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Review

Root uptake and transpiration: From measurements and models to sustainable irrigation

Steve R. Green^a, M.B. Kirkham^b, Brent E. Clothier^{a,*}

^a Sustainable Land Use, HortResearch, PB 11-030, Palmerston North 4442, New Zealand

^b Agronomy Department, Kansas State University, Manhattan, KS, USA

Dedicated to Wilford Gardner on the occasion of his 80th birthday on 19 October 2005.

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ABSTRACT

Water has been labelled 'blue gold', and 'blue gold' is destined to be the critical issue of the 21st Century. Globally, irrigation is responsible for 80% of the world-wide spending of 'blue gold'.

Development of sustainable irrigation practices will require that we understand better the biophysical processes of root-water uptake in soil, and transpiration from plant canopies.

Our review paper is divided into four parts: models, measurements, knowledge gaps and policy.

First, we present a retrospective on what has been done with root-water uptake models since the pioneering scheme of Wilford R. Gardner in 1960. His solution for water movement to a plant root was analytical. Since then, nearly all the models calculate water flow using numerical solutions of the Richards' equation. These schema include a water-uptake term specifically for the distributed uptake of water from soil by the root system. These models fall into two groups based on how the uptake term is handled. The most common formulations, called Type I, have evolved from the work of Gardner [Gardner, W.R., 1960. Dynamic aspects of water availability to plants. *Soil Sci.* 89, 63–73] and describe the microscale physics of water flow from the soil to, and through, the plant roots. The second form, Type II, comprises macroscopic, empirical functions that describe uptake based on responses to water potential. We discuss the merits and potential of these schemes. Yet, models are data hungry. Effective modeling requires apposite parameterisation to be effective. This can require substantive empiricism.

Second, we present new data on the functioning of root-water uptake and transpiration by kiwifruit vines. We describe new observations in the root zone, obtained using arrays of time domain reflectometry (TDR) sensors. As well, we present results obtained with new methods of sap-flow measurement inside the kiwifruit vine's roots. These reveal the uptake dynamics during partial root zone drying (PRD), a technique oft-touted to reduce irrigation volumes.

Next, we outline future research needs. This includes a requirement to infer better the matric potential at the soil-root boundary and its control on plant transpiration.

* Corresponding author. Tel.: +64 6 356 8080x7733; fax: +64 6 354 6731.

E-mail address: bclothier@hortresearch.co.nz (B.E. Clothier).

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We suggest that the role of reverse flow and specification of the root resistance also needs more researching. Further, linking the functioning of water uptake with the form of the root system will not be achievable until we know more about root resistance. Canopy area and architecture are critical for controlling transpiration, yet they are tiresome to measure. Improved measurement techniques, preferably remote, would enhance our ability to predict crop water-use and to assess more accurately the need for irrigation [Wesseling, J.G., Feddes, R.A., 2006. Assessing crop water productivity from field to regional scale. *Agric. Water Manage.* 86, 30–39].

Finally, we demonstrate how our scientific knowledge can be used to develop sustainable irrigation practices.

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1. Retrospective: root models since Gardner's landmark 1960 paper

Water is the lifeblood of plants (Clothier, 1990). It is the most important factor controlling plant growth (Richards and Wadleigh, 1952; Wesseling and Feddes, 2006). A plant gets its water by root uptake. Irrigation is required when the soil is incapable of supplying the plant's needs for water. Prediction of how water flows to plant roots has been a scientific challenge for decades. If we could predict the water flow, then we would not need to measure it. From our models, we would then be able to determine when to irrigate to optimise plant growth. However, models need to be confirmed by measurements. We review root-water uptake models, and then the new measurement technologies that are becoming increasingly available for measuring root-water uptake. We conclude with suggestions for future research, and then provide an example of how our science can be implemented in planning policies and irrigation practices.

Gardner (1960) was first to provide a solution for the movement of water to a plant root. Philip (1957) had earlier outlined the problem (Raats, *in press*). Gardner's equation, using

the modern terminology of matric pressure potential instead of suction, is (Baver et al., 1972, p. 404; Kirkham, 2005, p. 229):

$$\psi_b - \psi_a = \frac{q}{4\pi k} \ln\left(\frac{b^2}{a^2}\right), \quad (1)$$

where ψ_b (MPa) is the matric pressure potential midway between two roots, ψ_a (MPa) the matric pressure potential at the plant root–soil boundary, q the volume of water taken up per unit length of root per unit time ($\text{m}^{-3} \text{m}^{-1} \text{s}^{-1}$), and k is the hydraulic conductivity of the unsaturated soil ($\text{m}^2 \text{s}^{-1} \text{MPa}^{-1}$). The figure presented in Clothier and Green (1997, Fig. 1) provided a graphical representation of the biophysical set-up of Gardner's model. The Gardner model assumes the following: the roots are considered infinitely long cylinders a distance $2b$ apart; the roots have a uniform radius = a ; there is uniform water absorption along the root; water moves in a radial direction only; there is a uniform value for the initial soil-water content; it corresponds to an initial matric potential in the bulk soil. An advantage of Gardner's solution is that it is analytical. Gardner's 1960 paper is still widely cited, and it has become a "citation classic" (Gardner, 1985).

Most solutions for water flow to plant roots are now numerical. Nimah and Hanks (1973a) give a review of early numerical models. They divided root models into two types: microscopic studies, such as the analyses of Philip (1957) and Gardner (1960), which consider radial flow of water to a single root; macroscopic models, which consider removal of water by the root zone as a whole, without considering explicitly the effect of individual roots. Nimah and Hanks (1973a) developed a numerical model to predict water content profiles, evapotranspiration, water flow from or to the water table, root extraction, and root-water potential under transient field conditions. They modified the flow equation by adding an extraction term, following modifications made earlier by Whisler et al. (1968) and Molz and Remson (1970). The scheme predicted changes in root extraction, evapotranspiration, and drainage due to the variations in pressure head-water content relations and root depth. The model was tested over 2 years with alfalfa (*Medicago sativa* L.). Predicted and computed water content-depth profiles showed best agreement 48 h after any water addition. The poorest agreement for all crops tested was right after irrigation (Nimah and Hanks, 1973b).

