves and roots.

It should be noted, however, that this partitioning effect of BA was between leaves and roots only. The effect on stem weight ratio was neutral throughout the experiment. The effect on partitioning was apparent before any

significant effects were obtained on growth by leaves or roots. Indeed, neither was growth of roots suppressed (even later in the experiment) nor growth of individual leaves increased, in leaf area or specific leaf area. The first significant BA effects on attributes of individual organs or tissues was on specific root weight (root dry weight per unit length) which was reduced at the first harvest (Fig. 4.2 d) and later upon leaf area and leaf number which increased, the former at least by the second harvest (Table 4.1). Time would be required to activate apical meristems before increased growth, in terms of leaf number, or shoots, was visible, which could delay a measurable effect on shoot and/or leaf number. Nevertheless, the results clearly show that partitioning effects were set in train, well before the plant had developed additional photosynthetic potential. These facts, plus the apparent depletion of root dry weight at the first harvest, point strongly to an increase in sink strength of apical meristems caused by cytokinin enhancement of growth. This is not a new idea but these data appear unequivocal and they clarify the role of cytokinin in regulation of photosynthesis as one indirect stimulation.

The inhibitory effect on root growth of BA at low concentration was only temporary. Subsequently, the faster growth rate facilitated by increased leaf area in this treatment, resulted in an increased root dry weight per unit length and allowed root size to be maintained. In contrast, in the inhibitory treatments, reduced use of photoassimilates led to an accumulation of reserves in roots, which was reflected in increased root dry weight per unit length throughout the period of experiment. Similar indications can be observed in the root number per unit length. This effect, however, was only marginally significant.

Enhanced leaf growth resulting from BA occurred as production of leaves on shoot laterals, together with the stimulation of lateral production. The latter is a well known effect of cytokinins associated with the release of buds from apical dominance (Kender and Carpenter 1972; Baraldi *et al.*1988) and increased branching and sucker growth (Mynett 1977; Richards 1980). Other evidence also showed that high levels of total endogenous cytokinins was well correlated with the numbers of adventitious buds formed on cuttings (Hansen *et al.* 1988). This morphological alteration, however, did not cause any concomitant change in stem dry weight or stem weight ratio (see later). This observation also supports the

conclusion that the effect of BA is on stimulation of shoot and leaf primordia. In the inhibitory treatment however, both leaf initiation and expansion were suppressed.

In contrast to leaf and root growth, the stem was not affected by BA application, except at the highest, clearly non-physiological concentration. Similar results were obtained by Richards (1980) with apple seedlings in which he found an increased number of shoot suckers was not accompanied with the increase in stem weight. Even in stressed cucumber plants, exogenously-applied cytokinins did not improve stem growth (Carmi and Heuer 1981). This indicates that cytokinins are not involved in the growth, or more specifically, photoassimilate partitioning into the stem.

Regulation of photoassimilate partitioning by cytokinins appears to involve increasing the sink potential of the shoot meristems. The increase in the proportion of photoassimilates directed towards leaves, resulting from activation of shoot meristems and increased leaf number, led to a larger area of leaves and leaf mass. Initially, the high activity in leaves was facilitated by reduced supply of resources to the roots. Even though root weight was not reduced compared to the control, the proportion of photoassimilates directed to leaves was increased in relation to the roots, and initially, root weight per unit length reduced. This appears to be an expression of enhanced photoassimilate economy resulting from the adaptive potential derived from the plasticity of root function in a suitable root environment. Because root activity could adjust to match the higher photosynthetic potential of a larger plant without increasing root size, which was also observed by Richards (1977; 1978), savings could be made in the amount of photoassimilates invested in root growth, which could be reallocated for additional leaf area.

4.4.3. The Regulation of Shoot-root Allometry and BA

The results clearly show that exogenous cytokinins applied via the root system, control the shoot-root relationship via partitioning of photoassimilates. The fact that such exogenous cytokinins appear to be introduced into, and

supplement the level and the effects of, an endogenous cytokinin pool strongly suggests root-produced cytokinins also have this function. Nevertheless, it remains to be established if the above effects on shoot-root ratio affect the root to shoot allometric relation, and if so, how?

