



Dry mass production and water use of non- and drip irrigated *Thuja occidentalis* ‘Brabant’: Field experiments and modeling

A.A. Pronk^{1,4}, M. Heinen² & H. Challa^{3†}

^{1,4}Plant Research International, Wageningen University and Research Centre, P.O. Box 16, 6700 AA Wageningen, The Netherlands. ²Alterra, Soil Science Centre, Wageningen University and Research Centre, P.O. Box 47, 6700 AA Wageningen, The Netherlands. ³Farm Technology Group, Wageningen University, P.O. Box 43, 6700 AA Wageningen, The Netherlands. ⁴Corresponding author*

Received 10 February 2004. Accepted in revised form 17 May 2004

Key words: conifer growth model, decision support tool, eastern white cedar, sandy soil, two-dimensional soil water model

Abstract

Generally, irrigation increases dry mass production (*DM*) on sandy soils of horticultural crops and at the same time increases the risk of percolation losses of water and chemicals to below the root zone. However, the effects of irrigation are highly site-specific and not easily determined, which hampers the development of proper management tools and guidelines. A two-dimensional soil-water balance model combined with a crop growth model was parameterized and validated, and used to investigate *DM* and water use of *Thuja occidentalis* ‘Brabant’ in a field trial under non- and drip irrigated conditions. Measured leaf *DM* and leaf area index (*LAI*) were not affected by irrigation but irrigation increased stem *DM* and the specific leaf area. Simulated *DM* and *LAI* were in good agreement with the measurements. Simulated pressure head followed the measured pressure head, although model’s performance was better under dry than under wet conditions. Simulation experiments indicated that increasing irrigation threshold levels increased *DM* production and leaching relatively to no irrigation, when the irrigation threshold level was measured at 0.25 m depth.

Introduction

On sandy soils, dry mass production of many agricultural crops is often reduced by the limited amount of water in the root environment. In general, irrigation increases dry mass production. Field-grown nursery stock production can also benefit from irrigation as shown by Ponder et al. (1984), Hornig et al. (1997) and Pronk and Ravesloot (1998). Especially drip irrigation was found to improve dry mass production of several field-grown nursery stock crops (Pronk and Ravesloot, 1998).

However, irrigation may increase leaching of nitrogen (N) on sandy soils (e.g. Pang et al., 1997; Pionke et al., 1990; Sanchez et al., 1994; Smika and Watts, 1978). It is likely that this occurs in field-

grown nursery stock as well as when irrigation rates and/or methods are poorly matched to soil conditions and plant requirement. So far, most studies on irrigation strategies of field-grown nursery stock crops focus on dry mass production and on root growth and establishment after transplanting (Gilman et al., 1996; Ponder et al., 1984; Pronk and Ravesloot, 1998). Some studies suggest that leaching is not increased by irrigation, as tensiometer readings did not indicate downward water movement (Averdieck and Bohne, 1994; Hornig et al., 1997). However, in these studies pressure head was measured once a week only, while high-pressure head levels could occur within a week when high precipitation or irrigation rates are intermittently high. Leaching may have occurred within that week. If irrigation strategies are to be evaluated on both increasing dry mass production and leaching, lysimeters may be a better way to evaluate leaching.

† Deceased before publication. FAX No: +31-317475793.
E-mail: annette.pronk@wur.nl

Alternatively, the pressure head should be calculated in between measurements to estimate leaching, using soil-water balance models.

When irrigation strategies have to protect the environment by minimizing the percolation losses of water and chemicals to below the root zone, the combination of crop growth models and soil-water balance models can be a useful tool to evaluate the environmental performance of the various irrigation strategies.

Drip irrigation is common in field-grown nursery stock crops, with one emitter positioned at the stem base of the tree. This application method increases the hydraulic gradient in the soil from the emitter point to the area where no water is applied (Coelho and Or, 1996). To simulate the water dynamics in such drip irrigated system, two- or tree-dimensional soil-water models are necessary to include the horizontal transport of water (Ahuja and Nielsen, 1949). Combining a two dimensional soil-water balance model with crop growth models enables us to investigate the effect of drip irrigation on dry mass production and water use of the crop, and to develop irrigation strategies which are efficient and environmentally sustainable. To investigate dry mass production and water use of the crop under non- and drip irrigated conditions we undertook a field trial and compared dry mass production under dry (no irrigation) and wet (drip irrigation) conditions on a sandy soil with transplants of the ornamental conifer *Thuja occidentalis* 'Brabant'. We monitored pressure head at three depths continuously and used the results to validate the combined model for dry mass production for *Thuja* (CONifer GROwth, Pronk et al., 2003b) with the two-dimensional soil water balance model FUSSIM2 (Heinen, 2001; Heinen and De Willigen, 1998, 2001).

Materials and methods

Model structure

Two models, one to simulate dry mass production of ornamental conifers (CONifer GROwth Pronk et al., 2003b) and one to simulate the soil water balance (FUSSIM2, Heinen, 2001; Heinen and De Willigen, 1998, 2001), were coupled through a synchronization shell (FSE4, Rappoldt and Van Kraalingen, 2001). This shell allows the models to work independently while synchronizing data exchange. The driving variables (weather data) are known at a daily basis and therefore, communication between the two models oc-

curs once a day. The crop growth model CONGRO simulates daily dry mass production, partitioning of dry mass to the various organs. For the purpose of this study, daily water demand (T_p and E_p , Table 1) was implemented using independent trials and the concept of the water use efficiency (WUE). Daily water demand is imposed on the soil water balance model FUSSIM2. For the current water status in the soil, FUSSIM2 estimates the actual water uptake by the plant (T_a) and the actual water loss by evaporation (E_a). After this exchange of model information, the two models compute independently the changes during the day involved. When T_a is less than T_p , the CONGRO model reduces dry mass production by a factor equal to actual water removal divided by demanded water need (T_a/T_p , Van Keulen, 1986). The following subsections briefly summarize the essential characteristics of the two models. A list of abbreviations is included in Table 1.

Dry mass production and leaf area increase

CONGRO simulates potential dry mass of *Thuja occidentalis* 'Brabant' using the concept of a radiation use efficiency and actual weather data (Pronk et al., 2003b; Van Ittersum et al., 2003):

$$\frac{dDM}{dt} = F_{int} * RUE * DTR * F_{par}, \quad (1)$$

where dDM/dt is the crop growth rate ($g (DM) m^{-2} d^{-1}$), F_{int} is the fraction of photosynthetically active radiation (PAR) intercepted by small conifers grown in rows (Pronk et al., 2003a), RUE is the radiation use efficiency ($g (DM) MJ^{-1}$ (intercepted PAR)), DTR is the daily global radiation ($MJ m^{-2} d^{-1}$) and F_{par} is the fraction of PAR in DTR (Table 1). Dry mass is distributed to leaves, stems, fine (diameter <0.2 cm) and coarse roots (diameter >0.2 cm), with partitioning functions depending on thermal time during the growing period. A basal temperature of 4.4 °C is used to calculate the thermal time (Thomson and Moncrieff, 1982). Leaf area increase is calculated through the specific leaf area (SLA , $m^2 g^{-1}$). Daily dry mass increase is partitioned to the leaves (F_{lv}) by:

$$\frac{dLAI}{dt} = F_{lv} * SLA * \frac{dDM}{dt}. \quad (2)$$

Conifer stands at production nurseries grow for several years. However, DM increases only between budburst and dormancy (the end of October). Budburst after planting in the spring is induced at a temperature sum of 280-degree day, using the basal temperature

Table 1. List of abbreviations, input parameters and values used in the models

Abbreviation	Explanation	Unit
<i>DTR</i>	Daily solar radiation	MJ m ⁻² (ground) d ⁻¹
<i>PAR</i>	Photosynthetically active radiation	MJ m ⁻² (ground) d ⁻¹
<i>F_{int}</i>	Fraction intercepted photosynthetically active radiation	-
<i>LAI</i>	Leaf area index	m ² (leaf) m ⁻² (ground)
<i>DM</i>	Dry mass	g (dry mass) m ⁻² (ground)
<i>LDM</i>	Dry mass of the leaves	g (dry mass) m ⁻² (ground)
<i>SDM</i>	Dry mass of the stems	g (dry mass) m ⁻² (ground)
<i>FRDM</i>	Dry mass of the fine roots	g (dry mass) m ⁻² (ground)
<i>CRDM</i>	Dry mass of the coarse roots	g (dry mass) m ⁻² (ground)
<i>L_{rv}</i>	Fine root length density	m m ⁻³
<i>T_p</i>	Potential transpiration	m d ⁻¹
<i>T_a</i>	Actual transpiration	m d ⁻¹
<i>E_p</i>	Potential evaporation	m d ⁻¹
<i>E_p</i>	Actual evaporation	m d ⁻¹
<i>QL</i>	Growth rate of the length of the fine roots	m m ⁻³ d ⁻¹
<i>S</i>	Effective degree of saturation	-
<i>S_w</i>	Sink strength for water or root water uptake	m ³ m ⁻³ d ⁻¹
<i>θ</i>	Volumetric water content	m ³ m ⁻³
<i>θ_r</i>	Residual volumetric water content	m ³ m ⁻³
<i>θ_s</i>	Saturated volumetric water content	m ³ m ⁻³
<i>h</i>	Pressure head	m
<i>α</i>	Curve-shape parameter	m ⁻¹
<i>n</i>	Curve-shape parameter	-
<i>m</i>	Curve-shape parameter	-
<i>λ</i>	Curve-shape parameter	-
<i>K</i>	Hydraulic conductivity	m d ⁻¹
<i>K_s</i>	Hydraulic conductivity at saturation	m d ⁻¹

Table 1. Continued.