Cardon and Letey (1992) reviewed the literature on mathematical models that simulate water and solute movement through the soil, and coupled with simultaneous water uptake by plant roots. Nearly all the models calculate water flow by numerical solution of the Darcy-Richards' equation including a water uptake term written for flow in the vertical dimension, as follows:

$$C \frac{\partial h}{\partial t} = \frac{\partial}{\partial z} \left[K \frac{\partial h}{\partial z} - K \right] - S, \tag{2}$$

where K is the hydraulic conductivity ($m^{-1} d$), C the soil-water capacity (m^{-1}), h the soil-water pressure head (m), t time (d), z soil depth (m) taken positive downwards, and S is the root-water uptake term (d^{-1}).

Based on how the root-water uptake term, S , is handled, all models fall into one of two groups.

1.1. Type I models

The most common formulations, to which Cardon and Letey (1992) refer to as Type I, are based on the work of Gardner (1960, 1964) and describe the microscale physics of water flow from the soil to, and through, the plant roots. In general, these equations take the form of

$$S = BK'G, \tag{3}$$

where K' ($m^{-1} d$) is a conductivity term, G (m) the water pressure head gradient from the soil to the root (usually expressed as the difference in root and soil-water pressure head), and B (m^{-2}) is a water flow-geometry term. In the literature there are many examples of soil-water flow models that employ a Type I plant water uptake term (Gardner, 1964; Whisler et al., 1968; Nimah and Hanks, 1973a; Feddes et al., 1974; Hillel et al., 1976; Herkelrath et al., 1977; Rowse et al., 1978).

1.2. Type II models

The second major type of water uptake term, Type II, comprises empirical functions that describe plant water uptake based on a response to water potential (Cardon and Letey, 1992). These now seem favoured in simulation models (Feddes and Raats, 2004). The general form of such a term is

$$S = \alpha(h, \pi) S_{max}, \tag{4}$$

where $\alpha(h, \pi)$ is a dimensionless stress response function equivalent to the ratio between actual, S , and the maximum uptake, S_{max} . There are several models using this type of term reported in the literature (Feddes et al., 1976; Molz and Remson, 1970, 1971; van Genuchten, 1987).

Cardon and Letey (1992) compared the two types of models for sensitivity to salinity and water content. Type I was insensitive to salinity. There was no reduction in transpiration for increasing irrigation-water salinity from 0.0 to 6.0 dS/m, while applying water equal to potential transpiration. Type II was sensitive to salinity and showed a 35% reduction in water uptake by increasing water salinity under identical circumstances. Predicted reduction in water uptake due to matric potential was of the same magnitude as that due to salinity. Type I resulted in abrupt shifts in water uptake between full and zero transpiration, occasionally resulting in long periods of computed zero transpiration. This is not characteristic of field conditions! Cardon and Letey (1992) concluded that the Type I water uptake term may not be appropriate for models incorporating root-water uptake, particularly under saline conditions.

1.3. Hybrid models

Mathur and Rao (1999) also reviewed many models of water flow to plant roots. As previous researchers had done, they categorized models into microscope and macroscopic models. They noted various extraction models for when the soil's water content is not limited. For cases when water in the soil is limiting, the extraction term in models was reduced by a factor that is a function of the soil-water pressure head, and the hydraulic conductivity in the root zone. They also noted that some researchers have created a third category of models, a hybrid approach to take into account root density, root permeability, and root-water extraction in the extraction relationship. As an example of a hybrid model, they give the one by Singh and Kumar (1985), who used a one-dimensional finite-element method to determine water movement in an irrigated field following ponding. The root is assumed a line sink, and the root resistance term uses the root-contact factor of Herkelrath et al. (1977). This study was unusual, because it first used a microscopic analysis in a macroscopic root-water uptake model. The profile of soil-water content calculated for a 9-d simulation period did not compare well with the observed field data. This was attributed to an uncertainty in assigning appropriate soil hydraulic conductivity values that were obtained from experimental data. Mathur and Rao (1999) also reviewed the model presented by Gardner (1991). Gardner (1991) had suggested that only two parameters, namely the root depth parameter and an extractable water parameter, are

required to define the sink term in the governing equation. He assumed the water uptake process to be described by a distributed sink that moves downward through the soil.

Mathur and Rao (1999) noted that most models are similar even though they use different root extraction functions. They proposed a simple model with a linear root-water extraction term that varies with time. The model also incorporated a sinusoidal root growth function that takes into account the root growth with time. A linear root-water extraction term was later adopted, taking into account that root-water uptake is zero at the bottom of the root zone. By comparison with test cases this model was found to be reasonably good.

1.4. Coupled models

In a comprehensive commentary, Hopmans and Bristow (2002) assessed coupled root-water and nutrient-uptake models, and they reviewed mechanisms of ion uptake by plant roots. They reviewed Type I and Type II models, and discussed in detail models that combine water and solute uptake. Raats (1974) is an early example of such a scheme. Hopmans and Bristow (2002) also reviewed recent multidimensional approaches (Vrugt et al., 2001a,b).

Hopmans and Bristow (2002) noted that new experimental tools and better measurements are becoming available. Indeed, it seems that we are moving from a period of model development, to one of data-led discovery as we better observe root zone processes. Our vision of the greater complexities of root-uptake processes now warrant integration into our plant-functioning models. The developments and applications of innovative measurement techniques are documented by Clothier and Green (1997) and Mmolawa and Or (2000), who considered measurement of multidimensional plant root-soil interactions. Asseng et al. (2000) and Clausnitzer and Hopmans (2000) demonstrated the application of non-invasive measurement techniques to infer soil transport processes, and plant root-water uptake at spatial scales of less than 1 mm. Raats (in press) considered water uptake at two different spatial scales, and developed a basis for upscaling from the mesoscopic to the macroscopic scale.