The k value of allometric relationships between the shoot and root systems, and the leaf and root systems, were unaltered by BA. Nor were any changes detected in RGR ratios despite marked and rapid changes in shoot-root ratio. Since the regression equation of the allometric relation must change to give an increasing difference change in shoot-root ratio for a given plant size or age, the differences in shoot-root ratio observed between treatments must be due to changes in the intercept. It follows, therefore, that one needs to determine what is the cause, and physiological significance of a change in the value of the intercept in order to establish in what way cytokinin controls the allometric relation to affect a change in shoot-root ratio. While the RGR of individual organs were not significantly different at any stage during the experiment, the ratio of RGR_{LR} (Table 4.8) approached significance at the first harvest. At all subsequent harvests, and for all other RGR ratio no significant effects were observed.

By expressing size or growth of a plant organ as a function of the size or growth of another, as is done in allometric equations, one eliminates time as a variable. According to the most widely accepted hormone models of allometric growth, amendments to the rhizosphere, such as added nutrients, water or improved soil structure which facilitate root function, stimulate shoot growth and promote auxin production (Wareing 1970; Brouwer 1981; Richards 1986). Auxin thus synthesized would return via the phloem (Baker and Allen 1988) to the roots to stimulate root growth via the homeostatic mechanism. If the improved root conditions prevail, enhanced growth by roots and shoot would result in a change in the value of k and shoot-root ratio. In this experimental system, root conditions were not limiting. If the small increase in cytokinin level, that stimulated growth of the shoots initially, was followed by homeostatic balancing of root growth by auxin, an increase in root weight over the control would have been obtained. Although, there may have been a trend in that direction after an initial decrease in root weight, the data are not significant or convincing (Table 4.6).

Indeed, the available data appears to indicate that root growth did not adjust to the transitory increase in shoot growth. The shoot-root ratio increased rapidly up to the first harvest and then only slowly thereafter (Fig. 4.12 d). Thus, the initial response in shoot growth was not followed by a balancing increase in root growth, resulting from increased auxin production. This would result in a transitory increase in the value of k, but it is clear from figure (Fig. 4.7) that this was not sustained. On the other hand, since the initial increase in shoot growth was never balanced by a matching burst of root growth, the intercept of the allometric regression equation would have been displaced in the way the results show (Fig. 4.7).

The physiological interpretation of these data is complex. It could be argued that since there was no matching root growth response, that this was an artificially induced change of no physiological significance. The evidence in this connection, discussed earlier, however, is supported by these observations. Further, the data establish that there was a transitory change to a higher k value, followed (rapidly) by a return to the original k value which resulted in the change in the intercept; despite the fact that exogenous cytokinin was available at a more or less a constant level.

It is clear from studies of the periodicity of root and shoot growth that they do not necessarily occur simultaneously (Mullin 1963; Drew and Ledig 1980; Drew 1982). Chalmers (1987) noting those reports of non-synchronous growth by roots and shoots, proposed that shoot and root growth was complementary rather than synchronous or simultaneous. Of course, the hormone model of regulation of allometric growth by roots and shoot implies a sequential mechanism such as indicated in Figure 4.13 (i). Figures 4.13 (ii) through (iv), indicate what should occur if the mechanism was comprised simply of a sequence of promotion of root and shoot growth by auxin and cytokinin respectively. Since exogenous cytokinin was continually available to augment root-produced cytokinin, the relative growth rates of the components of the system would increase until a new rate limiting barrier (*e.g.* sunlight) was encountered. The data clearly indicates, however, that no root growth response occurred to compensate for the initial stimulation of shoot growth. Subsequent stimulation of growth by cytokinin in this treatment, appears

growth. Subsequent stimulation of growth by cytokinin in this treatment, appears to have been solely the result of the growth economy gained from the initial increase in shoot-root ratio.

The question therefore remains, why was root growth not stimulated in relation to the control, which would have led to a new growth equilibrium and higher value of k? From the preceding discussion it is clear that if exogenous cytokinin was not participating in or affecting the homeostatic balance between roots and shoot, a sequence of events similar to that indicated in Figs. 4.13 (i to iv) should occur and an increase in k would be obtained.