Parameters	Explanation	Unit	Value	Reference
RUE	Radiation Use Efficiency	$g (DM) MJ^{-1}$ (intercepted PAR)	3.3	(Pronk et al. 2003b)
F_{lb}	Fraction of daily DM partitioned to the leaves	-	function of thermal time	(Pronk et al. 2003b)
H	Plant height	m	function of time	(Pronk et al. 2003b)
$w_{r,1}$	Width of a crop row	m	function of time	(Pronk et al. 2003b)
$w_{r,2}$	Width of a crop row	m	function of time	(Pronk et al. 2003b)
SLA	Specific Leaf Area	$m^2 (leaf) g^{-1} (LDM)$	function of time	(Pronk et al. 2003b)
F_{par}	Average fraction of PAR in DTR	-	0.47	(Gijzen 1992)
k	Radiation extinction coefficient	$m^2 (ground) m^{-2} (leaf)$	0.48	(Pronk et al. 2003a)
w_p	Planting row distance	m	0.5	
D_r	Diffusion parameter in the horizontal direction	$m d^{-1}$	year 1: 0.33; year 2: 2.18	(Pronk et al. 2002)
D_z	Diffusion parameter in the vertical direction	$m d^{-1}$	year 1: 0.66; year 2: 1.38	(Pronk et al. 2002)
λ	Decay rate of the fine roots	d^{-1}	year 1: 0.031; year 2: 0.088	(Pronk et al. 2002)
K_1	Root hydraulic conductance	$m d^{-1}$	$11.5 \cdot 10^{-6}$	(Rudinger et al. 1994)
WUE	Water use efficiency	$kg DM kg^{-1} H_2O$	$7.6 \cdot 10^{-3}$	this study, Figure 5
a	Constant in transpiration reduction function	-	2.8	(based on data from Edwards 1993), Figure 2
$h_{r,1/2}$	Root water pressure head where $T_a = 0.5T_p$	m	-87	(based on data from Edwards 1993), Figure 2

mentioned above. The concept of Thomson and Moncrieff (1982) to initiate budburst following dormancy (at a temperature sum of 220-degree days after 1 January) is used. This concept was proven to work well for conifers under Dutch climatic conditions by Mohren (1987). Our simulations (and experimental data collection) start at planting and end at the end of October in the second year. No changes in model parameters were made when the tree growth model was linked to the soil water balance model.

Water movement in porous media

The two-dimensional simulation model FUSSIM2 (Heinen, 2001; Heinen and De Willigen, 1998, 2001) for water flow, solute transport, and uptake of water and nutrients by roots in variably saturated porous media, solves the Richards equation:

$$\frac{\partial \theta(h)}{\partial t} = \nabla \cdot [K(\theta) \nabla h(\theta)] - \frac{\partial K(\theta)}{\partial z} - S_w. \quad (3)$$

Equation (3) holds for variably saturated, heterogeneous, isotropic, rigid, isothermal porous media and incompressible water. In Equation (3) t is the time (d), z the vertical co-ordinate oriented positively downwards (m), θ the volumetric water content ($\text{m}^3 \text{m}^{-3}$), h the pressure head (m), K the hydraulic conductivity (m d^{-1}) and S_w the sink strength for water ($\text{m}^3 \text{m}^{-3} \text{d}^{-1}$). FUSSIM2 simulates soil water dynamics for a single, representative conifer. Root growth is considered to occur in a cylinder. For the purpose of this study, the FUSSIM2 model was modified to cylindrical co-ordinates in which the (x, z) co-ordinates were replaced by (r, z) co-ordinates and r represents the radius of the system (De Willigen and Heinen, 2001). Subsequently, water transport is simulated over the radius as well as over the vertical co-ordinates.

Water movement is determined by the interrelationships between h , θ and K . FUSSIM2 uses the $\theta(h)$ relationship given by Van Genuchten (1980):

$$S(h) = \frac{\theta(h) - \theta_r}{\theta_s - \theta_r} = \frac{1}{(1 + |\alpha h|)^m}, \quad (4)$$

where S is the effective degree of saturation (dimensionless), θ_r is a residual θ ($\text{m}^3 \text{m}^{-3}$), θ_s is θ at saturation ($\text{m}^3 \text{m}^{-3}$), and α (m^{-1}), n and m (both dimensionless) are curve shape parameters. FUSSIM2 uses Equation (4) for both the main drying curve as for the main wetting curve with only the α -parameter differing between the two curves: α_d and α_w , respectively, with $\alpha_d > \alpha_w$. The model of Mualem (1984)

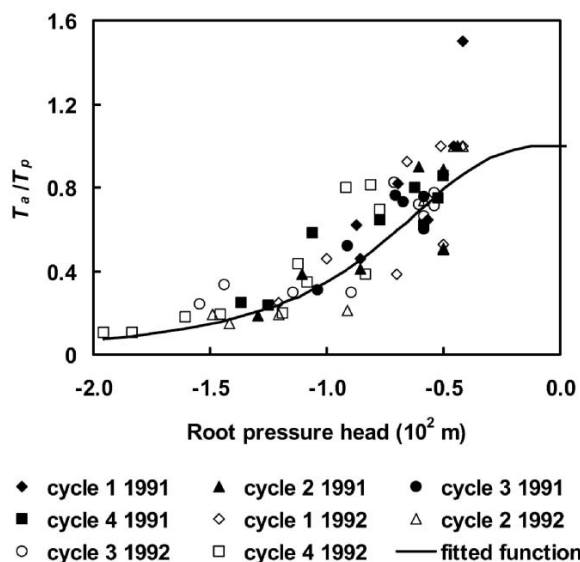


Figure 1. The transpiration reduction function $f_r(h_r)$, as a function of the root pressure head of 8 sets of measured drying cycles of *Thuja occidentalis* (data from Edwards (1993)). Solid symbols represent drying cycles in 1991, open symbols in 1992. $R^2 = 0.85$, $a = 2.8 \pm 0.3$, $h_{r,1/2} = -87 \pm 4.0$ m).

describes intermediate pathways in the hysteretic $\theta(h)$ relationship. For $m=1-1/n$, the Mualem (1976) $K(\theta)$ relationship is given by:

$$K(\theta) = K_s S^\lambda \left[1 - \left(1 - S^{1/m} \right)^m \right]^2, \quad (5)$$

where K is the hydraulic conductivity (m d^{-1}), K_s is K at saturation (m d^{-1}) and λ is a dimensionless curve shape parameter.

Water uptake by roots under potential and limited conditions

In Equation (3) the sink strength S_w represents uptake of water by the roots. De Willigen and Van Noordwijk (1987) obtained an approximate analytical expression for root water uptake, based on an analysis of water movement towards a single root. Their main focus was on the capabilities of the soil to transport water towards the root surface. The transport of water towards the root surface should be large enough to fulfill the demand of water. This approach can be up-scaled towards a whole root system (e.g. Heinen, 1997; Heinen and De Willigen, 1998). The main parameters and variables in this model are the root length density (L_{rv}) distribution (m m^{-3} ; see next section), the hydraulic conductance of the root K_1 (m d^{-1}), the potential transpiration rate T_p (m d^{-1}) and the soil

hydraulic properties (see above). The model yields an estimate of the root water potential, h_r (m), which is assumed to be uniform over the whole root system. When h_r decreases, reduction in water uptake will most likely occur. Therefore, the actual transpiration rate T_a can be assumed to be a function of the potential transpiration rate T_p and h_r according to:

$$T_a = f_r(h_r)T_p. \quad (6)$$

Campbell (1985, 1991) introduced the following reduction function:

$$f_r(h_r) = \left[1 + \left(\frac{h_r}{h_{r,1/2}} \right)^a \right]^{-1}, \quad (7)$$

where $h_{r,1/2}$ is a species-dependent root water pressure head at which $T_a = T_p/2$ and a is a species-dependent dimensionless parameter. This relationship was parameterized using data from Edwards (1993): $h_{r,1/2} = -87$ m and $a = 2.8$ (Figure 1).

Two-dimensional root growth

The root water uptake routine in FUSSIM2 needs the root length density distribution L_{rv} as a function of time. Based on known root dry matter production (e.g. from the CONGRO model) dry matter is transformed into total root length production by assuming a constant root radius, root dry matter content and root fresh bulk density. De Willigen et al. (2002) described a model that distributes roots in two dimensions according to a diffusion-type process. Heinen et al. (2003) showed that such a model works well for a variety of observed rooting patterns. This model has shown to be suitable to describe rooting patterns for *Thuja occidentalis* 'Brabant' (Pronk et al., 2002). In cylindrical co-ordinates, the L_{rv} distribution is given by:

$$\frac{\partial L_{rv}}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left(r D_r \frac{\partial L_{rv}}{\partial r} \right) + \frac{\partial}{\partial z} \left(D_z \frac{\partial L_{rv}}{\partial z} \right) - \Lambda L_{rv} + Q_L f(r, z). \quad (8)$$

In Equation (8) L_{rv} is the root length density of the fine roots (m m^{-3}), r the radial co-ordinate (m), D_r the diffusion coefficient in the r direction ($\text{m}^2 \text{d}^{-1}$), D_z is the diffusion coefficient in the z direction ($\text{m}^2 \text{d}^{-1}$), Λ the decay rate of fine young roots (d^{-1}) and Q_L the growth rate of fine roots at a given location in the root system ($\text{m m}^{-3} \text{d}^{-1}$). The function $f(r, z)$ becomes 1 at the position where roots enter the soil, otherwise $f(r, z)$ is zero.

Experimental site description

A field trial was conducted in 1998 and 1999 on the sandy siliceous mesic udic Plagept (Soil Conservation Service, 1975) at the experimental location within the cropping area of ornamental conifers at Horst in the Netherlands ($51^\circ 25' \text{ N}$, $06^\circ 05' \text{ E}$). A field description was made for the soil profile and a particle size distribution was established for three layers. The computer program 'Staringreeks' (Wösten et al., 2001), was used to estimate the Van Genuchten-Mualem parameters of Equations (4) and (5) (Table 2).

