

REVIEW PAPER

Contributions of roots and rootstocks to sustainable, intensified crop production

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Abstract

Sustainable intensification is seen as the main route for meeting the world's increasing demands for food and fibre. As demands mount for greater efficiency in the use of resources to achieve this goal, so the focus on roots and rootstocks and their role in acquiring water and nutrients, and overcoming pests and pathogens, is increasing. The purpose of this review is to explore some of the ways in which understanding root systems and their interactions with soils could contribute to the development of more sustainable systems of intensive production. Physical interactions with soil particles limit root growth if soils are dense, but root–soil contact is essential for optimal growth and uptake of water and nutrients. X-ray microtomography demonstrated that maize roots elongated more rapidly with increasing root–soil contact, as long as mechanical impedance was not limiting root elongation, while lupin was less sensitive to changes in root–soil contact. In addition to selecting for root architecture and rhizosphere properties, the growth of many plants in cultivated systems is profoundly affected by selection of an appropriate rootstock. Several mechanisms for scion control by rootstocks have been suggested, but the causal signals are still uncertain and may differ between crop species. Linkage map locations for quantitative trait loci for disease resistance and other traits of interest in rootstock breeding are becoming available. Designing root systems and rootstocks for specific environments is becoming a feasible target.

Key words: Biopores, QTL, resource use, root distribution, rootstock, root–shoot communication, root–soil contact, root systems.

Introduction

The increasing demands for food, fibre, and fuel, coupled with global environmental changes, are placing increasing strains on the ability of ecosystems to deliver all of the goods and services that are required (UK Foresight, 2011). Sustainable intensification will require new ways of thinking about plant husbandry and the development of practices that integrate biological and ecological processes into food, forage, and fibre production

(Pretty, 2008; Powlson *et al.*, 2011; UK Foresight, 2011).

As demands mount for greater efficiency in the use of water, nutrients, and other resources as major contributors to achieving this sustainable intensification (Pretty, 2008; Powlson *et al.*, 2011), so the focus on roots and their role in acquiring resources is increasing (Gregory, 2006a; Lynch, 2007; Gewin, 2010). There are clearly differences in patterns

of growth, architecture, and responses to soil properties between species and within genotypes (O'Toole and Bland, 1987; Gregory, 2006b), and some progress has been achieved in utilizing these differences to practical effect in cropping systems. For example, genotypes of common bean (*Phaseolus vulgaris*) with shallow root architecture have been shown to grow and yield better in soils of low P status than genotypes with deep architecture (Rubio *et al.*, 2001; Ho *et al.*, 2004; Henry *et al.*, 2010). In soybean, too, the most P-efficient genotypes had longer and larger root systems with a greater proportion of the root system in the topsoil (Ao *et al.*, 2010).

There are also opportunities to make greater use of the modifications that roots make to their immediate environment to aid the acquisition of water and nutrients and fend off pathogens (Ryan *et al.*, 2009; Richardson *et al.*, 2011). The rhizosphere is a complex zone of soil both influenced by and influencing roots, and there is increasing evidence of the changed properties of this zone including modification of rhizosphere pH, and the release of compounds that encourage the proliferation of beneficial microorganisms, improve nutrient availability, and protect against some pathogens (Hinsinger *et al.*, 2009; Ryan *et al.*, 2009; Hiltbold *et al.*, 2010; Hawes *et al.*, 2012). Ryan *et al.* (2009) detail some current and future targets for rhizosphere engineering including release of nitrification inhibitors to reduce emissions of N₂O (Subbarao *et al.*, 2009), exudation of organic anions such as malate and citrate to confer some tolerance to aluminium toxicity (Delhaize *et al.*, 2004; Magalhaes *et al.*, 2007), and release of enzymes such as phosphatases to enhance the availability of soil phosphorus (George *et al.*, 2007; Richardson *et al.*, 2011). Many plants exude phosphatase enzymes from their roots naturally and this can be associated with depletion of soil organic phosphorus (e.g. George *et al.*, 2002). Achieving greater hydrolysis of such organic P by plants could be beneficial on many soils (Richardson *et al.*, 2011).

Plant roots also have substantial effects on soil physical properties, ranging from localized increases in bulk density resulting from root expansion (Greacen *et al.*, 1968; Braunack and Freebairn, 1988; Young, 1998) to structure formation as a consequence of mucilage production, root hair formation, and localized wetting and drying (McCully, 1999; Hinsinger *et al.*, 2009; Bengough, 2012a). There is substantial potential for traits of the root tip region to be exploited to overcome soil mechanical impedance, soil water stress, and cell wall constraints to expansion (Acuna *et al.*, 2007; Bengough *et al.*, 2011; Leach *et al.*, 2011). Root tip traits beneficial to root penetration include those that decrease cavity expansion pressure (e.g. narrowly pointed root tips favour cylindrical deformation; Greacen *et al.*, 1968), frictional resistance (e.g. the lubrication action of mucilage and border cells; Vollsnes *et al.*, 2010), and axial cell wall tension (e.g. by softening of cell walls in the axial direction). Anchorage of the root tip so that the root can extend into new soil may also be a useful trait and an important physical function of root hairs facilitating the re-entry of a root from a macropore to the bulk soil, or into a compacted layer from a loose seedbed (Bengough *et al.*, 2011). Managing the physical properties

of the rhizosphere to stabilize soils, improve soil structure, and enable plants to access deep soil water are all attainable and desirable possibilities (Whalley *et al.*, 2006; Acuna *et al.*, 2007; Hinsinger *et al.*, 2009).

In addition to selecting for root architecture and rhizosphere properties, the growth of many plants in cultivated systems is profoundly affected by selection of an appropriate rootstock. Many fruit trees, grapevines, and fruits such as peppers, tomatoes, and aubergines are grown with scions grafted onto rootstocks that confer resistance to various pathogens and tolerance to salinity, regulate the size of the scion, and contribute to fruit quality. For example, the Malling rootstocks (M9, M27, etc.) confer resistance to woolly aphid on the scion and produce a range of tree sizes (Hatton, 1935; Preston, 1966). Rootstock selection offers a powerful tool for the sustainable intensification of fruit production because while the scion genotype can be used to select fruit properties, adaptation to water deficit and high salinity, tolerance of alkaline soils, and susceptibility to pathogens [e.g. fireblight (FB) in apple] can all be influenced by the choice of rootstock (Jensen *et al.*, 2012; Marguerit *et al.*, 2012; Tamura, 2012).