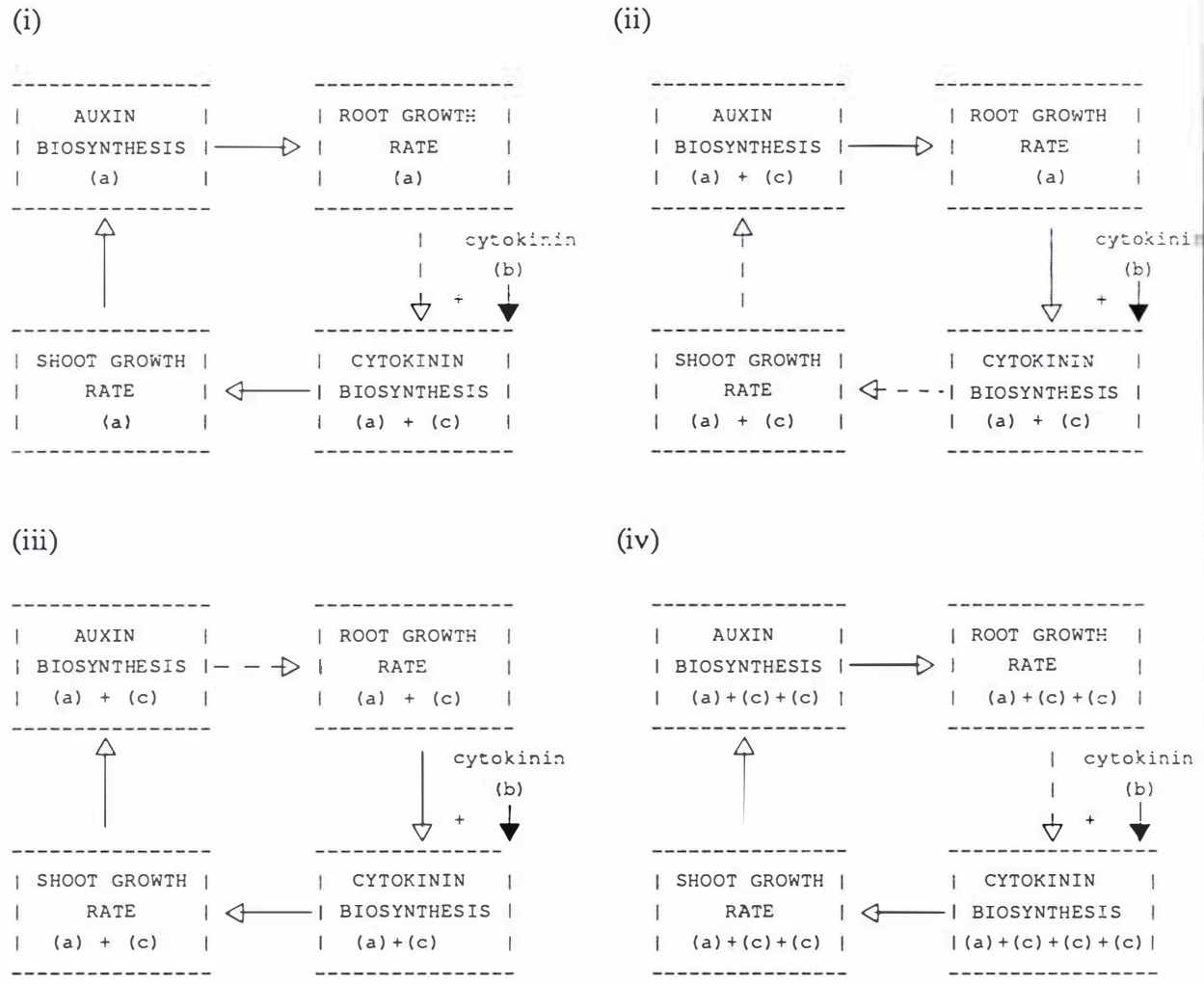
One possible explanation is that the exogenous cytokinin participates in a feedback system to suppress additional cytokinin synthesis that would otherwise follow increased shoot growth and auxin synthesis. Cytokinin produced as a result of root growth is exported from the root system and affects growth elsewhere. While exogenous cytokinin entering the root is clearly also exported, there is nevertheless a continuous source which will maintain an elevated (residual) cytokinin concentration in the root tissues. Cytokinin can inhibit root growth (Evans 1984) which may be a feedback mechanism to limit further cytokinin synthesis in situations where potential for shoot growth is reduced. This effect may be via the reduction of IAA in roots, through increased IAA oxidation (Evans 1984). If the apparent increase in cytokinin concentration in the root resulted in growth and consequent cytokinin synthesis being suppressed by the same order, this would result in the balancing of the new system, without additional root growth, at the same value of k (Fig. 4.14).