In their review, Hopmans and Bristow (2002, p. 107) cited Philip (1991), who had forewarned that the increasing application of computer models might eventually substitute for experimentation, thereby preventing their real-world application. This has not happened! Rather, Hopmans and Bristow (2002) now comment that inverse modeling back from data, may prove to be an even more-effective simulation tool. This process requires the combination of accurate experimentation with mechanistic modeling to yield appropriate measures of parameters, along with inferences of their uncertainties. Applications of such parameter estimation techniques are presented in Vrugt et al. (2001b) for characterizing multidimensional root-water uptake, and Hupet et al. (2005) to derive macroscopic water stress parameters. Inverse methods have been used to estimate root-water uptake (Ogata et al., 1960; Zuo and Zhang, 2002).

Still, we need detailed root-water and nutrient-uptake models that include root growth and its response to changing local soil conditions, such as water content, nutrient status, and mechanical impedance (Hopmans and Bristow, 2002, p.

156). Newer models are indeed including these factors. Li et al. (2001) included a root response to water stress. Meanwhile, an improved understanding of these processes may provide guidelines in “hot-spot” removal of specific toxic ions from soils for bioremediation purposes. Models are being developed that look specifically at root uptake of contaminants (Albrecht et al., 2002; Sung et al., 2002; Clothier et al., 2004).

Better understanding of root zone processes, needed in the quest to develop sustainable irrigation practices, will arise from coordinated use of modeling techniques and measurement protocols. We now discuss recent developments in the use of new measurement devices, both above and below ground. These are not only providing new knowledge, but also a better means of parameterising our modeling schema.

2. New observations and model parameterisation

Knowledge about water-use by plants is still required for the design of sustainable irrigation practices. New crops are now being irrigated in different locales, and new plant-canopy management practices are being used to maximize production and product quality. New measurement devices are providing us with direct measures of transpiration at remote locations in real-time, via wireless technologies. These data are yielding improved understanding of the processes of transpiration, and providing us with better means of parameterising our ever more-complex models of plant water-use. Here, we present some analyses of previously unpublished data we collected on kiwifruit vines over the summer of 1996–1997. These data reveal that we can successfully model stomatal behaviour, and upscale these results to the whole plant to predict transpiration, even though the canopy architecture of the kiwifruit vine is complex. Next, we show how arrays of time domain reflectometry (TDR) probes can provide us with a better picture of the complex spatial and temporal pattern of water uptake by the root system of the whole plant. These data will provide us with better information by which we can improve our macroscopic models of water uptake. Finally, we show how the use of miniaturized sap-flow probes can detect, in detail within individual roots, the root-water uptake processes that underpin the irrigation strategy of partial root zone drying (PRD), which is touted to reduce the need for irrigation volumes.

First, we only briefly outline details of our experimental set-up (Photograph 1), for the site and the experimental set-up are the same as that described by Green et al. (1997). The experiment was carried out in the Massey University research orchard near Palmerston North, New Zealand (40.2°S, 175.4°E), over 1996–1997. The soil is a Manawatu fine sandy loam consisting of about 0.4 m of sandy loam underlain by about 0.4 m of fine sand, with a gravelly coarse sand beyond about 0.8 m. The experimental data of Clothier et al. (1977) were used for the hydraulic conductivity and water retention characteristics in each soil layer. Three vines were selected from the middle of a block of similar-sized kiwifruit (*Actinidia deliciosa* ‘Hayward’). Each vine was about 8 years old and was trained on a T-bar trellis at a height of about 2 m, and a width of about 4 m. The ground beneath one vine was covered with a low

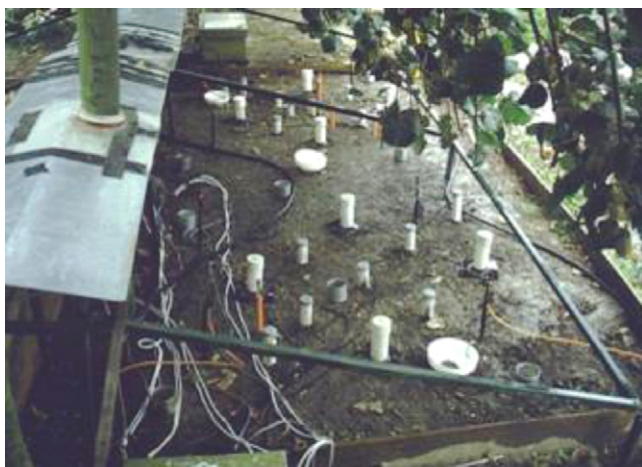


Photo 1 – The experimental set-up showing a semi-irrigation of just the east side of the ‘isolated’ and covered kiwifruit vine. Minirhizotron tubes, tensiometers, raingauges, and TDR probes can be seen, along with the cables leading to the heat-pulse sensors in the stem and roots. The frame supported covers to exclude rainfall.

rainout shelter made from waterproof plastic sheets. This prevented all rainfall and unwanted irrigation water from entering the root zone. We refer to this vine as the ‘covered’ vine. The soil surface surrounding the neighbouring ‘control’ vine was left uncovered and its root zone remained well-watered, both by irrigation and rainfall throughout the experiment. Total leaf area was estimated at regular intervals through the growing season using a vertical point-quadrant approach.

A trench of 4 by 4 m had been dug around each vine, to a depth of 1.2 m, some 6 months before the experiment was begun, to isolate and limit the horizontal extent of the root zone. The trench was lined with a 10 mm thick plywood wall and then backfilled with soil on the outside of the trench wall. Before the start of the experiment, we carefully excavated a small hole near the base of the covered vine to expose partially several surface roots at a depth of 0.1 m and a distance of about 0.3 m from the tree stem. Here, we report measurements from just two of these roots which emanated from opposite sides of the covered vine. One root was on the west-side, while the other root was on the east side. Miniaturized heat-pulse probes were installed to monitor sap flow in these two roots. The soil was then carefully repacked around the probes. Sap flow in both the tree stem and the roots was measured routinely using the compensation heat-pulse technique (Swanson and Whitfield, 1981; Green and Clothier, 1988). In the vine stem, two sets of probes, each consisting of a heater of 1.8 mm diameter and two temperature probes also of 1.8 mm diameter, were installed at heights of about 0.5 m above the ground. Sap velocity was measured at radial depths of 5, 12, 20, and 35 mm following the procedure given by Green and Clothier (1988).