The purpose of this review is to explore some of the ways in which understanding root systems and rootstocks and their interactions with soils could contribute to the development of more sustainable systems of intensive production. The three topics examined are: (i) physical contact between the root and soil; (ii) the use of rootstocks and root–shoot communication; and (iii) ‘designer’ root systems for sustainable intensified production.

Root–soil contact and root elongation

Importance and methods of assessment

Soil physical conditions have large effects on both the ease with which roots can extend through soils and the transfer of water, gases, and nutrients to and from the root. The mechanisms underlying such root responses are complex, but have been deduced in a series of controlled experiments and field studies (e.g. van Noordwijk *et al.*, 1992). Studies on the effects of root–soil contact using thin sections showed that water and nutrient uptake per unit root length decreased with decreasing root–soil contact (Kooistra *et al.*, 1992; Veen *et al.*, 1992). Kooistra *et al.* (1992) compacted sieved soil to bulk densities of 1.50, 1.43, and 1.08 Mg m⁻³ and used photographic prints of thin sections of soil to determine root–soil contact of maize roots. Root–soil contact increased from 60% to 87% with increasing bulk density. Similarly, Veen *et al.* (1992) grew maize in a sandy loam soil compacted to five bulk densities (1.54, 1.50, 1.43, 1.32, and 1.08 Mg m⁻³), corresponding to a range of soil porosity from 42.3% to 59.6%, at soil matric potentials between –10 kPa and –20 kPa. While root length decreased as bulk density increased, they found that water and nitrate uptake per unit root length after a growth period of 29 d decreased by 20–60% with decreasing bulk density and decreasing root–soil contact.

However, while porosity *per se* is important, the size of pores constituting the porosity also affects root growth and

activity. Large pores are not good for root growth, with roots preferring a network of narrow pores (e.g. White and Kirkegaard, 2010). For example, Stirzaker *et al.* (1996) found that barley plants grew better in compacted soil (bulk density 1.78 Mg m^{-3}) with narrow biopores made by lucerne or ryegrass roots than in compacted soil with wider pores made by canola or clover roots, or artificially with a wire of 3.2 mm in diameter. The dry weight of barley shoots grown in soils with narrow biopores was up to 96% of that of plants grown under optimal soil conditions (bulk density 1.37 Mg m^{-3}). Root responses to soil pore size and geometry depend on the way that forces are applied to the individual root tip, with recent evidence suggesting that roots are more sensitive to axial than to radial pressures (Bengough, 2012; Kolb *et al.*, 2012).

A penetrometer resistance of 2 MPa is typically adopted as an indicator of soil in which mechanical impedance is likely to be a major impediment to root elongation (Taylor and Ratliff, 1969; Bengough *et al.*, 2011). However, a recent study of UK topsoils cultivated for crops has indicated that strength in many soils exceeds 2 MPa even when water is readily available for uptake (Bengough *et al.*, 2011). In a wider range of 59 soils, penetrometer resistance was typically between 1 MPa and 3 MPa despite their moist condition, with root elongation of barley seedlings typically <50% of that in repacked soils (Valentine *et al.*, 2012). In field soils, seedling root elongation rate was most closely related to the volume of pores in the size range 60–300 μm (as estimated from water-release characteristics), and accounted for almost two-thirds of the variation in elongation rates. Two possible explanations were

offered for this result: (i) that roots take advantage of the low resistance in larger pores; or (ii) that root elongation is limited by hypoxia (and associated higher CO_2 partial pressure), as smaller pores may have been water filled. These findings agree with those of Stirzaker *et al.* (1996) who found that pores formed by plants can improve growth conditions in hard soils, but large pores are less advantageous than intermediate pores.

The determination of root–soil contact is very difficult because of the opaque nature of soils and the wide range of pore and particle sizes. Thin sections and 3D microtomographs allow visualization of the rhizosphere, but poor contrast between roots and soil makes it difficult to determine root–soil contact (van Noordwijk *et al.*, 1992). Schmidt *et al.* (2012) developed a non-invasive method to determine root–soil contact from 3D volumetric images with an accuracy of $\pm 3\%$. Root–soil contact was determined for young maize and lupin seedlings grown in loosely packed soil ($<1 \text{ Mg m}^{-3}$) sieved to different aggregate fractions (4–2, 2–1, 1–0.5, and $<0.5 \text{ mm}$) and wetted to a matric potential of -0.03 MPa . Root–soil contact decreased with increasing aggregate size (Fig. 1). Such contact appears to be beneficial as long as soil strength or matric potential do not limit root elongation. Maize grown for 4 d after germination in these soil conditions showed that roots elongated faster with increasing root–soil contact, as long as mechanical impedance was not limiting root elongation (Fig. 2), while lupin was less sensitive towards changes in root–soil contact. Closer root–soil contact probably allowed faster uptake of both water and nutrients (Veen *et al.*, 1992). However, under dry conditions (matric potential -1.6 MPa), preliminary experiments showed no significant