Field trial for model parameterization

Four treatments were included in the field trial (randomized block design, four blocks) with transplanted *Thuja occidentalis* 'Brabant': no irrigation (treatment A), drip irrigation according to local practices (treatment B), drip irrigation with 0.25 L per plant per day (treatment C) and drip irrigation with 0.5 L per plant per day (treatment D). Drip irrigation was applied at the stem base by placing one pressure compensated emitter (flow rate 2.4 L h^{-1}) per tree and not postponed at periods with high rainfall. Trees were planted on 24th of April 1998 at a row distance of 0.5 m and 0.4 m distance in the row, 81 trees per plot. Drip irrigation in treatments C and D was applied only in the period from mid May till mid August, 227 mm and 445 mm in 1998, respectively, and 227 mm and 445 mm in 1999. In treatment B drip irrigation of 15 mm was applied on 25 May 1998 and on 20 and 29 July 1999. Dry mass of leaves and stems (oven dried at 70°C for 48 h, 1 plant per plot per harvest time) and LAI, using a LI-COR model 3100 Area Meter (Lincoln, NB, USA), were determined periodically in all treatments. Trees were cut at the soil surface. The final harvest was in November 1999. The specific leaf area (SLA) was calculated as the LAI divided by leaf dry mass (LDM) at each destructive harvest time.

Soil pressure head (h) was measured in treatments A and D at three depths in replicate (0.15, 0.35 and 0.55 m) and at two distances from the tree: directly below and 0.25 m (half the planting row distance) from the tree. One reading per sensor per minute was taken and the averaged value over a period of 2 h (during the growing season) and 4 h (between growing periods) was stored in a data logger. Data collecting was carried out every two weeks during the growing period and monthly in the winter period. For the purpose of this study data were averaged to daily values.

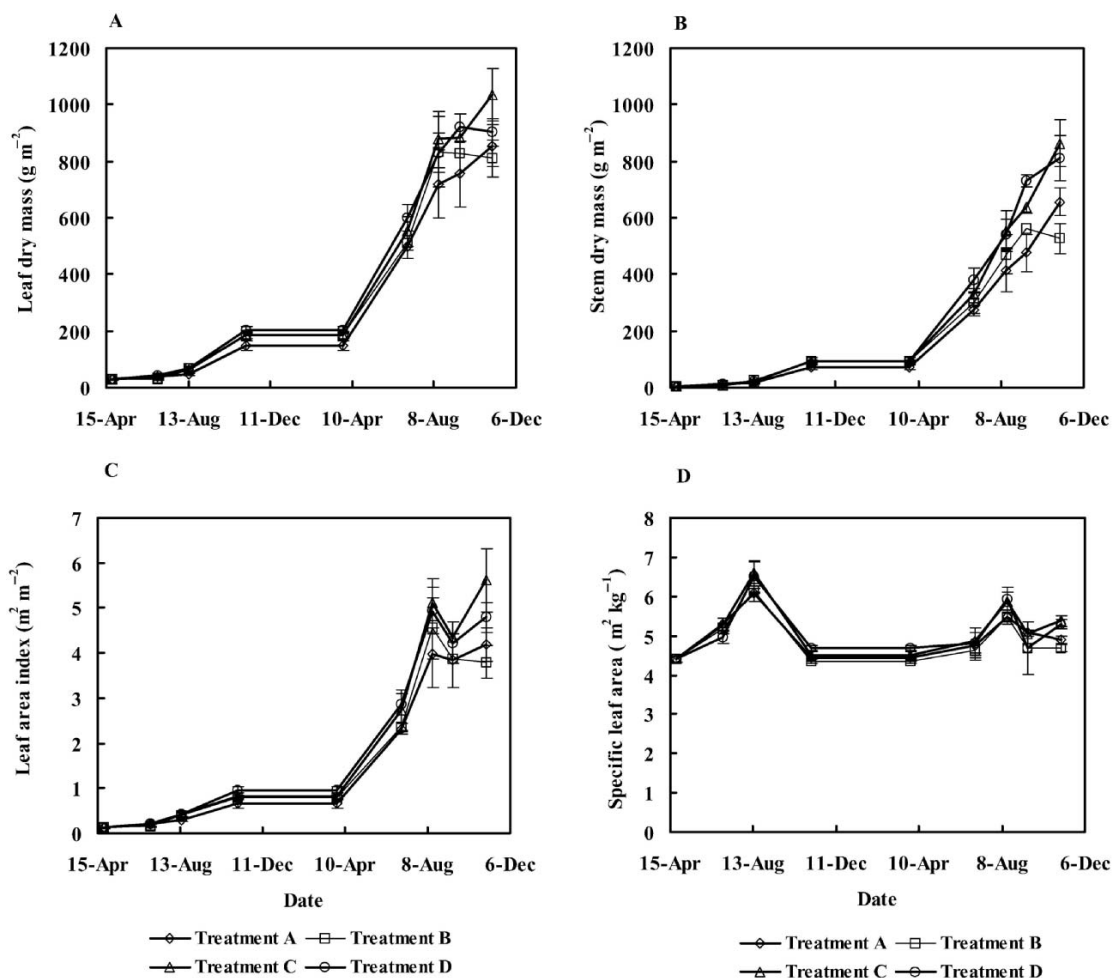


Figure 2. Measured leaf dry mass (A), stem dry mass (B), leaf area index (C) and specific leaf area (D) of the non- and drip-irrigated trees (treatment A and D, respectively). Error bars indicate standard error of the means and are not shown when smaller than the height of symbol.

At 0.15 m depth, h was measured with tensiometers whereas Watermark model 200 Granular Matrix Sensors were used at 0.35 and 0.55 m depths. Two additional Watermark sensors were placed in treatment D at a depth of 0.85 m, one at either distance. The Watermark sensor readings were corrected for temperature at corresponding depths according to Spaans and Baker (1992). The pressure head was calculated from the normalized block resistance using the calibration curve based on data of Spaans and Baker (1992). Missing data in the figures in the results section are either due to very dry conditions (<-75 kPa) when tensiometers were not working properly (as indicated in the product specifications), or to malfunctioning of the data logger.

Water use efficiency

A separate trial was carried out to determine the water use efficiency of *Thuja*. Therefore, daily water loss was measured on 12 and 29 July (10 plants) and 3 August (5 plants) in 1999 and on 13 June and 2 August (5 plants) and 5 September in 2000 (2 plants) of plants in containers. In all cases *Thuja occidentalis* 'Brabant' was used and only on 12 and 19 July 1999 5 plants of *Thuja occidentalis* 'Frieslandia' were included. The container was placed in a plastic bag and sealed around the stem to prevent water losses other than from the leaves. Plants were weighed at 8 a.m. and after 24 h. Leaf area of each plant was determined afterwards using a LI-COR model 3100 Area Meter. Total water loss per plant per day was calculated and net dry mass production per plant per day was calculated according

Table 2. The Van Genuchten parameters describing the hydraulic characteristics of the sandy siliceous mesic udic Plaggept soil for each soil layer, calculated with the program 'Staringreeks' (Wösten et al., 2001)

Depth (m)	θ_s ($\text{m}^3 \text{m}^{-3}$)	θ_r ($\text{m}^3 \text{m}^{-3}$)	α_d (10^{-2}m^{-1})	α_w (10^{-2}m^{-1})	n (-)	λ (-)	K_s (m d^{-1})
0-0.35	0.476	0.01	0.0225	0.1250	1.400	0.09	0.18
0.35-0.65	0.472	0.01	0.0202	0.0880	1.481	0.02	0.29
0.65-1.00	0.491	0.01	0.0161	0.0886	1.550	-0.042	0.21

to Equation (1). In this case, F_{int} was calculated for individual plants using the plant's geometry (height and width, Pronk et al., 2003a). WUE was found as the slope of the assumed linear relationship between the calculated dry mass production (DM) per plant per day and the measured transpiration (T_a) per plant per day:

$$WUE = \frac{dDM/dt}{T_a * 1000}. \quad (9)$$

Boundary conditions for the simulation model FUSSIM2

The simulations were carried out for one tree. The system under consideration had a surface area of 0.196 m^2 and a depth of 1 m. The water flux over the top of the soil was equal to the difference between input (precipitation and irrigation) and output (evaporation). In the model the irrigation was applied on 0.045 m^2 around the tree. Since the water table was at a rather constant level of 3.2 m below the soil surface, a free drainage bottom boundary condition was used. This simple condition does not need any input information. Its validity follows from the comparison between simulated and measured pressure heads. As an alternative validation for this condition a second simulation run was carried out in which the measured pressure head at 0.85 m below soil surface was used as bottom boundary condition (drip irrigated treatment only). The disadvantage of such type boundary condition is that it needs site specific input (i.e. time course of pressure head). No lateral transport was allowed across the cylindrical side of the system, which seems to be justified as all trees were equal in size and the site had no slope.

Statistical procedures

Analysis of variance was performed on LDM , SDM , LAI , SLA and h with the statistical program GENSTAT 6 to determine effects of treatments. Time was

included in the analysis as a factor. A logarithmic transformation on h was used to obtain a normal distribution of the residuals. Loss of measured data due to low values of h (<-75 kPa) increased the average pressure head, especially in treatment A and less often in treatment D.

The mean differences (M), the relative error (E), the correlation coefficient (r) and the number of simulations within 2.5 and 5 kPa of the observations (Addiscott and Whitmore, 1987) were used to evaluate the goodness of fit between measured and simulated h . For the goodness of fit we excluded all measured and accompanying simulated h values at conditions drier than -75 kPa, because the observed discrepancies between measured and simulated h values are artificially increased at lower h values due to physical limits of equipment with which h was measured.

Sensitivity analysis

After the coupling of a conifer growth model with a soil water balance model, the model's sensitivity for WUE , transpiration reduction function parameters and the site-specific characterization of the soil was tested.