We used the same procedure to measure root sap flow except that we used smaller size probes to accommodate the smaller diameter of the roots. As described by Green et al. (1997), the root probes were only 1.0 mm in diameter and had

three sensors, equally spaced, at depths of between 3.0 and 8.0 mm.

The soil’s volumetric water content, θ , was measured via TDR (Baker and Allmaras, 1990) using a cable tester (Tektronix Model 1502B, Beaverton, Oregon, USA). The TDR measurements were made routinely, every 1–2 d, and the temporal change in the depth distribution of θ over periods of almost 2 weeks were used to deduce the spatial pattern of water uptake by the roots of the covered vine. A total of 90 waveguides were installed vertically into the root zone soil. Each waveguide comprised three, parallel stainless-steel rods which were manually connected in sequence to the TDR via a 5 m coaxial cable. The shortest waveguides, of 0.1 m length, were made from stainless-steel rods of 2 mm diameter, with a spacing of 25 mm between the two outer rods. All the other waveguides, of 0.2 m length, were made from 6 mm diameter stainless-steel rods, with a distance of 100 mm between the outer two rods. The waveguides were installed in groups of three, arranged at different radial distances from the vine stem. Probes of length 0.1, 0.2 and 0.4 m were installed at 18 locations while probes of length 0.6, 0.8 and 1.0 m were installed at another 12 locations. A depthwise profile of θ was subsequently obtained by ‘differencing’ θ values from adjacent probes.

A meteorological station installed close to the experimental vine recorded 20-min averages of incoming radiation, wind speed, air temperature, and relative humidity. The incoming streams of net radiation, R_n ($W m^{-2}$), and global shortwave radiation, R_s ($W m^{-2}$), were measured, respectively, with a Radiation Energy Balance Systems Q*6 net radiometer (Seattle, WA, USA) and a silicon-cell pyranometer (model PY2100, Licor Ltd., Lincoln, NE, USA). These instruments were mounted on a mast in the middle of the orchard block, at a height of about 2 m above the vine. Air temperature and relative humidity were measured with a Campbell 207 probe, and wind speed was measured with a sensitive 3-cup anemometer.

The kiwifruit vines were manually irrigated during the experiment using a purpose-built mini-sprinkler system to deliver aliquots of 55 mm of water during a 2-h period. The control vine, which received rainfall, was irrigated just four times, on 28 January, 11 February, 5 March, and 20 March. For the covered vine we mimicked a PRD treatment. First, the east side of the vine was allowed to dry down. Then, on 12 February, both sides of the covered vine were irrigated, after which the west-side was allowed to dry, while a further three irrigations were applied just to the east side on 20 February, 5 March, and 20 March. Finally, on 2 April, both sides of the vine were again irrigated.

2.1. Stomatal behaviour

Plant water-use is primarily controlled, at the local scale, by the behaviour of the stomata on the leaves. We begin our upscaling analysis by first considering stomatal behaviour in relation to the ambient atmospheric environment. Here, we have parameterised the semi-empirical model of Winkel and Rambal (1990). Stomatal conductance (g_s , $mm s^{-1}$) is expressed as a function of quantum flux density (Q , $\mu mol m^{-2} s^{-1}$), the water vapour pressure deficit (D_A , kPa)

and the air temperature (T_A , °C) using a general multiplicative function:

$$g_s = g_{SM}g(Q)g(D_A)g(T_A), \quad (5)$$

where g_{SM} is maximum stomatal conductance and each $g(\cdot)$ is the partial function for the indicated independent variable ($0 \leq g \leq 1$). Average values of air temperature and vapour pressure deficit are used to simulate the combined T_A and D_A effects. A steady-state porometer (model Li 1600, Licor Inc., USA) was used to measure the leaf stomatal conductance at hourly intervals on the control vine throughout the growing season. We assumed Q for the sunlit leaves was equal to half the incoming global radiation, $R_g/2$, while the corresponding value for the shaded leaves was set equal to 0.1 times this value, as was found to be consistent with the light levels recorded by the photon sensor mounted on top of the porometer. The fitted relationship (Eq. (5)) provides a good rendition of the data (Fig. 1), across the range of ambient meteorological conditions experienced during the 10 d in which we carried out diurnal measurements. So we feel confident in our ability to model the stomatal functioning that controls well-watered transpiration at the leaf-scale. The next challenge is to upscale this understanding to predict the transpiration from the vine across its complex canopy which is supported on a T-bar.

2.2. Whole-vine transpiration

Total transpiration from the control vine was predicted using a modified version of the Penman-Monteith equation. For this calculation, the total leaf area of the vine was first divided into a fraction of sunlit leaves and a complementary fraction of shaded leaves. Uniform leaf properties were then assumed for each class of leaves (Sinclair et al., 1976; Green, 1993). Since kiwi leaves are hypostomatous we followed Jarvis and McNaughton (1986):

$$\lambda E_p = \sum_i a_i \left[\frac{sR_{n,i}r_{b,i} + \rho C_p D_a}{(s + 2\gamma)r_{b,i} + \gamma r_{s,i}} \right]. \quad (6)$$

The summation is made over a set of i uniform leaves each being a fraction, a_i , of the total leaf plan area and having an

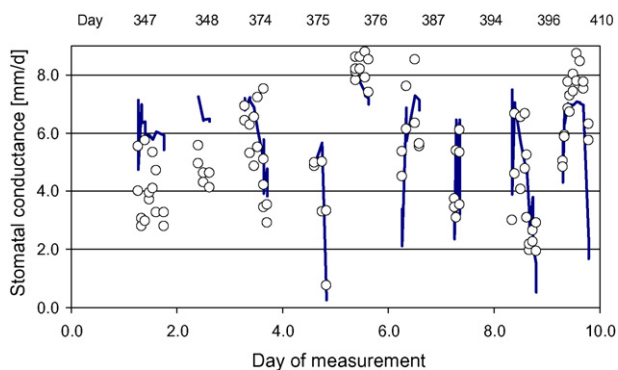


Fig. 1 – Stomatal conductance measured using a porometer (points), and modelled (lines) using a scheme based on air temperature, vapour pressure deficit and radiation (Eq. (5)) during 10 d of our experiment.