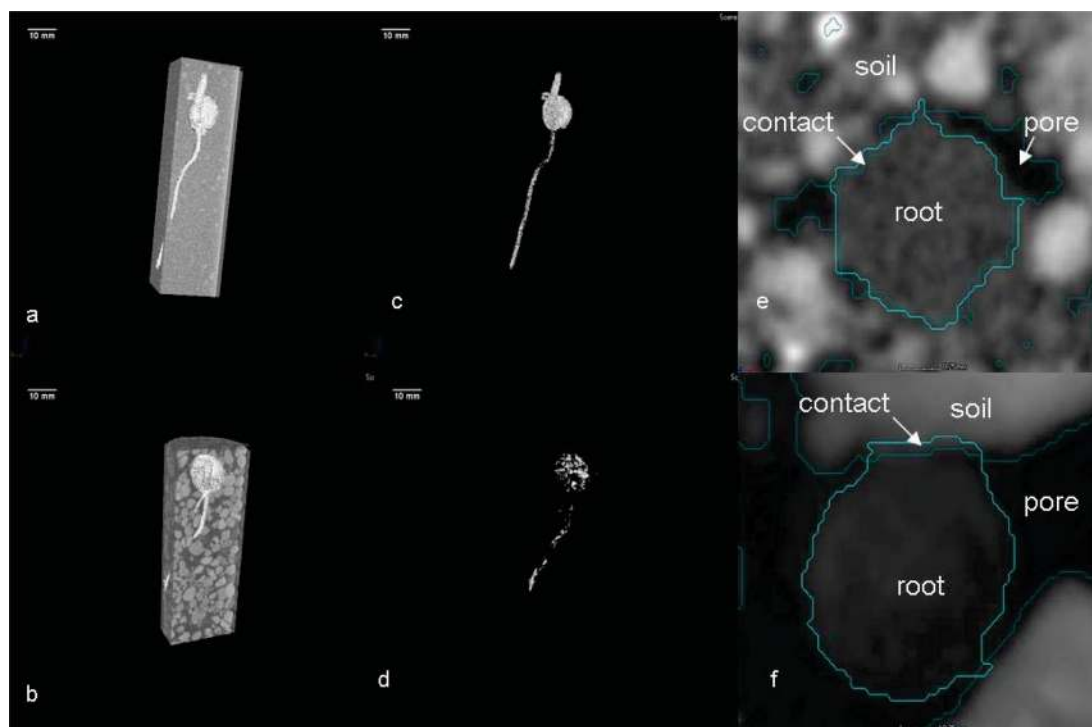


Fig. 1. A 3D segmented image of a maize seedling grown in soil aggregates of $<0.5 \text{ mm}$ diameter (a) and $4\text{--}2 \text{ mm}$ diameter (b), and the corresponding contact segmented out in 3D for $<0.5 \text{ mm}$ diameter aggregates (c) and $4\text{--}2 \text{ mm}$ diameter aggregates (d). e and f are close-up views (2D) of maize roots in contact with soil sieved to $<0.5 \text{ mm}$ and $4\text{--}2 \text{ mm}$, respectively.

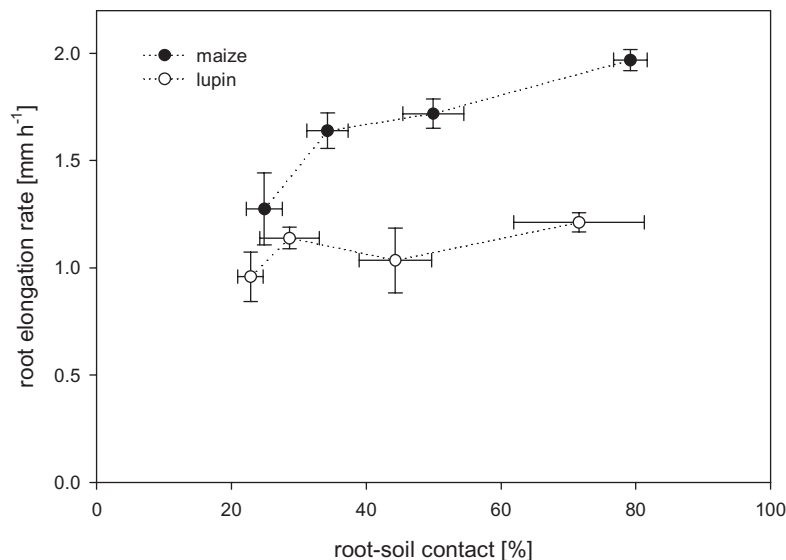


Fig. 2. Root elongation rate as a function of root–soil contact for maize and lupin seedlings grown in aggregate sizes of 4–2, 2–1, 1–0.5, and <0.5 mm at a matric potential of -0.03 MPa. Mechanical impedance was unlikely to be limiting root elongation, as the soil was loosely packed. Data of root–soil contact were derived from samples different from those of root elongation rates. The error bars show standard errors.

differences between root elongation rates in loose soil and vermiculite.

In dry soils, loss of contact at the root–soil interface may sometimes be advantageous in reducing the rate of water loss. Carminati *et al.* (2009) used X-ray tomography to show that the pore space around lupin roots increased in drying soil and therefore the roots lost contact with the surrounding soil. If the soil is approaching wilting point, such loss of contact may be advantageous for the plant, preventing water loss from the plant into the surrounding dry soil. Passioura (1988) suggested that the extent of any such root shrinkage will depend on the nature and location of the hydraulic resistances in the plant–soil system.

Field-based observations

There is a large literature on the need for ‘firm’ seedbeds to aid the establishment of seedlings. For example, Atkinson *et al.* (2009) investigated establishment of wheat (*Triticum aestivum*) under different management practices (ploughing or discing with rolling and/or power harrowing) and measured soil physical properties (shear strength, penetrometer resistance, bulk density, and water content) weekly from August to November. Soil structural data, such as porosity and average pore size of the sample, were obtained from thin sections. Discing increased the soil mesoporosity, but crop establishment was decreased. Overall, they found that crop establishment was significantly hampered when soil mesoporosity was >17–20%, and concluded that poor seed–soil contact was the cause. Schoonderbeek and Shoute (1994) used images from soil thin sections (Kooistra *et al.*, 1992) to determine the effects of farm management (conventional and integrated) on root–soil contact of wheat and macroporosity (>30 μm). Macroporosity was greater and root–soil

contact lower in soil in the integrated management system than in the soil managed conventionally. They also found greater root length densities in conventionally managed soil compared with those in the integrated system, and concluded that plants in soil with high macroporosity developed fewer, thinner, and shorter roots than in soils with lower macroporosity.

White and Kirkegaard (2010) used a core-break technique to investigate the abundance, spatial distribution, and root–soil contact of wheat roots at maturity growing in pores in a red Kandosol, a very hard soil in New South Wales with penetrometer resistances of between 3 MPa and 7.4 MPa. They found that 20% of the pores in the subsoil and 5% in the topsoil contained roots. In the upper 0.6 m of the soil profile, 30–40% of roots were clumped in pores and cracks, but in the subsoil this increased to 85–100%. These clumped roots had numerous root hairs that contacted the soil, whereas in cracks, root–soil contact was achieved by the root being pressed to the soil and root hairs were absent. They concluded that water from such subsoils might best be improved by targeting strategies to utilize pores (e.g. rapid growth and branching) rather than penetration of the hard soil matrix.