4.4.5. Leaf and Root Functional Relationships

In plants not receiving exogenous growth regulators the relationships between leaf area or leaf number and either root number or root length have been reported to be strong (Richards 1981, Chung *et al.* 1982). Similar results were obtained in this experiment. In the untreated plants R^2 for these attributes was generally low to moderately high (66 to 76%). These relationships are less convincing, however, than those derived from the log dry weights. A relationship

between leaf and root number has also been reported for plants treated with BA which changed as a function of the BA treatment (Richards and Rowe 1977 a). In this experiment, the slope representing this relationship also appeared to change with respect to the treatments, although not substantially. The R^2 values, however, were higher than those reported by Richards and Rowe (1977 a), but they remain less convincing than those obtained for k values which related shoot and root dry weights. These results cast some doubt on the conclusions reached in other work, at least to the extent, that root number or root length establish a strong case for a link to root function, *e.g.* cytokinin synthesis or water uptake, and leaf number or leaf area.

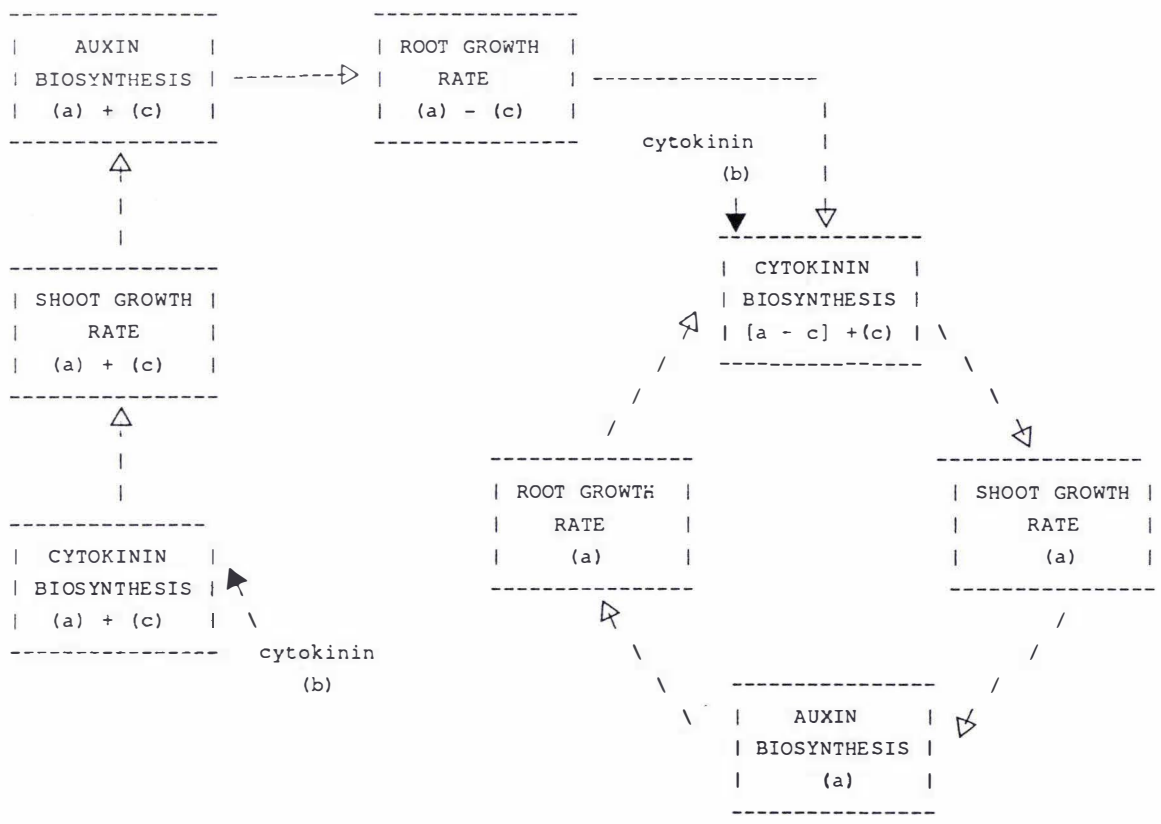
Proposed Homeostatic Mechanism for Cytokinin Regulation of Plant Growth