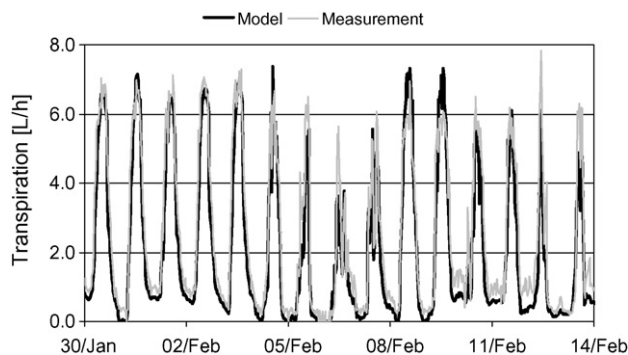


Fig. 2 – Sap flow in the control kiwifruit vine measured using heat-pulse devices along with the modelled transpiration using Eq. (6).

associated leaf stomatal (Eq. (5)) and boundary layer resistance equal to $r_{s,i}$ and $r_{b,i}$ ($s\ m^{-1}$), respectively. E_p represents the total transpiration flux ($kg\ m^{-2}\ s^{-1}$) from all the leaves, $R_{n,i}$ the net radiation flux density ($W\ m^{-2}$) of the i th set of leaves, D_a the ambient vapour pressure deficit of the air (Pa), λ the latent heat of vapourisation of water ($J\ kg^{-1}$), s the slope of the saturation vapour pressure curve ($Pa\ K^{-1}$) considered uniform throughout the tree, γ the psychrometric constant ($Pa\ K^{-1}$), ρ the air density ($kg\ m^{-3}$), and c_p is the specific heat capacity of air ($J\ kg^{-1}\ K^{-1}$). Leaf boundary layer resistances, r_b , were calculated from the empirical relation derived by Landsberg and Powell (1973), which accounts for the mutual sheltering of clustered leaves. Transpiration predicted by Eq. (6), when independently parameterised, and using Eq. (5) for stomatal functioning, faithfully tracks the integrated measurements of transpiration made with our sap flow sensors, despite the complex geometry of the canopy (Fig. 2). These results not only provide us with confidence in our ability to predict plant water-use, but they also highlight the ability, nowadays, to measure continuously plant water-use with relatively inexpensive equipment. Wireless technologies now make it possible to do this at remote locations, so that direct monitoring of transpiration can be carried out. New prospects for remotely deciding when to irrigate are becoming possible.

2.3. Uptake functioning of root systems

The spatio-temporal pattern of the changing soil-water content around the control vine (Fig. 3) reflects not only the timing of rainfall events and the four irrigations, but also it reveals the complex strategy used by the vine, across its entire root system, to access the water it needs to meet transpiration demands. The hyperactivity of the surface roots is revealed by the rapidly changing pattern of the averaged soil-water content at 0.2 m. Deeper down, at 0.6 m, there is a gradual, almost monotonic drying of the profile, which is really only interrupted by the four large irrigation events of 55 mm. Even deeper down, the pattern of water content change is further damped so that there is only a gradual, and lagged, drying down of the soil there. Indeed, the deep soil-water content reaches a nadir in very-late autumn (April). By May, the vines had lost their leaves, and the autumnal rains rapidly wet the

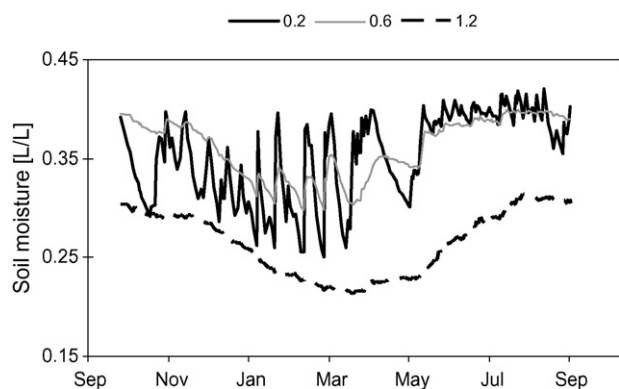


Fig. 3 – The seasonal pattern of soil-water content at different depths in the root zone of the control kiwifruit vine measured by time domain reflectometer (TDR) probes. The traces are for the depths of 0.2, 0.6 and 1.2 m.

surface soil, whereas this gradual wetting takes longer at depth, such that full recharge is not achieved until the following spring (September). These data from intensive arrays of TDR sensors, are providing a wealth of data with which to parameterise our macroscopic models of root-water uptake.

2.4. PRD under the microscope

Dirksen et al. (1979) used a network of 84 tensiometers around citrus trees to reveal that water savings could be made through high frequency irrigation, and regulated deficit irrigation (RDI) strategies. Nowadays, our enhanced ability to measure in detail and continuously, the pattern of soil-water content change around trees and vines, as well as by sap flow directly within roots, enables us to examine the biophysical processes invoked in RDI and PRD. As we seek ever more-parsimonious irrigation practices, PRD is thought to offer hope. The tenet of PRD is that roots, through hormonal signalling from a dry portion of the root zone, can enable the plant to adopt water conservative strategies, so that the need for irrigation is reduced.