In addition to the physical effects of root–soil contact, there are also chemical effects. In soils that are deficient in manganese, rolling seedbeds can increase yields. For example, Passioura and Leeper (1963) grew two oat varieties, Algerian (sensitive towards manganese deficiency) and Palestine (tolerant towards manganese deficiency), in Mn-deficient soil and showed that grain yields were up to 98% lower when grown in loose soil (bulk density 1.2 Mg m^{-3}) compared with denser soil (bulk density 1.5 Mg m^{-3}). The better root–soil contact in the more compact soil led to better access for roots to the immobile manganese.

Root–shoot communication in rootstocks

Empirically, the influence of roots on shoot behaviour can be measured and described, but there is not a clear understanding of the mechanisms by which this occurs. The composite fruit tree (clonal rootstock and grafted scion) has been used for many years as an experimental system to understand how root–shoot communication occurs. The most obvious influence is the ability of some *Malus* rootstocks, which generally lack vegetative vigour and produce little root biomass relative to more invigorating rootstocks, to cause scion dwarfing. This and many other phenotypic features, apparent in selected rootstocks, subsequently influences the behaviour of the grafted scion, through changes in precocity, flowering date, flower number, leaf and fruit nutrition, and fruit size (Hatton, 1935; Preston, 1966; Tubbs, 1973a, b). In practice, this descriptive knowledge enables choices to be made about which intensive *Malus* cropping systems are best able to cope with local abiotic and biotic challenges. However, to maximize fruit yields in future requires a mechanistic understanding of the control of scion behaviour by rootstocks. This control has been attributed to a wide range of potential mechanisms, ranging from hydraulic to multiple chemical signals (Table 1).

Hydraulic signals

The ways in which apple rootstocks influence the vegetative growth of grafted shoots (scions) are not known despite many investigations spanning eight decades (Beakbane, 1956; Tubbs, 1973a, b; Lockard and Schneider, 1981; Jones, 1974, 1984, 1986; Soumelidou *et al.*, 1994a, b; Atkinson *et al.*, 2003). Early studies centred on the ability of rootstocks to supply sufficient water to satisfy scion demand (Knight, 1926). Dwarfing rootstocks have a low xylem to phloem ratio, while the opposite is true for root systems that promote shoot growth (Beakbane and Thompson, 1947). Accordingly, a scion grafted onto a rootstock with a limited capacity for water uptake would operate under a continual mild water deficit that may limit shoot growth (Tubbs, 1973a, b; Olien and Lasko, 1984, 1986; Cohen and Naor, 2002).

A composite tree (rootstock and scion) necessarily includes a graft union; generally swelling of the stem above and below the union increases with the dwarfing potential of the rootstock. Xylem vessels within the union can be convoluted and run at different angles to the main axis of the tree (Simons, 1986; Soumelidou *et al.*, 1994b). Warne and Raby (1938) proposed that the graft union of an M.9 composite tree imposed

Table 1. Potential mechanisms leading to the control of scion growth by rootstocks.

Dwarfing mechanism	Signal	Species (perennials)	References
Hydraulic signalling	Axial resistance imposed by graft union	<i>Malus pumila</i>	Warne and Raby (1938); Beakbane (1956); Tubbs (1973a, b); Olien and Lasko (1984)
	Lower root LP	<i>Malus pumila</i> , <i>Prunus persica</i>	Olien and Lasko (1984); Atkinson <i>et al.</i> (2003); Nardini <i>et al.</i> (2006); Richards <i>et al.</i> (1986); Solari and DeJong (2006); Tombesi <i>et al.</i> (2010); Marguerit <i>et al.</i> (2012)
Rootstock-/interstem-sourced chemical signalling	Gibberellins	<i>Malus pumila</i> , <i>Pyrus</i> , <i>Prunus salicina</i>	Jones and Lacey (1968); Ibrahim and Dana (1971); Robitaille and Carlson (1976); Bulley <i>et al.</i> (2005); van Hooijdonk <i>et al.</i> (2010, 2011); El-Sharkawy <i>et al.</i> (2012)
	Cytokinins	<i>Malus pumila</i> , <i>Prunus persica</i>	Kamboj <i>et al.</i> (1999b); Sorce <i>et al.</i> (2002, 2007)
	Abscisic acid	<i>Malus pumila</i>	Yadava and Dayton, (1972); Kamboj <i>et al.</i> , (1999a)
	Indoleacetic acid	<i>Prunus persica</i>	Sorce <i>et al.</i> (2002, 2007)
	ACC/ethylene	–	–
	Brassinosteroids	–	–
	siRNA	–	–
Ions, pH	<i>Malus pumila</i> , <i>Prunus avium</i>	Bukovac <i>et al.</i> (1958); Atkinson and Else (2001); Jimenez <i>et al.</i> (2004, 2007); Fallahi <i>et al.</i> (2002); Ebel <i>et al.</i> (2000)	
Sequestration in rootstock shank, graft union	NO ₃ , Ca, IAA, cytokinins	<i>Malus pumila</i>	Jones (1974, 1984); Simons and Chu (1984); Simons (1986)
Metabolism in root, shank, graft union, interstock or shoot	Gibberellins	<i>Malus pumila</i> , <i>Prunus salicina</i>	Richards <i>et al.</i> (1986); El-Sharkawy <i>et al.</i> (2012)
Shoot-sourced chemical signalling	Polar IAA transport impeded in rootstock shank	<i>Malus pumila</i>	Soumelidou <i>et al.</i> (1994b); Kamboj <i>et al.</i> (1997)
	Abscisic acid	<i>Malus pumila</i>	Kamboj <i>et al.</i> (1997)
	Unidentified inhibitor	<i>Prunus avium</i> × <i>Prunus pseudocerasus</i>	Jones and Quinlan (1981); Webster (2004)

an axial resistance to sap flow that restricted water availability to the scion. Greater hydraulic resistances in the larger graft unions associated with more dwarfing rootstocks may increase the severity of shoot water deficits and reduce scion vigour further (but see [Atkinson *et al.*, 2003](#)).