TE:
homeostatic rate of hormone synthesis and corresponding root and shoot growth rate,
the constant rate of exogenous BA absorption,
the increased rate of export of cytokinin or metabolites from root system which reduces or increases shoot growth.

ure 4.13. The sequential events illustrated as if cytokinin and auxin had been duced in homeostatic manner and thereby k values would have been respondingly changed.

Proposed Mechanism of Cytokinins in Regulating Plant Growth With Respect to the Experimental Results



OTE:
= homeostatic rate of hormone synthesis and corresponding root and shoot growth rate,
= the constant rate of exogenous BA absorption,
= the increased rate of export of cytokinin or metabolites from root system which causes a reduced or increased corresponding shoot growth.

igure 4.14. Possible sequence of events induced by BA application as indicated by e results.

CHAPTER 5
GENERAL DISCUSSION

5.1. EVALUATION OF THE EFFECTIVENESS OF ALLOMETRIC MODELS AS AN APPROACH FOR STUDYING THE SHOOT-ROOT RELATIONSHIP

Several models have been formulated in an attempt to describe the coordination of growth, which explains the change in shoot-root ratios in response to external changes (Wilson 1988). Although these models are useful in that they indicate physical and/or functional changes which lead to shoot-root alteration (Wilson 1988), the mechanism which regulates organ growth and dimensions has never been discussed. In this work, analysis of the allometric relationship, which is one of these models, has been used to study this control mechanism. As with most studies using this approach, results revealed very high values of R^2, which underlined, in common with numerous previous studies, that the, so far undefined, link between shoot and root systems is very strong. The advantage of the allometric equation over the shoot-root ratio is well accepted (Ledig *et al.* 1970; Troughton 1977). It remains the same, independent of time. Any change suggests a change in growth of the organ in relation to the other. In plants this is usually due to a change in the root or shoot environment.

Results of this work also indicate that the allometric model is an appropriate approach for detecting and analysing dynamic changes in shoot-root relationships. Although alteration of the value for allometric relationships between shoot and root dry weight (k_T) alone may be difficult to interpret, when considered with other data, such as RGR(s), shoot-root and organ weight ratios, allometric model provides a robust rational for the formulation of mechanisms to explain the regulation of shoot-root equilibrium. In the sense that weight ratios were sensitive to transient changes in growth (Table 4.10), while the k_T value was not (Table 4.7), the data were rigorously complementary.

Since the k_T value provides an estimate of the ratio of the RGR(s) of the organs being studied, it can vary markedly over short intervals (Table 3.14 to 3.16).

Such fluctuations, however, will be confined to plants, in which the growth increment during a fluctuation in root or shoot growth, is a substantial proportion of total plant weight. In these circumstances the change to shoot growth which may precede or follow the complementary change in root growth will cause a substantial change in k. Over longer periods, however, alternating growth of the shoot and root system smooths out variations in k_T. In most mature plants, alternating growth between roots and above ground organs does not disturb the long term allometric relation, because the residual mass of the organs under study greatly exceeds short term growth increments.