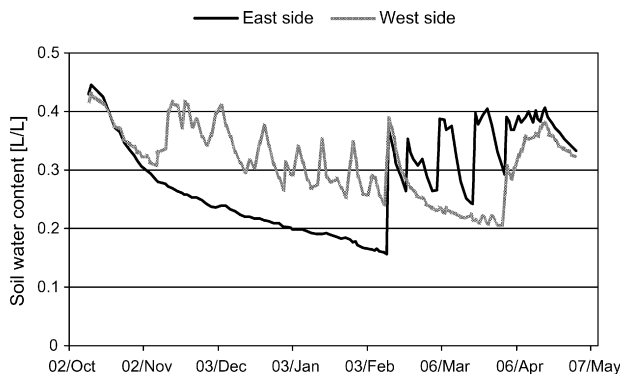


Fig. 4 – The pattern of TDR-measured soil-water content as influenced by partial root zone (wetting and) drying around the covered kiwifruit vine. Sap flow was measured in roots on both the east- and west-side of the vine (Figs. 5 and 6).

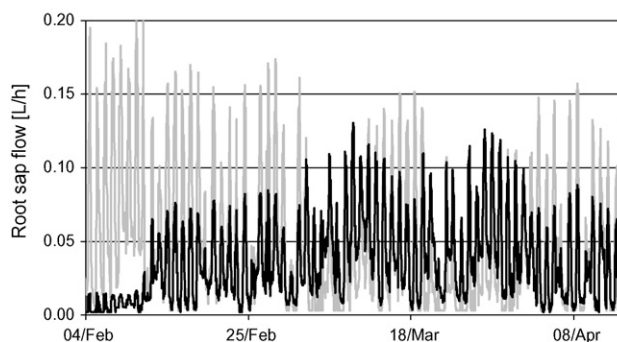


Fig. 5 – Heat-pulse measurements of the sap flow in both the east-side root (black line) and the west-side root (grey line) of the covered kiwifruit vine. Water had been withheld from the east side of the vine from early October. Then, on 12 February both sides of the vine were irrigated, and then three irrigations were applied to just the east side of the vine on 20 February, 5 and 20 March. A final full irrigation was carried out on 2 April.

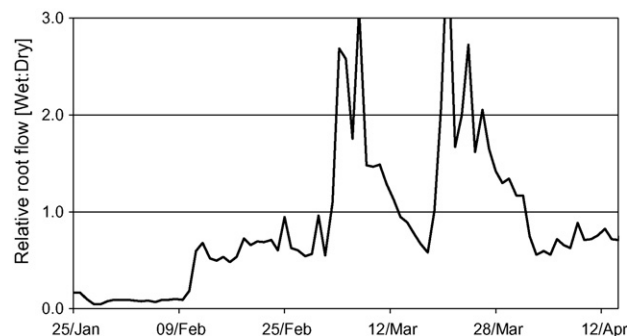


Fig. 6 – The impact of partial root zone (wetting and) drying (Figs. 4 and 5) on relative root sap flow of the east-side root to the west-side root.

The differing patterns of soil-water content around the covered vine in mid summer (Fig. 4) show that we allowed the east side of the vine to become very dry. Then, the soil all around the vine was fully wetted in early February. Then, the west-side allowed to dry down, while aliquots of irrigation were now applied to the east side. This is not strictly PRD, but our mimicking of it enables us to examine these differential wetting cycles of root functioning.

The diurnal pattern of sap flow in the two roots is shown in Fig. 5. The flows in the roots are of the order of 0.1 L h^{-1} , whereas vine transpiration was about 5 L h^{-1} (Fig. 2). That our measured root contributions are of the order of 2% of the vine’s transpiration suggests that there should be about 50, or so, such roots supplying the vine. This is, from our observations, reasonable. It can be seen that under the initially dry conditions, the maximum sap flow in the east root was of the order of 0.01 L h^{-1} . Later, when supplied with water, this root’s capacity was over 10-fold that.

In Fig. 6, we have plotted the daily totals of relative root-sap flow for the east root over the west root. By mid January, the soil on the east side of the covered vine is dry ($\theta < 0.2 \text{ m}^3 \text{ m}^{-3}$),

and the flow in the east root is just 10% of its opposite. The first full irrigation wetted both sides of the vine, and the sap flow ratio rose to around 0.5, as the once-dry root increases its contribution. The semi-irrigation on 20 February did little to alter this ratio, as the water content on the now-dry west-side was around $0.25 \text{ m}^3 \text{ m}^{-3}$. However, the flow ratio changed dramatically following the second semi-irrigation of 5 March. Now the water content on the dry-side had dropped close to $0.2 \text{ m}^3 \text{ m}^{-3}$, and the east-side root increased its flow such that it was carrying nearly three times the flow of its opposite. This dramatic cycle was repeated with the third semi-irrigation. At this average θ of about $0.2 \text{ m}^3 \text{ m}^{-3}$, the mean potential would only have been around -1 bar, so this response is somewhat surprising. Locally, there would have been much drier pockets from which signals may have originated. The final full wetting of both sides resulted in the ratio returning to 0.5–0.7, as it was following the first full irrigation on 12 February. A reassuring closure.

These data reveal the great flexibility that the kiwifruit vine has in securing the water it needs to meet transpiration demands. The relative flows between the east and west roots ranged rapidly, from 0.1 to over 3, depending on local conditions. Certainly there is much biophysical complexity in the functioning of the root zone that we need to unravel in order that we develop sustainable irrigation practices. Despite the difficulty of its implementation, PRD appears one, amongst many strategies, that is worthy of pursuing.

Having these new observations, and possessing comprehensive modeling schemes, what more is there that we need to know? Much, if we are to transform irrigation practices so that they become sustainable.