The sensitivity of predicted cumulative potential and actual transpiration (T_p and T_a , respectively), LAI , leaf-, stem-, fine- and coarse root dry mass (LDM , SDM , $FRDM$ and $CRDM$) to changes in different model-input parameters was tested for the entire growing period. Mean values for temperature and radiation from the Horst research site from 1993 to 2002 were used in the sensitivity analysis. The initial LAI , LDM , SDM , $FRDM$ and $CRDM$ were set at $0.18 \text{ m}^2 \text{ m}^{-2}$ and 42, 8, 11.2 and 9.8 g m^{-2} , respectively. The initial pressure head was set at field capacity ($h = -10 \text{ kPa}$) and drip irrigation was applied of 0.5 L per plant per day between mid May and half August. The simulation started at the day of planting and ended one and a half-year later. The effects of a change in model input parameters under well-watered conditions were inves-

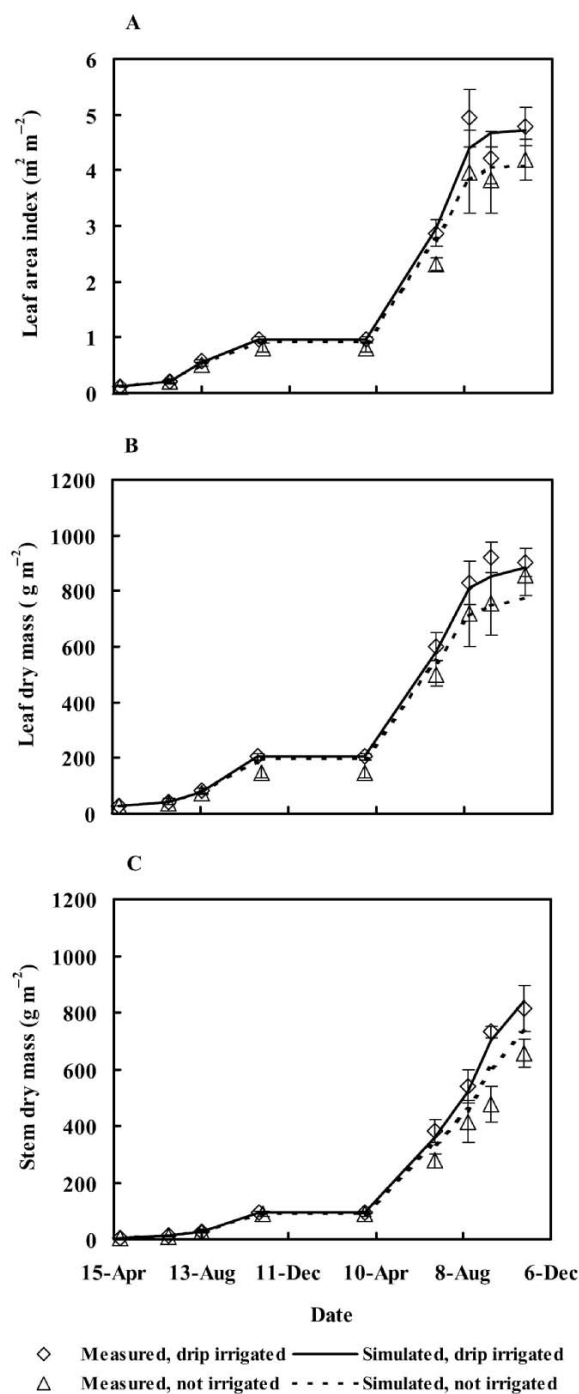


Figure 3. Measured and simulated leaf area index (A), leaf dry mass (B) and stem dry mass (C) under non- and drip-irrigated trees. Error bars indicate standard error of the means and are not shown when smaller than the height of symbol.

tigated by calculating the relative partial sensitivity of the model output, the elasticity (EL) as:

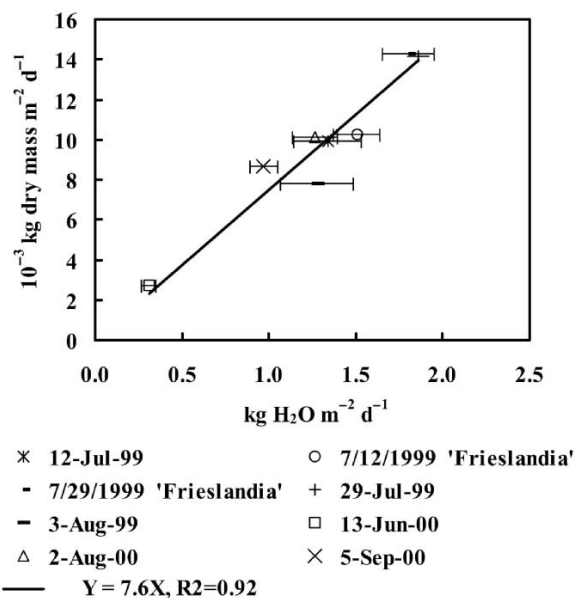


Figure 4. The water use efficiency as the slope of the linear regression between measured transpiration and calculated dry mass of *Thuja occidentalis* 'Brabant' and 'Frieslandia' when indicated in the legend. Error bars indicate standard error of means and are not shown when smaller than the height of symbol.

$$EL = \frac{I}{O} \frac{dO}{dI}, \quad (10)$$

in which dO/O is the relative change in model output, and dI/I the relative change in the input value or input data. Sensitivity was calculated as the mean EL of four levels of change in the model input for WUE , a , K_1 and $h_{r,1/2}$ of -10% , -5% , 5% and 10% . For K_s and the ratio between α_w and α_d (by changing α_d) the range was increased to 10 levels of change, -75% , -50% , -25% , -10% , -5% , 5% , 10% , 25% , 50% and 75% , because of the larger variability of these soil parameters.

Model irrigation scheduling

Simulations were carried out in which irrigation was initiated by simulated h at 0.15 and 0.25 m depth below the tree with an application rate per irrigation event of 0.5 L per plant. Threshold values ranged from -15 to -100 kPa with 5 kPa intervals between the scenarios. No irrigation was applied when precipitation on that day exceeded 20 mm. Multiple applications were applied on the same day when simulated h was not yet in agreement with the threshold level. Although total water loss was not validated as such, absolute values on water loss were not considered but we compared total water loss at 1 m depth and dry

Table 3. Probability of *F*-test for the effect of treatment and time on measured leaf dry mass (*LDM*), stem dry mass (*SDM*), leaf area index (*LAI*) and the specific leaf area (*SLA*)

Source of variation	<i>LDM</i>	<i>SDM</i>	<i>LAI</i>	<i>SLA</i>
Treatment	0.339	0.044	0.183	0.019
Time	<0.001	<0.001	<0.001	<0.001
Linear	<0.001	<0.001	<0.001	<0.001
Quadratic	<0.001	<0.001	0.005	<0.001
Treatment × time	0.815	<0.001	0.567	0.847

mass production with the simulation results of the non-irrigated treatment (c.f. treatment A).

Results

Measured dry mass production and leaf area

LDM and *LAI* increased in time (Figure 2A, C) but no differences treatment related or interaction between time and treatment were found (Table 3). *SDM* increased in time as well (Figure 2B) and an interaction between time and treatment was found (Table 3): *SDM* of treatment B ceased to increase by mid August of the second growing season and was lower than the *SDM* of treatments A, C and D at the final harvest. *SDM* of treatments A, C and D continued to increase although the increase of treatment A was smaller in the second growing season compared to the increase of treatments C and D. *SLA* varied in time (Figure 2D), and treatment had an effect on *SLA* (Table 3). The *SLA* of treatment B was lower than the *SLA* of treatments C and D. However, the *SLA* of treatment A was not different from the *SLA* of treatment B or D. No interaction between time and treatment was found.

Simulated dry mass production and leaf area

In general, the correspondence between simulated and measured *LAI*, *LDM* and *SDM* was good (Figure 3).

The largest discrepancy between simulated and measured *LAI* was found mid August (second growing season), when simulated *LAI* underestimated measured *LAI* with 11.5% in treatment D (Figure 3A). However, no discrepancy was found at the final harvest. The largest discrepancy in treatment A was found in June (second growing season), when simulated *LAI* overestimated measured *LAI* by 19%. The slope of

the linear regression (forced through the origin) relating simulated to measured *LAI* was 1.00 ± 0.022 ($R^2 = 0.98$).

The discrepancy between simulated and measured *LDM* of treatment D was small (<5%). In treatment A, *LDM* was overestimated with 16.8% in June of the first growing season. However, at the end of the second growing season *LDM* was underestimated with 9.5%. The slope of the linear regression relating simulated to measured *LDM* was 0.96 ± 0.013 ($R^2 = 0.99$), indicating a systematic underestimation of 4%.

The discrepancy between simulated and measured *SDM* of treatment A increased during the second growing season and an overestimation of 10.7% at the final harvest was found (Figure 3C). The slope of the linear regression relating simulated to measured *SDM* was 1.03 ± 0.03 ($R^2 = 0.97$), indicating a systematic overestimation of 3%.

Water use efficiency

Water loss varied between 0.33 and 1.85 kg m⁻² per day depending on the actual weather conditions. *WUE* was $7.6 \cdot 10^{-3}$ kg dry mass kg⁻¹ H₂O ($R^2 = 0.92$, Figure 4).

Measured pressure head

For 1998, differences in *h* between treatments were only found during a sunny and relatively dry period that lasted from 5 August to 20 August (data not shown). Larger differences in *h* between treatments were found in 1999 (Figures 5 and 6). The *h* at 0.15 m depth became very low early May in treatments A and D (Figures 5A and 6A). This happened before drip irrigation started. After drip irrigation started, *h* measurements in treatment D were close to field capacity but occasionally decreased to very low values during hot and dry periods. In these periods, the fixed application rate of treatment D was insufficient to maintain field capacity and *h* values below -75 kPa were found on 26 May, 16–22 July and 3 August 1999 (Figure 6A).