In experiments to determine whether hydraulic resistances contribute to the contrasting growth-controlling capacities of M.9 (dwarfing) and MM.106 (semi-invigorating) rootstocks, 3-year-old rootstocks were grafted with Queen Cox scions. Xylem sap was collected by placing root systems of whole potted trees inside specially designed split-lid pressure chambers. A series of decreasing pneumatic pressures was applied to the roots to generate a range of sap flow rates that encompassed those of whole tree transpiration. Sap was collected above and below the graft union to collect the expelled sap along with sap exuding osmotically from unpressurized, detopped roots.

After removal of the scion above the graft union, sap flow rates decreased linearly with decreasing applied pressure until 0.4 MPa. At this and lower pressures, the response of sap flow to applied pressure was not linear; similar responses occurred when sap was collected below the graft union ([Fig. 3](#)). Since sap flow was a function of applied pressure, the linear portions of these curves provide an estimate of root hydraulic conductance (L_p) over the range of flow rates in intact trees. Slopes of the linear parts of the pressure–flow curves were calculated for each tree, above and below the graft union, and were averaged within rootstocks. The L_p calculated below the graft union represents the hydraulic conductance of the rootstock; MM.106 had a greater L_p than M.9 ([Table 2](#)). The L_p calculated above the graft union represents the hydraulic conductance of the rootstock and the graft union combined (i.e. in series). Values of L_p were not statistically different above and below the graft union in either rootstock ([Table 2](#)) but, when the size of the root systems was taken into account, the hydraulic conductance per unit dry weight of root was nearly 2-fold greater in M.9 than in MM.106 rootstocks ([Table 2](#)).

The more swollen graft union in M.9 composite trees did not impose a greater axial resistance to water flow than the smaller union in MM.106 composite trees (see also [Atkinson *et al.*, 2003](#)). These data imply a lower conductance per unit cross-sectional area in the larger diameter unions of M.9. Overgrowth of the graft union may be a compensatory mechanism to overcome these hydraulic limitations ([Atkinson *et al.*, 2003](#)). The negligible hydraulic resistance imposed by the M.9 graft union (see also [Gur and Blum, 1975](#)) contrasts with earlier reports (e.g. [Knight, 1926](#); [Warne and Raby, 1938](#)). This disparity may result from the different methods used to calculate hydraulic conductance. The present measurements were made at flow rates comparable with those occurring in transpiring trees, as were those by [Gur and Blum \(1975\)](#). All previous reports used excised pieces of stem tissue, and sap flow was induced experimentally by the application of positive or negative pressures. Such flows must have rarely amounted to more than 5% of the transpirational flow rates expected in composite trees, so it is unclear to what extent the results represent natural conditions in intact trees (but see [Atkinson *et al.*, 2003](#)).

These estimates of xylem hydrostatic potential measured in leaves upstream of the graft unions were similar in scions grafted onto M.9 and MM.106 rootstocks. Furthermore, calculated values of leaf area per unit root hydraulic conductance were similar in both rootstocks (data not shown). These findings suggest that scions grafted on to dwarfing M.9 rootstocks do not suffer from mild water deficits compared with those on MM.106, a factor previously implicated in the capacity of M.9 to reduce scion vigour ([Tubbs, 1973a, b](#); [Olien and Lasko, 1984, 1986](#)). These experiments suggest that the contribution of hydraulic functional capacity to the growth-controlling capacities of M.9 and MM.106 rootstocks was negligible.

Rootstock-sourced chemical signals

The ways in which rootstocks confer their growth-controlling effects are almost certainly via altered root-to-shoot and shoot-to-root chemical signalling, and there are several hypotheses about the causal signals ([Table 1](#)). A differential

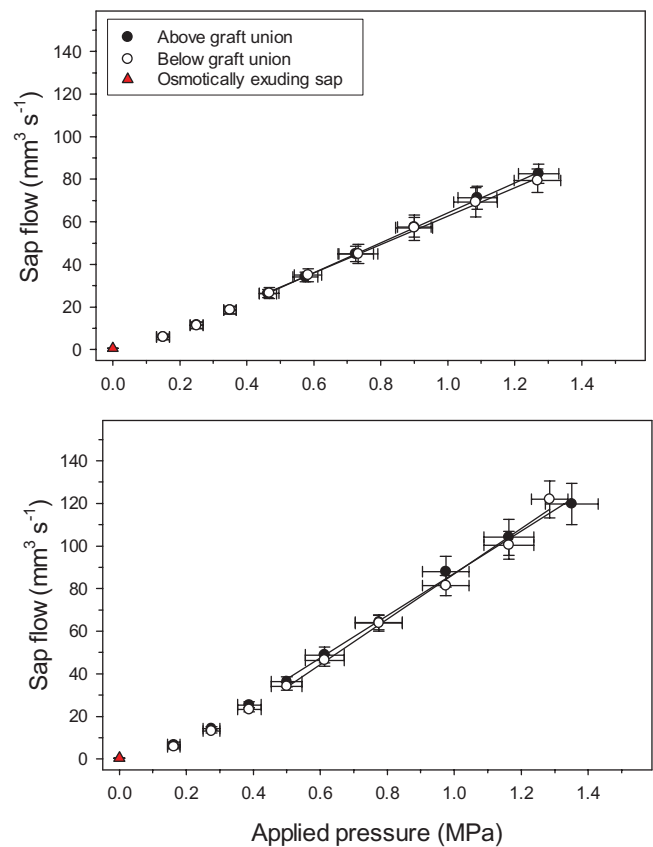


Fig. 3. Flow rates of xylem sap collected above and below the graft union and from detopped roots of (A) M.9 and (B) MM.106 rootstocks. The increase in sap flow in response to applied pressures was linear above 0.4 MPa applied pressure in both rootstocks. Regression analysis of these points was used to determine the values of the slopes of the relationships between applied pressure and sap flow rate, and hence the hydraulic conductances of the rootstocks ([Table 2](#)). Results are means of eight replicates with associated standard errors.

Table 2. Hydraulic conductances of M.9 and MM.106 rootstocks derived from sap flow rates above and below the graft union. Flow rates were varied by applying a series of pressures (0.05–1.4 MPa) to detopped root systems in split-top pressure chambers. Values of L_p were calculated from regression analyses of the linear portions of pressure versus flow curves.