3. Scientific challenges for the future

3.1. What is the matric potential at the soil–root interface?

As measurement methods become increasingly miniaturized, we will be able to take measurements on a microscopic scale. The Gardner (1960) approach has been criticized because measurements could not be made around an individual root. With the dual-probe heat-pulse technique, we now can measure soil-water content within 15 mm of a surface, such as a root or soil surface (Song et al., 1999b). Theoretically, the instrument can take a measurement as close as the distance between the probes, which is usually 6 mm (Philip and Kluitenberg, 1999). Time domain reflectometry is also providing water contents at higher levels of resolution (Vetterlein and Jahn, 2004). Schack-Kirchner et al. (2005) documented a modified TDR system that had an accuracy of about 2 mm. A large root system should allow us to verify Gardner's equation using the available small instrumentation. Large taproots, such as those of sunflower (*Helianthus annuus* L.) (Song et al., 1999a), or the structural roots of kiwifruit (*A. deliciosa*) (Clothier and Green, 1994) could be used. Miniaturized equipment would not only allow monitoring of water uptake around a root, but also of the solute uptake. TDR has been used for many years to measure low solute concentrations (Vogeler et al., 2000), but now it also can monitor solutes in highly saline soil (Jones and Or, 2004).

3.2. Is nocturnal root-water uptake important?

Most soil–vegetation–atmosphere transfer (SVAT) (Levine and Salvucci, 1999; Hupet et al., 2002), or soil–plant–atmosphere continuum (SPAC) (Coelho et al., 2003) models assume no root-water uptake at night, because transpiration is assumed to be zero. It has long been known that plants with crassulacean acid metabolism (CAM) plants keep their stomata open at night. Most plants have the C_3 or C_4 type of photosynthetic system, and it has commonly been thought that they keep their stomata closed at night. However, this may not always be the case, as Green et al. (1989) showed that, on average, kiwifruit used 20% of its water during the hours of darkness. Downward convective transfer of drier air from above sustained the nocturnal transpiration from the open stomata. Our Fig. 2 here demonstrates nocturnal transpiration by our control vine during the nights of 1, 2, 10, 11 and 12 February. Using the dual-probe heat-pulse technique, Song et al. (1999a) recorded a small amount of nocturnal transpiration in sunflower. Snyder et al. (2003) measured significant nighttime stomatal conductance and transpiration in a range of plants in the western USA with both the C_3 and C_4 types of photosynthetic systems. They commented that the substantial night-time water loss deserves further investigation.

3.3. Site-specific water uptake by roots

Large-scale models (Feddes et al., 2001; Zhu and Mohanty, 2004) are valuable when we do not need to consider small-scale spatial variation. However, spatially variable models are needed, too, as we become more precise in our application of water, fertilizers, and pesticides to the soil. This, per force, means looking at roots on a small scale, yet integrating their functioning over a field. Approaches such as that of Wilderottter (2003), who developed a model that allows the calculation of the water uptake of an entire root system while preserving the local impact of single roots, are appropriate. Methods to conserve water, such as deficit irrigation and partial root zone drying (Zegbe-Domínguez et al., 2003; Zegbe et al., 2004) and drip irrigation (Or and Coelho, 1996), will require that root models incorporate local variations in water content. More work like that done by Morgan et al. (2003) needs to be carried out. They looked at spatial distribution of plant-available water, but also considered root-water uptake. Site-specific models will require a better understanding of root morphology and development. Data are becoming available. The increase in rooting depth with time has been documented for 48 crop species (Borg and Grimes, 1986). This is crucial information for determination of the depth of stored water that is available to the plant. Wu et al. (2005) compared seven models with different plant-root architectures. Sustainable irrigation is about applying the right amount of water at the precise location where it is needed.

3.4. What is reverse flow?

With miniaturized sap-flow gauges, we now have vision of better acuity in measuring sap flow in the root (Green and Clothier, 1995, 1999; Moreno et al., 1996; Green et al., 1997, 2003a; Fernández et al., 2001). With these, and other types of

gauges, we can determine the direction of movement of water and solutes within plants, and plant parts. In a study to determine water and ^{15}N labelled-N uptake by potatoes (*Solanum tuberosum* L.), Kirkham et al. (1974) found unexpectedly high concentrations of nitrate-N in the soil solution throughout the 800-mm long columns. They attributed this to contamination, but it might have been a result of back diffusion or back leakage out of the roots, because of the high level of nitrogen in the plant. How a plant regulates its uptake and loss is poorly understood. We need to look further at outward flux. Tracers could be used, such as in the study by Thorburn and Ehleringer (1995). Measurements of stable isotope ratios in root water showed that the water taken up by the roots was not derived entirely from the surrounding soil. This indicated movement and the possibility of mixing of water within the root system. Further studies, such as the one done by Kirkham et al. (1974) who put the ^{15}N label at just two different depths in the columns appear merited. The presence of roots at greater depths ought to be revealed by an increasing penetration of label at a rate much faster than that due to leaching. Such studies would have a bearing on ion uptake and fertilizer studies.

Related to reverse flow is hydraulic lift. This occurs when plant roots extract water from a moist subsoil and release it into a dry topsoil. Song et al. (2000) documented its occurrence with dual-probe heat-pulse sensors placed around sunflower roots. Many years ago, at the U.S. Salinity Laboratory in Riverside, California, an unpublished experiment with pepper (*Capsicum frutescens* L.) revealed significant hydraulic lift up into the upper root zone (Gardner, W.R., pers. commun., 2000). The effect on water potential was significant, and they recognized that water indeed goes both ways through root membranes, depending upon solutes and active transport processes. Gardner ended this personal communication by stating that, "... I still believe, after two decades, that the most important problems are at the interface between the physics and the biology."