It is well known that the change in k_T value is determined by changes in external environment (Hunt and Burnett 1973; Szaniawski 1985; Saunders, pers.comm.). Evidence has shown that as long as the environmental change persists, there will be a change in k_T value (and shoot-root ratio) (Ledig *et al.* 1970; Hunt and Burnett 1973; Szaniawski 1985). The results from this study, however, raise the question whether a change of shoot-root ratio is always accompanied by the change in k_T value, and if not, under what circumstances this could occur. Using a consistent environment with a continuing high level of exogenous plant growth regulator, shoot-root ratio was altered in contrasting ways, by GA_3 and BA. Although treatment with GA_3 did not alter the k_T value in relation to the change in shoot-root ratio, k_S was altered in a consistent and predictable way. Because GA_3 stimulated partitioning towards the stem, partially, although indirectly, at the expense of leaves (section 3.3.2.6), this would tend to cancel changes in the value of k_T. Nevertheless, since these data also showed that the direct effect of GA_3 was on partitioning of assimilates towards the stem at the expense of the roots, it is this relationship that is of interest, with respect to the GA mechanism, and therefore should produce the change in k_S, that indeed was measured.

In contrast, the direct effect of BA was upon the allometric relation between leaves and roots (k_L). In this experiment, however, neither k_L nor k_T was affected by the physiologically important treatments of BA, despite significant and relevant changes in shoot-root ratio. On the other hand, BA treatments significantly altered the value of ln a, which is the intercept on the ordinate of the allometric regression line.

The above mathematical solution rules out any biological explanation for these BA treatment effects, which involves any persistent change in relative growth rates of the shoot versus the roots. In these experiments, the results pointed to *a brief period of growth by the shoot that was not subsequently balanced by growth of the roots*. This initial period of enhanced carbon economy with respect to leaf production resulted in an increase in leaf area, photosynthetic potential, and consequently overall plant growth. This advantage was maintained, but not increased for the remainder of the experiment. Thus, it is clear that changes in the intercept of the allometric regression also point to important developmental events, and that allometric analysis highlights their occurrence. consequently, the lack of a statistically significant change in k value did not diminish the usefulness of the allometric regression coefficient. This potential contribution of changes in intercept has not been considered in other studies (*e.g.* Ledig *et al.* 1970; Troughton 1977; Reiss 1989), except in one recent report (Huges, Nichols and Woolley, 1991).

Consideration of the value of k at the organ level, provides information of the relative preferences with which assimilates are directed to different organs. In this study, comparisons of the k values of allometric relationships between organs assisted in indicating which growth regulators (cytokinins or gibberellins) regulated partitioning between which parts of the plant. The results showed that cytokinins regulated growth between leaf and root system (Table 4.10). In contrast, GA_3 did not exert direct control over partitioning to shoot meristems and leaf development, but stimulated stem growth substantially, initially at the expense of root growth and only later, and probably indirectly, affecting leaf growth (Table 3.17).

5.2. GIBBERELLINS AND CYTOKININS IN THE CONTROL OF SHOOT GROWTH AND PLANT GROWTH : A PROPOSED MECHANISM

Growth of tomato plants responded differently to BA and GA_3 in several important and definitive ways.

(1). While BA clearly affected the allometric relation between roots and leaves, it was neutral with respect to stem growth. In contrast, GA_3 applied to shoots or

roots increased the k_S value of the allometric relation between stem and roots directly by stimulating partitioning of dry weight towards the stem at the expense of the roots and only indirectly at the expense of leaves. Effects of GA_3 on leaf growth were clearly attributable to increased apical dominance or reduced leaf initiation. Treatments with GA_3 did not appear to diminish the competitive potential of individual leaves with respect to their capacity to compete with the stem for the available photoassimilates. In natural systems, gibberellins could suppress or enhance leaf growth by this indirect mechanism, depending upon the location of the expanding cells favoured by enhanced dry weight partitioning.

These conclusions are compatible with most reports of other studies of the mechanism of action of cytokinins and gibberellins. Taken together they suggest a complementary model of GA and cytokinin involvement in the regulation of vegetative growth, mediated by the specific effects of each growth substance upon dry weight partitioning. Leaf initiation and growth is promoted at the expense of roots, by increasing cytokinin level in relation to gibberellins, while relatively higher active gibberellin levels would promote growth of the stem at the expense of the roots and, perhaps also, leaves. The growth processes involved in the cytokinin response include increased leaf initiation, which consequently enhanced leaf growth and leaf area, increased shoot initiation and total production. Root growth, although reduced as a proportion of total growth and, at least initially, reduced absolutely, was ultimately increased due to the enhanced productive potential of the whole plant. On the other hand, gibberellic acid increased apical dominance, stem growth, internode length, and indirectly, reduced leaf number and consequently leaf area. The above hypothesis clearly extends the model proposed by Woolley and Wareing (1972 a; b) who proposed that the relative levels of gibberellins and cytokinins control apical dominance.