Although 1998 was wet and cloudy compared to the 10-year average (Table 4), the pressure heads of treatment A were lower than in treatment D at 0.15 m depth (Table 5). No differences were found at 0.55 m depth and position had no effect on *h*. In 1999, *h* measurements below the tree in treatment A were lower than in treatment D (Table 5). Furthermore, *h* between the tree was higher (wetter conditions) than below the

Table 4. Precipitation and radiation per month and for the four month together at the research location during the growing seasons 1998 and 1999 of the experiment and the ten-year average for the period 1993–2002

	Precipitation (mm)			Radiation (MJ m^{-2})		
	1998	1999	1993–2002	1998	1999	1993–2002
May	27	68	61	534	554	512
June	112	58	62	477	571	556
July	64	71	61	447	651	534
August	67	95	71	477	451	477
Total	270	292	255	1935	2227	2079

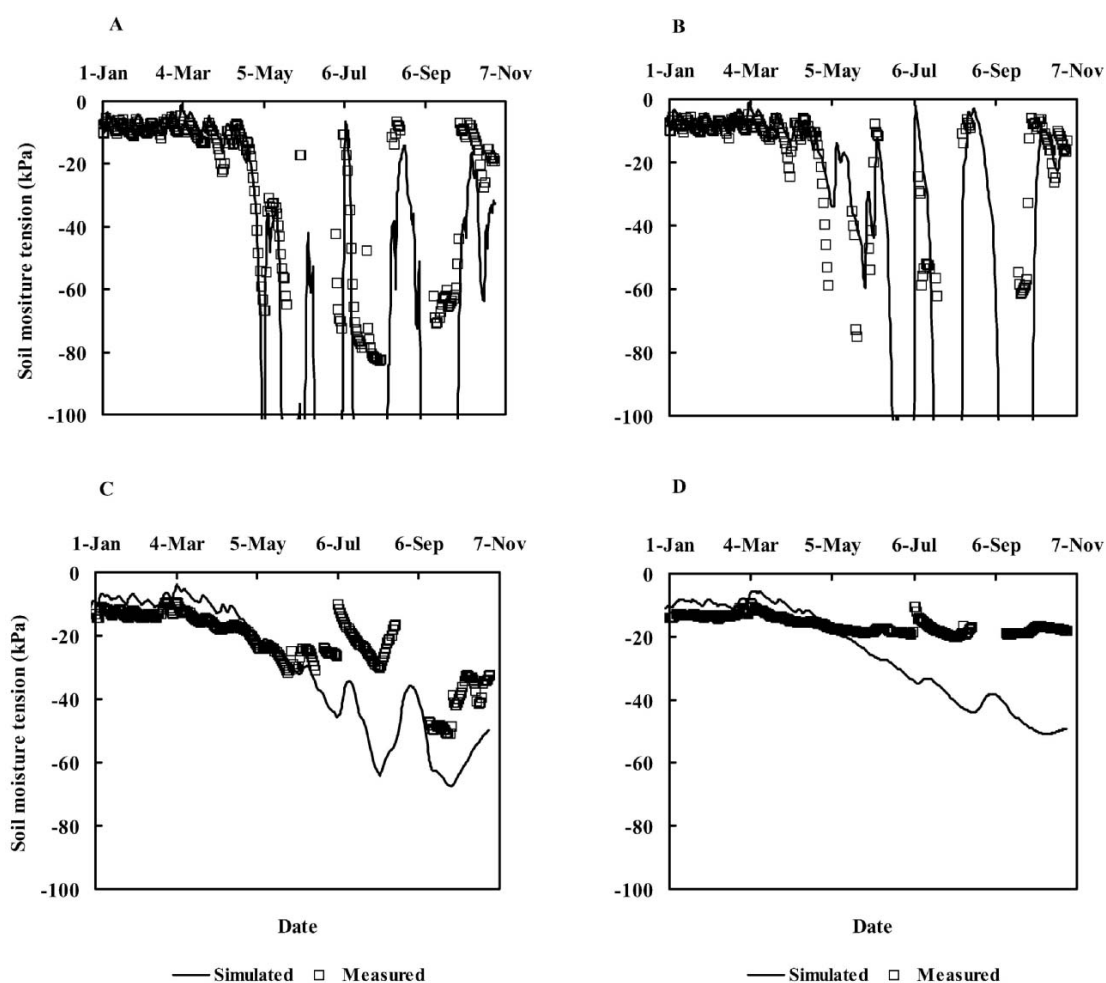


Figure 5. Measured and simulated pressure head in the non-irrigated plots (treatment A) at 0.15 m depth below (A) and near (B) the tree, 0.35 m depth (C) and 0.55 m depth (D) in 1999.

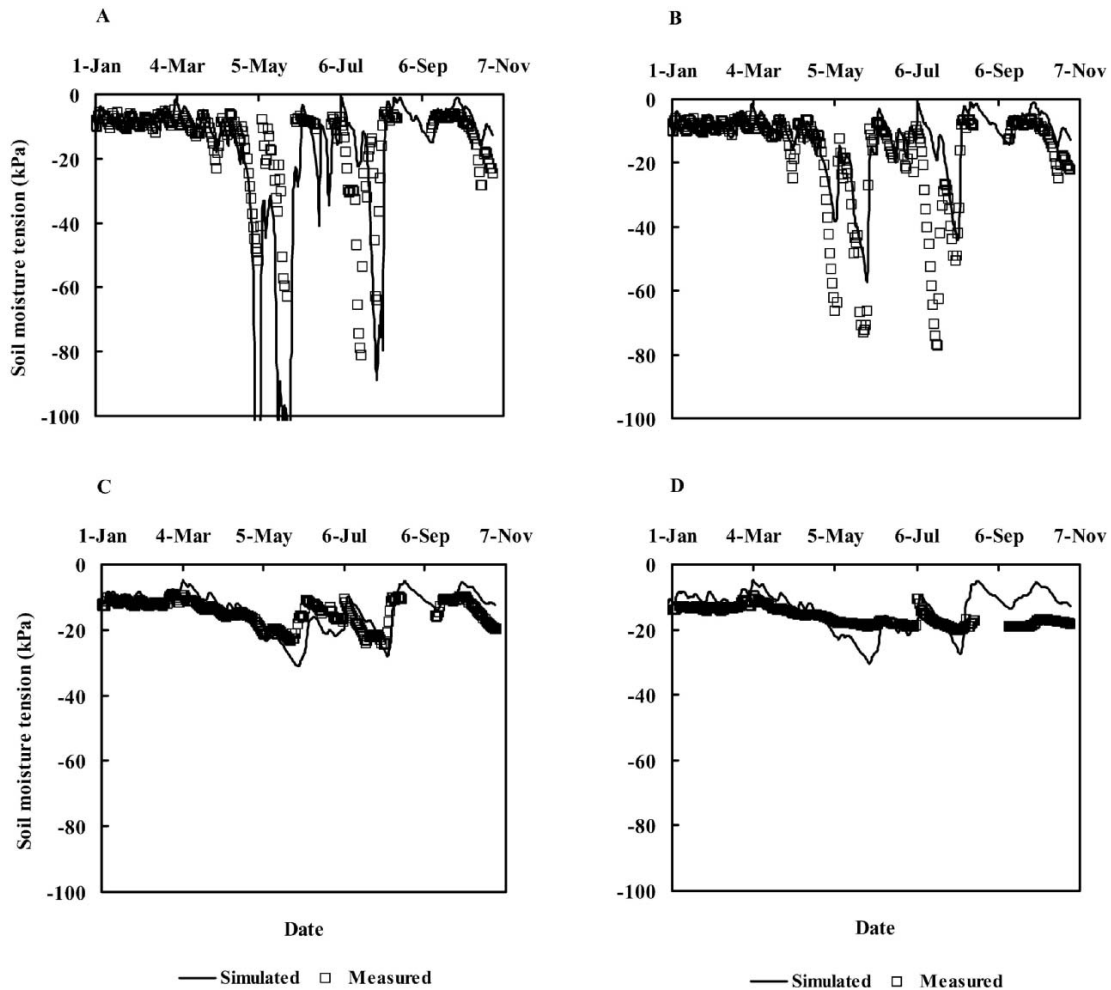


Figure 6. Measured and simulated pressure head in the drip-irrigated plots (treatment D) at 0.15 m depth below (A) and near (B) the tree, 0.35 m depth (C) and 0.55 m depth (D) in 1999.

tree in treatment A. The opposite was found in treatment D. The driest conditions were found in treatment A at 0.35 m depth. No differences within treatments were found below or between the trees at 0.35 m depth and no differences between treatments or position were found at 0.55 m depth. Because of that, h data below and between the trees were averaged per treatment at 0.35 and 0.55 m depths (Figures 5 and 6). The measurements at 0.85 m depth were close to the measurements at 0.55 m depth (data not shown).

Simulated pressure head

The simulated h followed similar wetting and drying patterns as the measured h (Figures 5 and 6). At the beginning of May in the second growing season, the simulated h between the trees at 0.15 m depth indicated

wetter conditions than the measured h (Figures 5B and 6B, both treatments), whereas the simulated h below the tree at the same depth, was in agreement with the measurements (Figures 5A and 6A). The model predicted wetter conditions than were measured in both treatments at depths of 0.35 and 0.55 m the winter period (Figures 5C, D and 6C, D). Half way through the second growing season, however, the simulated h indicated drier conditions in treatment A at 0.35 and 0.55 m depth. Differences between measured and simulated h were found at large precipitation intensity (Figure 7A). The simulated h showed a slow recovery to field capacity. Simulated h was in better agreement with the measurements when smaller amounts of precipitation rates occurred repeatedly (Figure 7B).

