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Root restriction and root-shoot relationships in tomato (*Lycopersicon esculentum* Mill.)

A thesis presented in partial fulfilment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY
in
Horticultural Science

at Massey University.

Bruce R MacKay
1995

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Mac
DC20

We shall not cease from exploration
And the end of all our exploring
Will be to arrive where we started
And know the place for the first time.
—T.S.Eliot *Four Quartets*

Abstract

The potential for controlling plant growth and productivity by manipulating root growth and development has not been realised because of a lack of understanding of how root growth influences shoot growth. Until such responses are understood, matching container design and volume to desired plant output will continue to be based solely on anecdotal evidence. A series of experiments were conducted to explore the role of physical root restriction on the vegetative growth and development of tomato (*Lycopersicon esculentum* Mill. 'Moneymaker'). Concurrent with these experiments, a statistical model was developed for non-destructively estimating leaf area, cluster analysis was adapted to improve experimental precision, and an improved form of growth analysis developed. Additionally, a review of oxygen and major nutrient uptake rates by tomato established the operational parameters of a hydroponic system developed specifically for the study.

Rooted tomato cuttings were grown in 0.025 or 10 litre (control) containers in the hydroponic system. After 31 days in 0.025 litre containers, plants were de-restricted into either 0.05 or 10 litre containers, or retained in the 0.025 litre containers. Plants with physically restricted root systems had lower total plant biomass and total leaf area, were shorter in both height and total root length, and had fewer roots, leaves, and lateral shoots than unrestricted plants. Restriction reduced root number after 31 days, but reductions in root length and dry biomass did not occur until after 45 days. Leaf dry biomass was reduced in restricted plants after 45 days; reductions in stem height, leaf area, number and total dry biomass) were apparent after 67 days. Short periods (31 days) of root restriction had long term (67-99 days) effects on leaf growth. Leaf expansion was more sensitive than leaf biomass accumulation to root restriction. A strong linear relationship, independent of root restriction, was observed between the relative rates of root elongation and leaf expansion. Similar relationships with the relative rates of increase in root number and dry biomass were due to their covariance with root elongation. These data are consistent with the hypothesis that root elongation is functionally linked to leaf expansion via the synthesis of hormones in actively growing root apices.

The influence of partial root restriction on leaf expansion was also examined. One or both halves of a split root system was enclosed in a 30 cm^3 polyethylene cell. Leaf expansion was reduced in plants with only a portion of their total root system physically restricted. Compensatory growth in the unrestricted portion of the root systems resulted in total root growth at final harvest being similar to plants with all their root system unrestricted. Analysis of the relative rate of leaf expansion (R_A) of individual leaves along the stem axis revealed two distinct phases in response to root restriction. In the first phase, apparent about 28 days after treatments were initiated (DAI) and observed in leaves that started expansion 3, 7, and 14 DAI, R_A was reduced in plants with one or both root sub-systems in a restriction cell. The second phase, detected 42 DAI and observed in leaves that started expanding 21 and 28 DAI, was characterised by a higher R_A in plants with a portion of their root system restricted compared to unrestricted plants. Proportionately more assimilate was partitioned to stems of plants with two restricted root sub-systems compared to plants with either a single or non-restricted root sub-system. No differences in leaf water potential or photosynthesis of leaves were observed among treatments.

Conclusions drawn from these data support the involvement of chemical signals in maintaining coordination between root and shoot growth in container-grown plants. These conclusions are discussed with reference to the literature, and a model is proposed to explain root-shoot coordination in terms of root-sourced cytokinin and shoot-sourced auxin. Avenues for future research to test hypotheses arising from this model are identified and discussed, as are possible horticultural ramifications.

Emphasis was placed in the study on improving analytical methodology of growth analysis of whole-plant studies. Experimental precision was increased in these experiments by using cluster analysis to allocate plants to blocks based on leaf area, with a developmental study showing that the mean coefficient of variation of groups formed from cluster analysis was between two and fives times smaller than that of groups formed from visual assessment. A statistical model for non-destructively estimating the leaf area of tomatoes was developed based on the length of the mib-rib of each compound leaf and its position on the stem. Although the model was accurate to within about 2.5% of actual leaf area, it was not stable in time. It was concluded that when non-destructive estimation of tomato leaf area is required, the prediction model must be developed while the main experiment is being conducted. A hybrid method of growth analysis, incorporating both functional and univariate statistical approaches, provided more flexibility and information than standard functional or classical analytical methods. The hybrid method yielded replicated estimates of growth analysis indices, providing opportunity for further evaluation of the derived data using multivariate analytical techniques including path, canonical correlation, and canonical discriminant analysis.

keywords: **allometric relationships, assimilate partitioning, biometrics, Chanter function, cluster analysis, containerised plants, hydroponics, leaf expansion, local error control, plant growth analysis, relative growth rate, Richards function.**