Rootstock	Above graft union		Below graft union	
	(mm ³ MPa s ⁻¹)	(mm ³ g ⁻¹ MPa s ⁻¹)	(mm ³ MPa s ⁻¹)	(mm ³ g ⁻¹ MPa s ⁻¹)
M.9	69.1	0.69	67.6	0.67
MM.106	103.8	0.34	99.2	0.33
LSD ($P < 0.05$)	34.45	0.14	32.38	0.14

ANOVA was used to analyse differences between slopes [degrees of freedom = 12 (M.9) and 14 (MM.106)] The effect of the graft union on L_p was not statistically different in either rootstock (LSDs not shown).

ability to synthesize or metabolize endogenous plant hormones has been implicated in the ‘dwarfing effect’ (Jones, 1974, 1984, 1986; Lockard and Schneider, 1981; Soumelidou *et al.*, 1994a, b; Atkinson and Else, 2001; Sorce *et al.*, 2002, 2007; van Hooijdonk *et al.*, 2011; El-Sharkawy *et al.*, 2012). The idea that a dwarfing rootstock reduces concentrations of growth-promoting hormones [e.g. auxin, gibberellins (GAs), and cytokinins] and/or increases concentrations of growth-inhibiting hormones [e.g. abscisic acid (ABA) and ethylene] at the active sites for shoot growth in the composite trees has been tested many times, but definitive evidence for the hormonal control of scion vigour is still lacking.

For example, the intensity of the putative signal may differ from extremely dwarfing and very invigorating rootstocks, but can be similar from semi-dwarfing and semi-invigorating rootstocks, despite a marked difference in tree stature (e.g. van Hooijdonk *et al.*, 2011). This is due, in part, to the difficulties of extrapolating hormone concentrations measured in slowly flowing, osmotically exuding sap to hormone deliveries into canopies of intact, transpiring, composite trees. To determine accurately the passage of signals from roots to shoots in the transpiration stream, information on both the concentration and the delivery rate of putative signals is needed (Else *et al.*, 1995).

ABA concentrations are higher in the tissues of the more dwarfing rootstocks (Yadava and Dayton, 1972; Kamboj *et al.*, 1999a). ABA is generally considered to be a potent growth inhibitor (but see Sharp *et al.*, 2000) and has been shown to limit extension growth by suppressing the accumulation of GA₁ (Benschop *et al.*, 2005), but whether rootstock-sourced ABA and scion-derived GAs interact to regulate shoot extension in grafted scions is not yet known.

It will also be important to elucidate the role of the graft union on the intensity of root- and shoot-sourced hydraulic and chemical signalling. Repeated measurements of xylem sap constituents over the entire growing season (van Hooijdonk *et al.*, 2011) using an untargeted metabolomics approach would yield valuable information on altered signalling from dwarfing rootstocks. This approach is likely to be more fruitful than measuring tissue concentrations of key hormones since these do not often correlate with measured differences in vigour (see Pearce *et al.*, 2004). Recent advances in next-generation sequencing now provide the opportunity to link changes in the transcriptome to those

in the metabolome of composite trees, and this multidisciplinary approach should provide new insights into the mechanistic basis of the dwarfing response. Work utilizing hormone mutants as rootstocks in horticultural crops such as tomato (see Aloni *et al.*, 2010; Ghanem *et al.*, 2011) will also help to elucidate the nature of dwarfing signals, although the molecular mechanisms underpinning dwarfing may differ between species as well as between annuals and perennials. For example, the molecular mechanisms modulating dwarfing in apple appear to be different from those in pear, although both are controlled by a major gene (Pilcher *et al.*, 2008; Wang *et al.*, 2011). No published study has yet identified the mechanism by which dwarfing is conferred, though there are tantalizing hints that dwarfing (as in many other species) can be conferred by disruption of GA regulation via DELLA-mediated regulation of growth responses (Zhu *et al.*, 2008). Furthermore, levels of GA have been shown to differ in ungrafted rootstocks (Yadava and Lockard, 1977). In *Arabidopsis*, DELLAs have been shown to be transported in the phloem, but DELLA homologues in apple are located on linkage groups different from those known to confer dwarfing, ruling out DELLA as the primary locus conferring dwarfing (Haywood *et al.*, 2005; Huang and Yu, 2009). Despite the lack of molecular information, there are still usable markers for dwarfing in apple and pear, and these should prove useful in future breeding programmes for dwarfing *Malus* and *Pyrus* rootstocks.

Genetic control of pest and disease resistance in rootstocks

Rootstocks greatly influence overall plant health so that resistance/tolerance to a range of pests and diseases are important selection criteria in rootstock development of both annual and perennial crops. For example, root-knot nematode (*Meloidogyne* spp.) resistance is of interest in tomato (Medina-Filho and Stevens, 1980) and also in stone fruit (Esmenjaud *et al.*, 1997), and molecular markers have been identified to aid pre-selection in both genera (Williamson *et al.*, 1994; Claverie *et al.*, 2004). The importance of pest- and disease-resistant rootstocks is particularly important where the productive cropping period may be several decades

long, as is often the case in temperate tree fruit crops. In the case of apple, rootstocks suffer from a number of specific soil-borne diseases such as collar/crown rot caused by *Phytophthora cactorum* and replant disease, as well as others that affect the scion such as FB (*Erwinia amylovora*). Woolly apple aphid (WAA) is a pest of the scion and the rootstock but it is most damaging to the latter, in particular in the southern hemisphere. Thus, some pests and diseases have long been the focus of breeding programmes (see, for example, Crane *et al.*, 1936) and are still the focus of intensive study. Two case studies for apple follow, for which some level of molecular detail is available.