Table 5. The geometric mean (antilogarithm of the mean of the logarithmic transformed data) of pressure head (kPa) measured at different depths in treatment A (no irrigation) and treatment D (drip irrigation 0.5 L per plant per day) below and between the trees in 1998 and 1999. Different letters denote significant difference (5%) of the means within a year. No LSD is given because analysis was done on logarithmic transformed data to obtain a normal distribution of the residuals

Years	Treatments	Position	Pressure head at different depths (m):		
			0.15	0.35	0.55
1998			0.15	0.35	0.55
	A: no irrigation	Below	-13.5	-15.0	-12.9
	A: no irrigation	Between	-12.2	-13.2	-13.4
		Mean	-12.9 bc	-14.1 c	-13.2 bc
	D: drip irrigation	Below	-9.8	-12.2	-13.2
	D: drip irrigation	Between	-10.6	-12.8	-12.5
		Mean	-10.2 a	-12.6 b	-12.9 bc
1999					
	A: no irrigation	Below	-15.6 cd	-20.8 e	-15.3 c
	A: no irrigation	Between	-11.7 ab	-19.8 de	-16.3 cd
	D: drip irrigation	Below	-10.8 a	-14.1 bc	-15.3 c
	D: drip irrigation	Between	-13.7 bc	-14.9 c	-16.4 cd

Table 6. Statistical indices for the goodness of the fit between the observed and simulated pressure head (kPa) of treatment A (no irrigation), treatment D (drip irrigation 0.5 L per plant per day) and of all data. M is the mean difference between simulated and observed (kPa, standard error between brackets), E is the relative error (%), r the correlation coefficient and ± 2.5 or ± 5 are the number of simulations within 2.5 and 5 kPa of observations, respectively

	M (kPa)	E (%)	r	± 2.5 (%)	± 5.0 (%)	Number of observations
A: no irrigation	-0.03 (0.23)	6	0.69	19	49	2394
D: drip irrigation	-2.5 (0.10)	18	0.67	34	67	3574
All data	-1.5 (0.11)	13	0.68	28	58	5968

The correlation coefficients (r) between measured and simulated h of treatment A, treatment D or both treatments together, were positive (Table 6). The mean difference (M) for treatment A was not different from zero, indicating that there were no systematic differences between measured and simulated h . M was significantly less than zero for treatment D and all data together and indicated systematic deviations. However, the simulations were within about 18% of the measurements (E) and most were within 5 kPa of the measured values (Table 6). The simulated patterns of the pressure head with the alternative bottom boundary condition using measured pressure heads at 0.85 m below soil surface were similar to the ones presented above. Also, the leaching predicted by both types of

bottom boundary condition were comparable (data not shown). Therefore, all other result in this manuscript refer to simulations with the free drainage bottom boundary condition.

Sensitivity analysis

Sensitivity analysis showed that WUE had a large influence on cumulative T_p and T_a whereas a , $h_{r,1/2}$, K_1 , K_s and α_w : α_d were less important (Table 7). The sensitivity of all investigated input parameters showed a linear response in the tested range except for K_s and α_w : α_d .

A decrease of WUE of 10% increases the cumulative T_p with 9.8%. Although an EL of 1 is expected

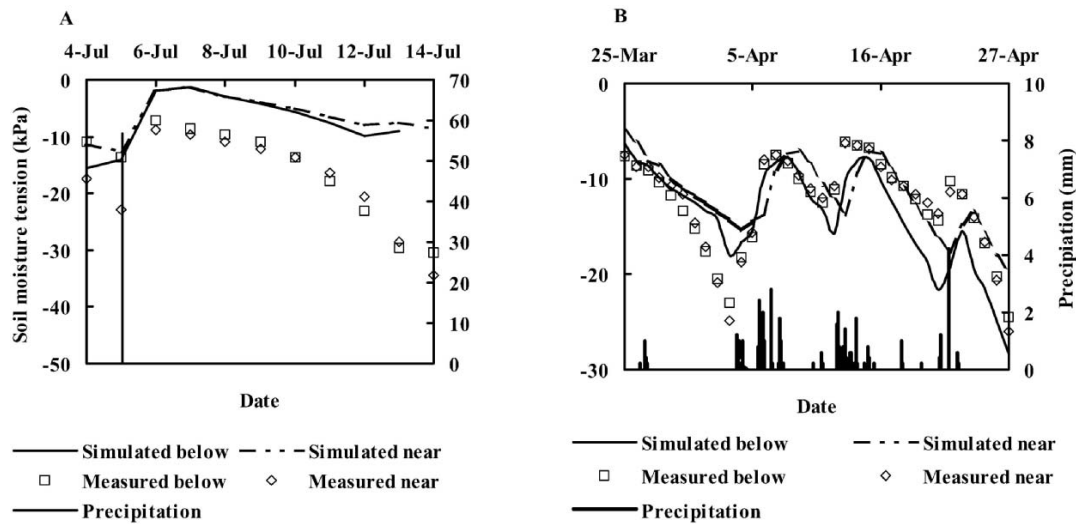


Figure 7. Pressure head measured below and near the tree, and simulated below and near the tree in the non-irrigated at 0.15 m depth when 57 mm of precipitation occurred (A) and when small (<10 mm) amounts of precipitation occurred (B).

under well-watered conditions, it is less than 1. There are two possible reasons for this effect. First, the root system may be unable to fulfill the demand for water because there are not enough roots. In that case, $T_a < T_p$, less dry mass is produced, followed by less LAI and thus T_p is reduced. Second, h decreases and the root system can not fulfill the water demand. Again, T_a is less than T_p and thus T_p is reduced through a reduced LAI . A similar effect was found for the cumulative T_a for the same reasons only slightly stronger (Table 7).

There was a negative effect of the change in the input parameters a and K_1 on model output parameters whereas a positive effect was found for $h_{1/2}$. However, the sensitivity of the model output to these input parameters was within about 0.03. The effect of change in the site-specific characterization of the soil was small, but increased when input parameters were changed from -50% to -75% due to a non linear response of the model output (Table 7).

Results on model irrigation scheduling

Irrigation was applied only a few times in the first growing season (1998) and increased dry mass production by 5% at the most (Figure 8A, C). Leaching in the first growing season increased up to 13% at an irrigation threshold level of -15 kPa (Figure 8B, D). At the end of the second growing season, however, leaching was increased by 25% whereas dry

mass increased by 15%. When the irrigation threshold level was decreased to -100 kPa still an increased dry mass production was found of 15%, compared to no irrigation, when the irrigation threshold level was measured 0.15 m below the tree (Figure 8A). A response was found when the irrigation threshold was measured at 0.25 m depth (Figure 8C). However, 7% increase in dry mass production was found with an irrigation threshold of -100 kPa in the second growing season. Leaching decreased faster with decreasing threshold levels when measured at 0.25 m compared to 0.15 m depth (Figure 8B and C).

The decrease in leaching with decreasing threshold values was not monotonic. For example, in the first growing season the leaching at a threshold of -24 kPa was larger than at -20 kPa (Figure 8B). This occurred when an irrigation event was postponed due to a lower threshold value, finely applied but then shortly followed by an extended period of wet conditions, for instance the winter period. When the irrigation event took place earlier (higher threshold value), the soil profile was drier when the extended period of wet conditions arrived and consequently less leaching was simulated. Due to this delayed irrigation, the increased leaching was in some scenarios even larger than the amount of applied irrigation.

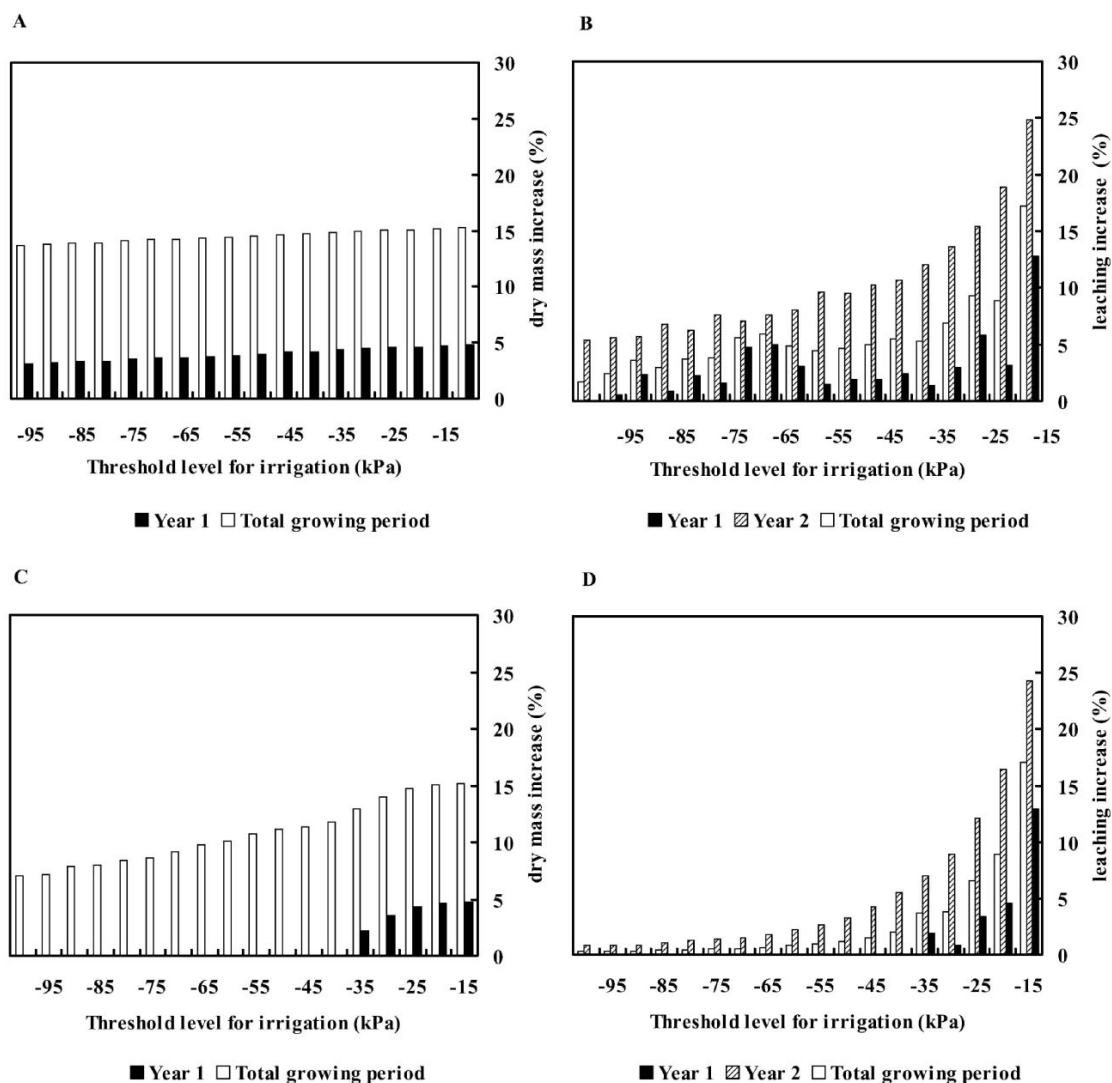


Figure 8. Dry mass increase (%) in the first growing season and the total growing period and increase in leaching (%) in the first and second growing season, and the total growing period, compared to the non irrigated treatment with threshold levels measured 0.15 m (A and B) and 0.25 m (C and D) below the tree. Irrigation threshold levels ranged from -15 to -100 kPa with 5 kPa intervals.