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List of abbreviations

$\bar{E}_A$	mean net assimilation rate ($g_w \cdot m^{-2} \cdot day^{-1}$)
$\bar{R}_W$	mean plant relative growth rate ($g \cdot g^{-1} \cdot day^{-1}$)
ε_{ij}	residual error (of RCB model)
ε_{ja}	among-treatment error
ε_{jw}	within-treatment error
λ_i	*i*th eigenvalue of canonical discriminant function
χ^2_{obs}	observed chi-square value
ψ_W	leaf water potential (MPa)
ACC	1-amino-cyclopropane-1-carboxylic acid
ANCOVA	analysis of covariance
ANOVA	analysis of variance
BA	benzyladenine
CCA	canonical correlation analysis
CDA	canonical discriminant analysis
CDF	canonical discriminant function
$CDF_{1(31)}$	first canonical discriminant function of data at 31 DAI
C_p	Mallows statistic
CR	continuously restricted
CRD	completely randomised design
CV	coefficient of variation
CV_{HT}	coefficient of variation for plant height
CV_{LA}	coefficient of variation for leaf area
DAI	days after initiation (of experiment)
DCR	double cell restricted root system
DFT	Deep Flow Technique (hydroponic system)
E_A	net assimilation rate ($g_w \cdot m^{-2} \cdot day^{-1}$)
g_L	leaf dry weight (g)
g_R	root dry weight (g)
g_{ST}	stem dry weight (g)
g_W	plant dry weight (g)
INDEX	relative leaf position on stem
k	allometric coefficient
LAR	leaf area ratio ($m^2 \cdot g_W^{-1}$)
LIP	leaf insertion position
LNAREA	$\log_e$ leaf area (cm^2)
LNMRIB	$\log_e$ leaf mid-rib (cm)
LPI	leaf plastochron index
LWR	leaf weight ratio

MSE	mean square of error
n	number of observations
NAA	naphthaleneacetic acid
NFT	Nutrient Film Technique
NSC	Non-Split Control
OLS	ordinary least squares
$P_{1(13)}$	first predictor canonical variable of data at 13 DAI
P_{ij}	path coefficient between variables i and j
$R_{1(13)}$	first response canonical variable of data at 13 DAI
R^2	coefficient of multiple determination
R^2_{adj}	adjusted coefficient of determination
R_A	relative leaf expansion rate $(m^2 \cdot m^{-2} \cdot day^{-1})$
R_{av}	mean relative growth rate (over a given period).
RCB	randomised complete block design
RD	restricted-derestricted
RDD	restricted-derestricted-derestricted
$R_{I(RN)}$	relative rate of increase in root number
$R_{I(variable)}$	relative rate of increase of variable (e.g. leaf or root number)
r_{ij}	correlation coefficient between variables i and j
R_L	leaf relative growth rate $(g \cdot g^{-1} \cdot day^{-1})$
RPF	root produced factor
R_R	root relative growth rate $(g \cdot g^{-1} \cdot day^{-1})$
R_{RL}	relative root extension rate $(m \cdot m^{-1} \cdot day^{-1})$
R_S	shoot relative growth rate $(g \cdot g^{-1} \cdot day^{-1})$
RSM	root specific mass $(mg \cdot m^{-1})$
R_{ST}	stem relative growth rate $(g \cdot g^{-1} \cdot day^{-1})$
R_W	plant relative growth rate $(g \cdot g^{-1} \cdot day^{-1})$
RWR	root weight ratio
SCR	single cell restricted root system
SE	standard error of mean
SEOD	standard error of difference between means
SLA	specific leaf area $(m^2 \cdot g_L^{-1})$
SLW	specific leaf weight $(g_L \cdot m^{-2})$
SOC	Split Only Control
SPF	shoot produced factor
SR	shoot:root ratio
SRL	specific root length $(m \cdot g_R^{-1})$
SWR	stem weight ratio
UR	unrestricted (control)

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Fig. 6.4. Leaf area at point of inflexion of L_3, L_7, and L_{14} leaves. Bars are ± SE 235

Fig. 6.5. Expansion ontogeny of leaves commencing development (a) 21 days or (b) 28 days after treatment application. Each point is the mean ± SE from 10-12 plants. *Key:* □:DCR, ▵:SCR, ◇:SOC. 237

Fig. 6.6. Expansion ontogeny of (a) total plant leaf area, (b) leaves present at treatment initiation, leaves commencing expansion (c) 0-20 DAI, and (d) >21 DAI. Each point is the mean ± SE from 10-12 plants. *Key:* □:DCR, ▵:SCR, ○:SOC, ◇:NSC. 245

Fig. 6.7. Relationship between shoot dry weight and root dry weight. Each value is the block mean of 2-3 plants. Y=18.7 + 6.39X, R^2=0.92. *Key:* □:DCR, ▵:SCR, ○:SOC, ◇:NSC 249