Fireblight resistance (*Erwinia amylovora*)

Resistance to FB is also desirable in a rootstock, as infection can occur in both scion and rootstock, and the tree can be killed by girdling of the rootstock by the pathogen (Norelli *et al.*, 2003). The most common source of FB resistance has been a cultivar *Malus* × *robusta* cv Robusta 5 (henceforth R5), a hybrid of *Malus baccata* and *Malus prunifolia* (Norelli *et al.*, 1986). R5 was identified as highly resistant to the predominant FB strain and has been used as a parent in most rootstock breeding programmes including EMR and Geneva (NY). The resistance is of a quantitative nature, and a major associated quantitative trait locus (QTL) has been mapped to linkage group (LG) 3 (Peil *et al.*, 2007) explaining >65% of the variance associated with FB resistance from R5. Inoculation with strains known to differ in their pathogenicity on R5 revealed that there were in fact two QTLs present on LG3, and a further QTL on LG7 (Gardiner *et al.*, 2012). Candidate genes underlying LG3 include a resistance gene of the LRR (leucine-rich repeat) family of receptor-like proteins (RLPs), implicated in resistance in many other species (Gardiner *et al.*, 2012), and a peroxidase gene (MxdPrx8) that is differentially regulated between the susceptible rootstock ‘M.26’ and the resistant ‘G.41’. In the resistant rootstock, this gene is rapidly down-regulated in response to FB infection, while it is oppositely regulated in the susceptible genotype. Class three peroxidases, such as MxdPrx8, are implicated in defence responses in model systems, though it is still unclear exactly what role these genes have in resistance to FB in *Malus* sp. (Triplett *et al.*, 2009). As noted previously, R5 is susceptible to minor strains of FB (Norelli *et al.*, 1986) which could become more prevalent as cultivars carrying R5-derived resistance are increasingly abundant. Therefore, breeders have aimed to introduce FB resistance from other sources including the ornamental apple cultivar ‘Evereste’. A major QTL, Fb_E, explaining 50–70% of the phenotypic variation in a progeny from a cross between ‘M.M.106’ and ‘Evereste’ was mapped to LG12 by Durel *et al.* (2009). Subsequently, Parravicini *et al.* (2001) identified nucleotide-binding site (NBS)-LRR and serine/threonine kinase genes in this area as candidate genes for the trait.

Durel *et al.* (2009) also identified a separate QTL explaining ~40% of the variation of FB resistance derived from ‘*M. floribunda* 821’ in the distal part of LG12.

Woolly apple aphid (*Eriosoma lanigerum*)

The WAA is a major pest of apples, forming galls on roots and branches, generally reducing tree vigour, shoot extension, and yield, and increasing susceptibility to disease (Klimstra and Rock, 1985; Brown *et al.*, 1995). Rootstocks such as ‘M.793’ (John Innes) and the Malling-Merton series (e.g. M.M.106) were developed to incorporate resistance into WAA ‘Northern Spy’, while in later rootstocks *Malus baccata* and *Malus sieboldii* have proved useful donors of major gene resistance (Crane *et al.*, 1936; Bus *et al.*, 2008). The resistance genes denoted as *Er1–Er4* have been mapped to LG7 (*Er4*; Bus *et al.*, 2010 from ‘Mildew Immune Selection’), LG8 (*Er1* from ‘Northern Spy’ and *Er3* from *M. sieboldii*), and LG17 (*Er2* derived from *M. robusta* 5; Bus *et al.*, 2008). As in the case of FB, WAA resistance is known to have broken down in some areas to all three major gene resistance types; however, pyramiding of markers, coupled with the identification of new resistance from wild *Malus* species, as well as the pyramiding of minor race resistance genes should prove effective for future resistance breeding (Bus *et al.*, 2008).

Linkage map locations for these and other traits of interest in rootstock breeding are presented schematically in Fig. 4 using the simple sequence repeat (SSR) and single nucleotide polymorphism (SNP) map of Antanaviciute *et al.* (2012) to estimate the position of genes and QTLs published in various apple populations.

‘Designer’ root systems for sustainable intensified production

With the global demands for food and fibre increasing, and the realization that this increase will largely be achieved by increasing yields (Godfray *et al.*, 2010; UK Foresight, 2011), the role of roots and rootstocks in accessing resources efficiently and contributing to yield has received increasing prominence (Lynch, 2007; Gewin, 2010). There are many potential targets for such approaches utilizing a wide variety of root traits including basal-root gravitropism (Ho *et al.*, 2004; Lynch, 2007; Ao *et al.*, 2010), the presence of root hairs (Gahoonia *et al.*, 2001; Brown *et al.*, 2012), cortical aerenchyma (Lynch, 2007), and greater branching at depth (Wasson *et al.*, 2012). The choice of rootstock is also achieving greater prominence as horticultural production intensifies and the demand for fruits and vegetables increases.

For rootstocks of fruit trees, current breeding objectives include effective vigour control (most desirable are dwarfing to semi-vigorous, depending on the orchard management system and environmental stresses), optimal fruit size and yield efficiency, good anchorage, resistance to pests and diseases [especially WWA (*E. lanigerum*), FB (*E. amylovora*), crown rot (*P. cactorum*)], and replant disease. The effects of different rootstocks on marketable yields in a range of fruit (e.g. apple, apricot, peach, grape, tomato, cucumber, and melon) crops are well documented, but it has only recently been recognized that rootstock genotype can alter specific aspects of post-harvest fruit quality of a scion (Goncalves *et al.*, 2006). The