Discussion

Short periods of water stress in young coniferous trees do not lead to permanent losses of leaf elongation rates and subsequently to production losses (Miller, 1965). This suggests that h in the rooting environment in 1998 was not a production-limiting factor. Longer periods of water stress, however, as observed in the second growing season, reduced *SDM* (treatments A and B) although *LAI* and *LDM* were not reduced. Reduced leaf area in response to drought stress, is a common reaction of plants to reduce water loss by transpiration (El Sharkawy and Cock, 1987). The leaf area can be

reduced through reduced expansion growth but also by shedding of older leaves. However, shedding of older leaves by increased lignification of leaf material was not observed in our trial.

The h in treatment A was lower below the tree than between the trees, indicating a horizontal gradient of the pressure head and thus a water flow towards the tree. In treatment D, wetter conditions were found below the tree than in between the trees, also indicating a horizontal gradient of the pressure head and thus water flow away from the area where daily irrigation was provided. To simulate these measured horizontal gradients, it was necessary to use a soil moisture bal-

Table 7. Output of the model at reference conditions and the mean elasticity (Equation 10) of model output to a change in Water Use Efficiency (WUE , kg kg^{-1}), a (-), the root water pressured head at which $T_a = 0.5T_p(h_{r,1/2})$ the root hydraulic conductivity (K_1 , cm d^{-1}), the saturated conductivity of the top soil (K_s , m d^{-1}) and the ratio between alpha wet (α_w , m^{-1}) and alpha dry (α_d , m^{-1})

	LAI ($\text{m}^2 \text{m}^{-2}$)	LDM (g m^{-2})	SDM (g m^{-2})	$FRDM$ (g m^{-2})	$CRDM$ (g m^{-2})	ΣT_p (m)	ΣT_a (m)
Reference output	4.9	911	854	1540	343	0.476	0.475
Partial sensitivities							
WUE	-0.022	-0.023	-0.020	-0.017	-0.020	0.984	0.974
a	-0.032	-0.034	-0.029	-0.025	-0.029	-0.017	-0.030
$h_{r,1/2}$	0.017	0.018	0.015	0.013	0.015	0.009	0.016
K_1	-0.015	-0.016	-0.014	-0.012	-0.013	-0.009	-0.014
K_s (-50 to 75%)	0.001	0.001	0.001	0.001	0.001	0.001	0.001
K_s (-75 to -50%)	0.004	0.004	0.003	0.004	0.002	0.002	0.003
$\alpha_w: \alpha_d$ (-50 to 75%)	0.000	0.000	0.000	0.000	0.000	0.000	0.000
$\alpha_w: \alpha_d$ (-75 to -50%)	0.003	0.003	0.003	0.003	0.002	0.002	0.003

ance model that simulated both vertical and horizontal water transport. This phenomenon of horizontal gradients in the soil profile is well known in drip-irrigated systems (Brandt et al., 1971; Coelho and Or, 1996).

The combined plant-soil model was able to simulate dry mass production in treatment D successfully (Figure 3). The model slightly underestimated LAI and LDM in treatment A, whereas SDM was slightly overestimated. A lower LAI results in a reduced dry mass production and subsequently in a reduced LAI . This effect is amplified by the negative feedback of a lower LAI on F_{int} , resulting in a lower dry mass production. The model partitioned dry mass to the various sinks independent of pressure heads. Irrigation is known to change dry mass partitioning between the various organs (Jones, 1992). Further adjustments in dry mass partitioning depending on h need to be made.

The systematic deviations between simulated and measured h indicate that the model predicts higher h values during wet conditions than were observed. Preferential flow in water repellent soils contributes to an increased transport of water into the deeper subsoil (Ritsema and Dekker, 2000). Our h measurements suggest that precipitation amounts, which are larger than those to obtain field capacity are transported to the deeper subsoil more rapidly than is simulated (Figures 5D and 7A). This effect (preferential flow) is currently not implemented in the model and may contribute to the systematic deviation between simulated and measured h . Another source of error may be the assumed bottom boundary condition of free drainage

(unit gradient). Free drainage is only valid if the gradient in total soil water potential equals one. This may not be the case during sharply fluctuating conditions near the soil surface, like large amounts of precipitation or irrigation, or high losses of water due to uptake or evaporation. In addition, errors in the soil physical characterization due to the fitting procedure may have contributed to the systematic deviations.

From the limited sensitivity analysis it appeared that the model was most sensitive to WUE (Table 7). *Thuja* produced $7.6 \cdot 10^{-3}$ kg dry mass per kg water transpired which is high compared to the WUE of agricultural crops ($1.1 \cdot 10^{-3}$ to $2.7 \cdot 10^{-3}$ kg $DM \text{ kg}^{-1} \text{ H}_2\text{O}$; Jones, 1992; Van Keulen and Van Laar, 1986). Stilma (2001) found values for WUE of *Thuja occidentalis* 'Brabant' of $8.26 \cdot 10^{-3}$ to $9.09 \cdot 10^{-3}$ kg dry mass per kg water transpired. In that study, WUE was measured on potted plants as dry mass increase and total water transpired over a period of 6 weeks. The values thus obtained are slightly higher than our values for WUE . The instantaneous WUE (net photosynthesis measured as CO_2 uptake/transpiration measured as water loss) of deciduous forests are generally in the order of 6–12 mg $\text{CO}_2 \text{ g}^{-1} \text{ H}_2\text{O}$ (Baldocchi et al., 1987). This is equivalent to $2.7 \cdot 10^{-3}$ to $5.5 \cdot 10^{-3}$ kg dry mass per kg water, assuming an assimilation requirement for overall dry mass of 1.5 kg carbohydrates per kg dry mass (Penning de Vries et al., 1983). These values are lower than our values but evergreen species tend to have higher instantaneous WUE than deciduous species (DeLucia et al., 1988; Gower and Richards, 1990). Another

estimate for *WUE* is the carbon isotope composition ($^{13}\text{C}/^{12}\text{C}$). Marshall and Zhang (1994) showed that *Thuja* had the lowest carbon isotope discrimination and presumably the highest *WUE* of all investigated evergreen species.

These results support our findings that *Thuja* uses water very efficiently to produce dry mass. Decreasing irrigation threshold levels did not automatically decrease leaching (Figure 8B, D) although that may be expected. Irrigation followed by prolonged wet periods increased leaching to larger amounts than were irrigated. This effect was found more often and more pronounced when the irrigation threshold was situated at 0.15 m depth rather than at 0.25 m depth. The depth at which the irrigation threshold was situated had a large effect on dry mass production and leaching at decreasing threshold levels as well. These two aspects indicate that irrigation scheduling is more complicated than just using the best irrigation threshold level. The depth at which the irrigation threshold is measured and the actual and future weather data are very important and need to be taken into account as well as to develop irrigation guidelines with minimal environmental impact.

Conclusions

Irrigation was not always necessary to increase dry mass production of *Thuja occidentalis* 'Brabant' under Dutch climatic conditions, as our results of 1998 showed.

Pressure head measurements and model calculations revealed that the need for irrigation may occur sooner than half May in the second growing season in warm and dry spring conditions. Calculations with the combined model could support growers in their decisions to irrigate during the growing season to increase dry mass production. However, several modifications need to be made to the model: dry mass partitioning between leaf and stem dry mass and preferential flow are the two major aspects that need further development.

The combined model was able to predict effects of irrigation on dry mass production. With this tool we quantified the benefits of irrigation on dry mass production but also on leaching. Results on leaching however were only considered relatively to the non-irrigated simulation, which limits statements on environmental benefits by optimal irrigation strategies. However, irrigation increased leaching and therefore

the risk of nitrogen losses, as was found by many other researchers (Pang et al., 1997; Sanchez et al., 1994; Smika and Watts, 1978). This combined model, however, indicated that developing optimal irrigation strategies is more complicated when leaching is considered, because leaching can increase at lower irrigation threshold levels. The results on model irrigation scheduling do not allow the conclusion that there is one unique combination of irrigation threshold value and depth at which the value is to be monitored in order to obtain optimal production at minimal leaching. The user has to make his or her own trade-off decision what strategy to apply.

Acknowledgements

This work was supported by the Dutch program LNV-DWK 317 for Manure and Minerals and performed at the Applied Plant Research Nursery Stock Unit. We thank Prof. Dr O. Oenema (Soil Quality Group, Wageningen University) and Dr E. Heuvelink (Horticultural Production Chains Group, Wageningen University) for critically reading the manuscript.