(2). Both cytokinins and gibberellic acid increased shoot-root ratio compared to the control. Cytokinin, however, failed to alter the k_L. In contrast, GA_3 altered the k_S value upon which it was acting, directly. The effect of BA was clearly limited to an initial stimulation of leaf growth which was not subsequently balanced by compensating root growth. It was proposed (section 4.3.4) that the response to BA was rapidly curtailed by a feed-back mechanism, possibly affecting the rate of

endogenous cytokinin synthesis. On the other hand, GA_3 continued to affect k_S throughout the experiment leading to a persistent change in the k_S value and the shoot-root ratio, suggesting no feedback mechanism was activated. This evidence of a feedback reaction affecting the mechanism of cytokinins, but not that of gibberellins, on the tomato plant shoot-root ratio, suggests that cytokinins, not gibberellins, is responsible for controlling the relationship, when root activity or root size is the rate limiting variable.

During the experiment, the root environment was not altered, except for the addition of BA. Growth changes following treatment with BA indicated that endogenous cytokinin synthesis, or turnover, adjusted rapidly to keep the total root concentration derived from endogenous and exogenous sources the same as in the control. Treatments resulted in two contrasting out comes, both of which were consistent with the established effects of exogenous cytokinin treatments reported by others (*e.g.* Woolley and Wareing 1972 a; b). At the low BA concentration, it could be argued that the feedback mechanism, regulating the total concentration of cytokinin at a point within the root, was unsaturated by the exogenous supply of cytokinin. Under this condition, cytokinin transport to the shoot was initially enhanced, and *de novo* synthesis inhibited, thereby maintaining the total BA concentration at the level prevailing in that environment in the control treatment. No net increase in the root cytokinin concentrated resulted, and the transitory increase in cytokinin gave the growth responses obtained. On the other hand, high concentrations of BA saturated the feedback mechanism. Neither enhanced transport, nor suppressed *de novo* synthesis, could prevent accumulation of BA in root tissues. Under these circumstances, the root became a sink for photoassimilates, as proposed by others (Wittwer and Dedolph 1963; Tognoni *et al.* 1967; Richards 1980) and consequently, the shoot-root ratio and also total production decreased.

Considering the shoot-root relationship is dynamic, changing in response to changes in the root environment, a feedback loop between the mechanism and the function or size of the two systems, must be required. It has been proposed that responses of tomatoes to the application of BA indicate that cytokinin is involved in the shoot-root balance mechanism, and the endogenous level of

cytokinin adjusts to changes in the root environment. Nevertheless, the proposed model is not simply one in which root meristem activity (responding to soil conditions) produces cytokinins in proportion to that activity. The model specifies, that a particular root environment corresponds to a particular root cytokinin concentration, as part of the feedback loop. Once the appropriate cytokinin concentration was exceeded (by feeding exogenous cytokinin), endogenous cytokinin synthesis was suppressed or reduced. Furthermore, subsequent growth measurements suggested that in the presence of an exogenous source of cytokinin, endogenous production adjusted, so that the resultant total cytokinin concentration was similar to the untreated control. If so, this suggests that cytokinin synthesis and or turnover in the roots is involved in detection of environmental changes in the rhizosphere.

In contrast, this study with GA_3 suggested that while gibberellins may be involved in the alteration of shoot-root ratio, these effects do not link with changes in the rhizosphere. Nevertheless, the results suggest that different morphological and developmental effects will result, depending upon whether gibberellin arrives at the site of action directly from sites of synthesis in the top of the plant, or via the xylem, from the root system. The results, however, do not clarify whether the root system has a direct or indirect role in the synthesis and or activation of gibberellin. On the other hand, there is much circumstantial evidence that proximity to the root system is an important factor in regulation of phenomena such as juvenility which are known to be associated with gibberellins (Chalmers 1985).

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