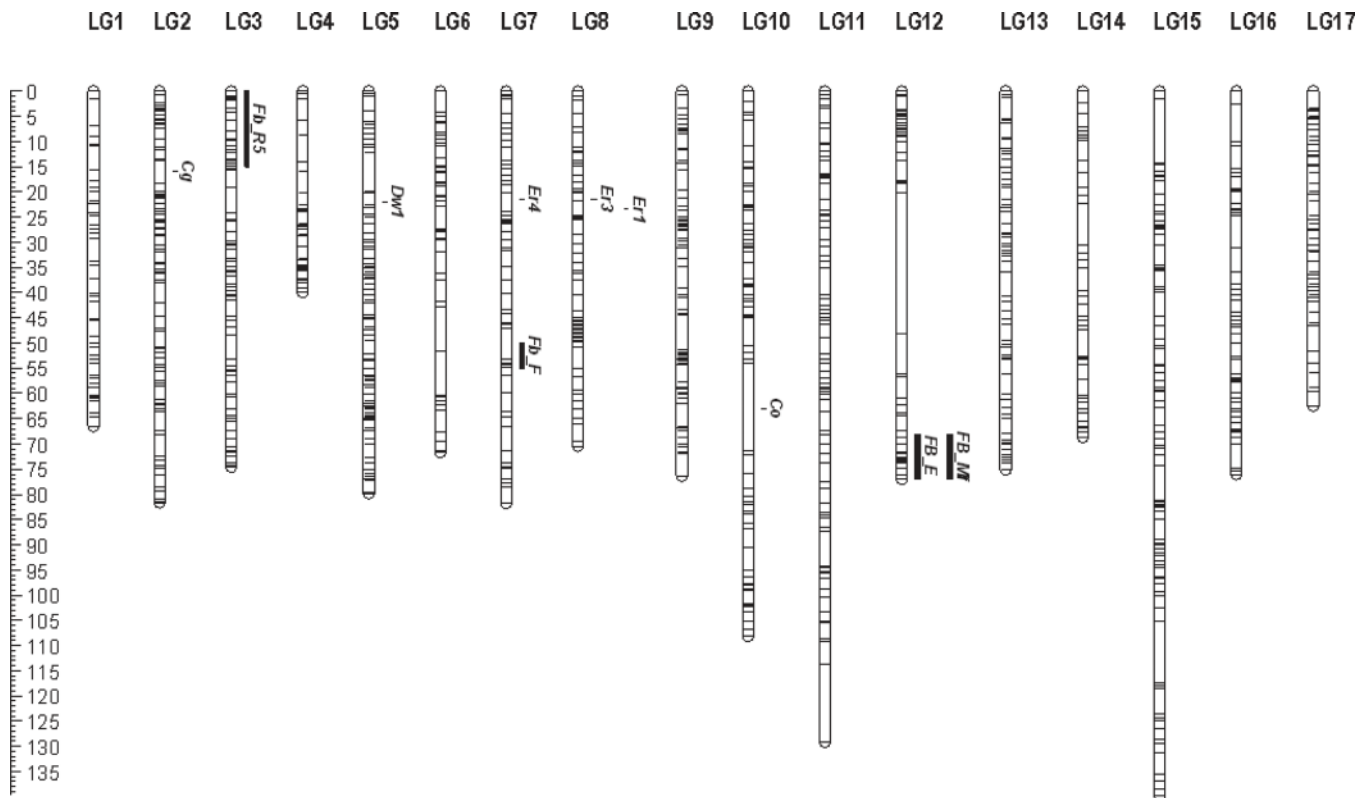


Fig. 4. Schematic linkage map of apple using SNP and SSR marker data as in [Antanaviciute et al. \(2012\)](#) with the scale in centiMorgans (cM) given on the left. Genes and QTL positions were estimated from linkage information provided by [Moriya et al. \(2010\)](#) for grown gall resistance (*Cg*), by [Rusholme-Pilcher et al. \(2008\)](#) for dwarfing (*Dw1*), by [Bai et al. \(2012\)](#) for columnar growth habit (*Co*), by [Bus et al. \(2008, 2010\)](#) for woolly apple aphid resistance (*Er1-4*) and, for fireblight resistance, by [Peil et al. \(2007; Fb_R5\)](#), [Khan et al. \(2007; Fb_F\)](#), and [Durel et al. \(2009; Fb_E and Fb_Mf\)](#).

matching of rootstocks to scions to deliver fruit of a specified nutritional quality is a likely productive area of future research. Rootstock control of other quality traits (e.g. flavour volatile production, susceptibility to pathogens during storage) has not yet been investigated but could contribute to food security by improving nutrition and reducing waste.

More effective utilization of the mechanisms underlying root–shoot and shoot–root communication also offer opportunities to increase yields and fruit quality. In wheat, the *Rht-B1b* and *Rht-D1b* alleles used widely in semi-dwarf genotypes reduce the response to GAs via dominant gain-of-function mutations in DELLA genes. [Wojciechowski et al. \(2009\)](#) demonstrated a direct effect of these dwarfing alleles on root growth during seedling establishment, rather than a secondary partitioning effect. Shortening of internodes, rather than a reduction in the number of nodes per shoot, has been well characterized in cereals ([Peng et al., 1999](#)), but the genes regulating precocity and scion growth in dwarfing apple and other crops are not yet known, although they must be a priority if intensified production systems are to be developed. [Pilcher et al. \(2008\)](#) identified the *Dw1* locus as a major component of dwarfing in apple, and the emerging linkage maps should allow rapid progress ([Antanaviciute et al., 2012](#)).

One aspect of root systems that has been relatively ignored is what happens as crops approach maturity. Because roots in

soil are difficult to study, most screens and experiments are undertaken with seedlings, but the functioning of systems during the filling of reproductive organs is crucial in realizing yield potential especially as ‘terminal drought’ is a common feature of many arable regions. In cereal crops, the downward descent of the root system typically ceases at around the time of flowering and start of grain growth ([Gregory et al., 1978](#)). However, whether the root system continues to grow in mass and length during grain filling is less certain. In a study with six modern cultivars of wheat grown on a sandy loam, [Ford et al. \(2006\)](#) found that while root mass remained constant between anthesis and maturity, root length increased in both of the two seasons of study (but significantly in only one), suggesting that proliferation of fine roots occurred concurrent with death of thicker, mature roots; overall, they found no evidence for a decline in root mass or length during grain filling. There were significant differences between cultivars in the distribution of roots within the soil profile, with one cultivar, Shamrock, having a significantly larger root system below 40 cm in both seasons. Late-season performance of roots is important for both water and nitrogen uptake because of their contributions to grain yield and grain quality. On deep soils, many studies have indicated the desirability of increasing root length at depth to better capture and use water available in the subsoil (e.g. [Richards, 2008; Wasson et al., 2012](#)),

and root lengths of ~ 1 cm root cm^{-3} soil have been shown by models and experiments to ensure uptake of all the available water at moderate rates of evaporation (van Noordwijk and de Willigen, 1987; Gregory and Brown, 1989; Tardieu *et al.*, 1992).

Past study of roots has been bedevilled by a lack of techniques (Gregory, 2006a). However, recent technological improvements in non-invasive techniques, such as X-ray microtomography, have permitted the response of different plant species, genotypes, and individual roots to soil properties to be more readily examined, providing details of root angles and root system spread (Hargreaves *et al.*, 2009), root diameters (Tracy *et al.*, 2012), and root–soil contact (Schmidt *et al.*, 2012). Field and laboratory phenotyping of roots and rootstocks to complement genomic studies are emerging as techniques to speed up the selection of ideotypes that can be a part of intensified production systems (Gregory *et al.*, 2009; Wasson *et al.*, 2012).

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