References

- Addiscott T M and Whitmore A P 1987 Computer simulation of changes in soil mineral nitrogen and crop nitrogen during autumn, winter and spring. *J. Agricul. Sci. Cambridge* 109, 141–157.
- Ahuja L R and Nielsen D R 1949 Field soil-water relations. *Agronomy (Madison)* 30, 143–190.
- Averdieck H and Bohne H 1994 Untersuchungen in einem Alleebaumquartier unter Berücksichtigung der Geholzqualität (in German; Studies on additional irrigation of an avenue tree nursery field with special reference to tree quality). *Baumschulpraxis* 24, 122–124.
- Baldocchi D D, Verma S B and Anderson D E 1987 Canopy photosynthesis and water-use efficiency in a deciduous forest. *J. Appl. Ecol.* 24, 251–260.
- Brandt A, Bresler E, Diner N, Ben Asher I, Heller J and Goldberg D 1971 Infiltration from a trickle source: I. mathematical models. *In Soil Science Society of America Proceedings*, pp. 675–682.
- Campbell G S 1985 *Soil Physics with BASIC. Transport Models for Soil-plant Systems*. Elsevier Science Publishers B.V., Amsterdam. 150 pp.
- Campbell G S 1991 Simulation of water uptake by plant roots. *In Modeling Plant and Soil Systems*. Eds. J Hanks and J T Ritchie. pp. 273–285. American Society of Agronomy, Madison, WI.
- Coelho F E and Or D 1996 A parametric model for two-dimensional water uptake intensity by corn roots under drip irrigation. *Soil Sci. Soc. Am. J.* 60, 1039–1049.
- De Willigen P and Heinen M 2001 Cylindrical coordinates: FUSSIMR. *In FUSSIM2 Version 5. New Features and Update User's Guide*. Eds. M Heinen and P De Willigen. pp. 17–24. Alterra report 363, Alterra, Green World Research, Wageningen.

- De Willigen P, Heinen M, Mollier A and Van Noordwijk M 2002 Two-dimensional growth of a root system modelled as a diffusion process. I. Analytical solutions. *Plant Soil* 240, 225–234.
- De Willigen P and Van Noordwijk M 1987 Roots, Plant Production and Nutrient Use Efficiency. pp. 282. Agricultural University Wageningen, Wageningen.
- DeLucia E H, Schlesinger W H and Billings W D 1988 Water relations and the maintenance of Sierran conifers on hydrothermally altered rock. *Ecology* (N Y) 69, 303–311.
- Edwards D R 1993 The Water Relations of *Thuja occidentalis* L. in Response to Repeated Water Stress Conditioning. pp. 167. University of Guelph, Guelph, Ontario.
- El Sharkawy M A and Cock J H 1987 Response of cassava to water stress. *Plant Soil* 100, 345–360.
- Gijzen H 1992 Simulation of Photosynthesis and Dry Matter Production of Greenhouse Crops. CABO-DLO, Wageningen. 70 pp.
- Gilman E F, Yeager T H and Weigle D 1996 Fertilizer, irrigation and root ball slicing affects Burford holly growth after planting. *J. Environ. Hortic.* 14, 105–110.
- Gower S T and Richards J H 1990 Larches: deciduous conifers in an evergreen world. *Biosci.* 40, 818–826.
- Heinen M 1997 Dynamics of Water Nutrients in Closed, Recirculating Cropping Systems in Glasshouse Horticulture: with special attention to lettuce grown in irrigated sand beds. Wageningen Agricultural University, Wageningen. 270 pp.
- Heinen M 2001 FUSSIM2: brief description of the simulation model and application to fertigation scenarios. *Agronomy (Madison)* 21, 285–296.
- Heinen M and De Willigen P 1998 FUSSIM2. A Two-Dimensional Simulation Model for Water Flow, Solute Transport and Root Uptake of Water and Nutrients in Partly Unsaturated Porous Media. Quantitative Approaches in Systems Analysis No 20. DLO Research Institute for Agrobiological and Soil Fertility and the C.T. de Wit Graduate School for Production Ecology, Wageningen. 140 pp.
- Heinen M and De Willigen P 2001 FUSSIM2 version 5: New Features and Updated user's Guide. Alterra report 363, Alterra, Green World Research, Wageningen. 164 p.
- Heinen M, Mollier A and De Willigen P 2003 Growth of a root system described as diffusion. II. Numerical model and application. *Plant Soil* 252, 251–265.
- Hornig R, Bohne H and Behrens V 1997 Effect of irrigation on growth and yield of Forsythia X intermedia 'Spectabilis' and soil nitrogen content on two sites. *Gartenbauwissenschaft* 62, 113–119.
- Jones H G 1992 Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology. Cambridge University Press, Cambridge. 428 p.
- Marshall J D and Zhang J W 1994 Carbon isotope discrimination and water-use efficiency in native plants of the north-central Rockies. *Ecology* (N Y) 75, 1887–1895.
- Miller L M 1965 Changes in radio-sensitivity of Pine seedlings subjected to water stress during chronic gamma irradiation. *Health Phys.* 11, 1653.
- Mohren G M J 1987 Simulation of Forest Growth, Applied to Douglas Fir Stands in the Netherlands. Agricultural University Wageningen, Wageningen. 184 pp.
- Mualem Y 1976 A new model for predicting the hydraulic conductivity of unsaturated porous media. *Water Resour. Res.* 12, 513–522.
- Mualem Y 1984 A modified dependent-domain theory of hysteresis. *Soil Sci.* 137, 283–291.
- Pang X P, Letey J and Wu L 1997 Irrigation quantity and uniformity and nitrogen application effects on crop yield and nitrogen leaching. *Soil Sci. Soc. Am. J.* 61, 257–261.
- Penning de Vries F W T, Van Laar H H and Chardon M C M 1983 Bioenergetics of growth of seeds, fruits and storage organs. *In* Potential Productivity of Field Crops under Different Environments. Eds. S J Banta and W H Smith. pp. 37–59.
- Pionke H B, Sharma M L and Hirschberg K J 1990 Impact of irrigated horticulture on nitrate concentrations in groundwater. *Agric. Ecosyst. Environ.* 32, 1–2.
- Ponder H G, Gilliam C H and Evans C E 1984 Trickle irrigation of field-grown nursery stock based on net evaporation. *Hortsci.* 19, 304–306.
- Pronk A A, De Willigen P, Heuvelink E and Challa H 2002 Development of fine and coarse roots of *Thuja occidentalis* 'Brabant' in non-irrigated and drip irrigated field plots. *Plant Soil* 243, 161–171.
- Pronk A A, Goudriaan J, Stilma E and Challa H 2003a A simple method to estimate radiation interception by nursery stock conifers: A case study of eastern white cedar. *NJAS* 51, 279–295.
- Pronk A A, Heuvelink E and Challa H 2003b Dry mass production and leaf area development of field-grown ornamental conifers: measurements and simulation. *Agric. Sys.* 78, 337–353.
- Pronk A A and Ravesloot M B A 1998 Fertigation of field grown nursery stock on sandy soils in the Netherlands. *In* Fertilization for Sustainable Plant Production and Soil Fertility, Gent, Belgium, 7–13 September 1997, 1998. Eds O Van Cleemput, S Hanaklaus, G Hofman, E Schnug and A Vermoesen. pp. 480–486. Proceedings of the 11th International World Fertilizer Congress.
- Rappoldt C and Van Kraalingen D W G 2001 FSE 4.0. User Guide and Technical Documentation. Technical Document. Alterra, Wageningen. 63 p.
- Ritsemá C J and Dekker L W 2000 Preferential flow in water repellent sandy soils: principles and modeling implications. *J. Hydrol. (Amst.)*, 308–319.
- Rudinger M, Hallgren S W, Steudle E and Schulze E D 1994 Hydraulic and osmotic properties of spruce roots. *J. Exp. Bot.* 45, 1413–1425.
- Sanchez C A, Roth R L and Gardner B R 1994 Irrigation and nitrogen management for sprinkler-irrigated cabbage on sand. *J. Am. Soc. Hortic. Sci.* 119, 427–433.
- Smika D E and Watts D G 1978 Residual nitrate-N in fine sand as influenced by N fertilizer and water management practices. *Soil Sci. Soc. Am. J.* 42, 923–926.
- Soil Conservation Service 1975 Soil Taxonomy. A Basic System of Soil Classification for Making and Interpreting Soil Surveys. USDA. 754 pp.
- Spaans E J A and Baker J M 1992 Calibration of Watermark soil moisture sensors for soil matric potential and temperature. *Plant Soil* 143, 213–217.
- Stilma E 2001 Description of Conifer Growth Compared to Roses Supported by Experimental Research, with Emphasis on Radiation Interception and Water Use Efficiency. Plant Production Systems Group, Wageningen University, Wageningen. 71 pp.
- Thomson A J and Moncrieff S M 1982 Prediction of bud burst in Douglas-fir by degree-day accumulation. *Can J. For. Res.* 12, 448–452.
- Van Genuchten M T 1980 A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Sci. Soc. Am. J.* 44, 892–898.
- Van Ittersum M K, Leffelaar P A, Van Keulen H, Kropff M J, Bastiaans L and Goudriaan J 2003 On approaches and applications of the Wageningen crop models. *Eur. J. Agron.* 18, 201–234.

- Van Keulen H 1986 A simple model of water-limited production. *In* Modelling of Agricultural Production: Weather, Soils and Crops. Eds. H Van Keulen and J Wolf. pp. 130–152. Pudoc, Wageningen.
- Van Keulen H and Van Laar H H 1986 The relation between water use and crop production. *In* Modelling of Agricultural Production: Weather, Soils and Crops. Eds. H Van Keulen and J Wolf. pp. 117–129. Pudoc, Wageningen.

- Wösten J H M, Veerman G J, De Groot W J M and Stolte J 2001 Waterretentie- en doorlatendheidskarakteristieken van boven- en ondergronden in Nederland: de Staringsreeks. Alterra report no 153, Alterra, Green World Research, Wageningen. 86 p.

Section editor: P.J. Gregory