3.5. What is the root resistance?

In most cases, an Ohm's law analog is assumed to determine the resistances in the soil-root-stem-leaf-atmosphere continuum. This follows the analysis of van den Honert (1948). Thus, a plot of transpiration versus the potential difference between any two points in the system should result in a line, and the slope of this line is the resistance (Zhang and Kirkham, 1999). This physical analog works in many cases (Kirkham, 1983). However, a plant root has living membranes that affect the uptake of solutes and cannot be considered a completely non-living system (Brisson et al., 1993). A non-linear type of relationship for flux through plant roots has often been reported in the literature (Gardner, 1973). This is probably a natural consequence of the semi-permeable nature of the root membranes. Dalton et al. (1975) presented a theory describing the hydraulic and osmotic transport of water and the diffuse, convective, and active transport of solutes across root membranes. The theory predicts a non-linear relationship between the flux of water and the pressure difference across root membranes. de Willigen et al. (2005) discuss both the physical and physiological aspects of water and solute flow

through the root, including this non-linear relationship. Hopmans and Bristow (2002) describe models that couple water and nutrient uptake. One of them is HYDRUS-2D (Rassam et al., 2003). With new, miniaturized instrumentation, we should be able to determine the solute uptake and release at the root surface. The transport will reflect the movement across the semi-permeable root membrane. Gardner (pers. commun., 2000) believes that an important question in soil-plant-water relations relates to what is happening at the end of the xylem to the dissolved salts. The pioneering work of Dalton et al. (1975) needs further study.

Again, according to Gardner (pers. commun., 2003), trying to correlate water uptake with root distribution is a lost cause because we cannot measure the root resistance. Experimentation confirms this observation (Shein and Pachepsky, 1995). However, with the new instrumentation, we should be able to infer it better from our measurements. Gardner himself addressed the problem of root resistance (Gardner, 1991). He said, "An increase in root resistance with depth could contribute to plant survival where an extended period of drought follows seasonal recharge of the soil profile. A highly 'efficient' root system with low vertical resistance could continue to extract water at the potential rate until the water stored in the profile was exhausted, but before the plant had a chance to set seed or leaving too long a dry period for survival. A higher resistance in the root system would tend to ration the water more slowly, limiting growth, water uptake would continue, thus enhancing prospects for survival until the profile is refilled." At the end of his paper, Gardner (1991) rued that "... because of the complexity of the root-soil flow system and our present ignorance about how root systems in the soil really operate, it is not possible to prove using extant data that this moving sink model of uptake is correct. None of our models describe the soil-plant flow system from first principles. The test of our empiricisms is not only how well they fit the existing data, but also how well they can be extended to describe new situations." With the new measurement tools, we should be able to calculate resistances and then describe the soil-plant flow system from first principles, such as Gardner used in his 1960 paper.

Armed with better understanding from improved observations of root and plant functioning, along with integrated modeling schemes, we will be able to provide stakeholders and end-users with policies and practices for sustainable irrigation.

4. Policies and practices for sustainable irrigation

To conclude our review, we present the results of a study that was commissioned by a regulatory authority, the Marlborough District Council of New Zealand, to determine whether new grape-vine management strategies should result in a change of policy for the allocation of irrigation consents to vineyards. This demonstrates how scientific study can influence regulatory policy (Green et al., 2003b).

The Council had noted that some Marlborough grape growers are now using more intensive vineyard systems on the poorer soils, as a means to achieve yield gains by using

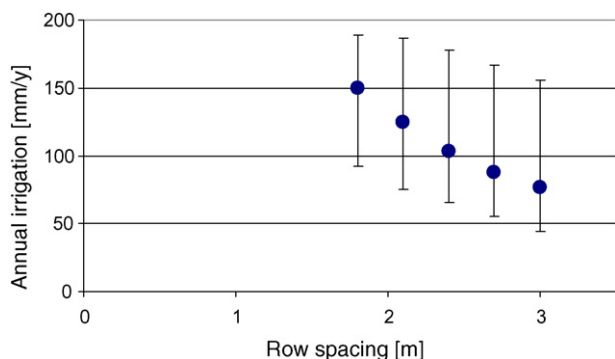


Fig. 7 – The influence of row spacing on the annual irrigation requirements of Sauvignon Blanc grape-vines on a Wairau silt loam soil in Marlborough, New Zealand. Canopy architecture was held constant as the row spacing diminished. The symbols represent the annual average irrigation demand. The error bars represent the range spanning 80% of the years.

higher density plantings. The traditional row spacing of 3 m was being narrowed to 2.4 m, or less. This raised the important policy question of “what impact will an increase in planting density have on the water demands for grapes, and the requirement to allocate an irrigation consent?” To answer this question we chose a modeling approach that required a comprehensive understanding of the complex interactions between canopy architecture, plant processes, soil-water mechanisms, and the long-term impact of weather patterns. The results of our modeling exercise are presented in Fig. 7, where the annual requirement for water is plotted against the row spacing between the vines. The model simulations, in daily timesteps, were carried over 30 years using a long-term weather record. Indeed, on average, as the rows of vines become closer together, the need for water doubles from around 75 mm/year at a 3 m spacing, to 150 mm/year at 1.8 m. However, the Council allocates irrigation at an 80% security level. In the case of the 20% of driest years, as shown by the error bars in Fig. 6, the slope of the line is not as steep, ranging from about 155 mm/year for 3 m rows, to about 190 mm/year at 1.8 m. Since the current policy for grapes is 220 mm/year, the Council were confident that a change in their allocation schedule was not merited. From science to policy in one step.

5. Conclusions

Parsimonious use of ‘blue gold’ will ensure irrigation policies and practices are sustainable, so that into the future one third of the world’s food can continue to come from just 15% of the earth’s land area. New measurement techniques and novel devices will provide two-fold impetus to this quest for sustainable practices. First, new observations will enhance our understanding of the biophysical mechanisms that control irrigation efficiency, so that we can then model them better and prescribe sustainable policies and practices. These same tools can also act as monitoring devices that we will be able to interrogate remotely, and in real-time, to provide

decision support information for irrigation scheduling. There are significant challenges facing irrigation. Irrigation scientists will be integral in the participatory processes with end-users and stakeholders that will lead to sustainable actions. Our journal of Agricultural Water Management will continue to provide a high-impact vehicle for the endeavours of irrigation scientists.

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