Jones, T., McIvor, I., McManus M., 2016. Drought tolerance and water-use efficiency of five hybrid poplar clones. In: *Integrated nutrient and water management for sustainable farming*. (Eds L.D. Currie and R.Singh). http://flrc.massey.ac.nz/publications.html. Occasional Report No. 29. Fertilizer and Lime Research Centre, Massey University, Palmerston North, New Zealand. 13 pages.

DROUGHT TOLERANCE AND WATER-USE EFFICIENCY OF FIVE HYBRID POPLAR CLONES

Trevor Jones[1], Ian McIvor[1], and Michael McManus[2]

[1]Plant & Food Research, Private Bag 11600, Palmerston North 4442
[2]Massey University, Private Bag 11222, Palmerston North 4442
trevor.jones@plantandfood.co.nz

Abstract

The physiological responses to soil water deficits of four new experimental hybrid poplar clones of *P. maximowiczii* × *P. trichocarpa* and *P. trichocarpa* × *P. nigra*, and the drought-tolerant *P. deltoides* × *P. nigra* ‘Veronese’ poplar clone that is widely used for soil conservation in New Zealand, were evaluated in a greenhouse pot trial, with well-watered, moderate and severe (90, 60 and 40% of field capacity) soil water deficit treatments. The biomass growth, water-use efficiency, leaf stomatal conductance and water potential of the trees were measured to determine the drought tolerance of the poplar clones.

The ‘Veronese’ poplar clone was sensitive to water stress, with greater leaf abscission and suppression of new leaf development, and higher root-to-shoot ratios under soil water deficits, and was well adapted for drought-prone areas. The four new experimental hybrid poplar clones were not as sensitive to moderate soil water deficits, due in part to lower water use and better water-use efficiency, and in some clones were able to combine these with high biomass productivity. The new hybrid poplar clones appear to be adapted to moderately drought-prone areas, where there is an advantage in combining high productivity and high water-use efficiency to better utilise the available water during the growing season.

Introduction

Soil water deficit is a major factor limiting the survival and growth of plants in many environments. Pastoral hill country in New Zealand is subject to periodic summer drought conditions which can produce significant soil water deficits (Garnier 1958). This can reduce the survival and growth of poplar trees (Ceulemans & Deraedt 1999) and compromise the effectiveness of poplar (*Populus* spp.) trees for soil conservation.

The physiological response of poplar trees to water deficits differs among poplar species and hybrids (Kelliher and Tauer 1980; Pallardy and Kozlowski 1981; Blake et al. 1984; Hinckley et al. 1989; Gebre and Kuhns 1991; Braatne et al. 1992; Yang et al. 2010), with wide variability in the water-use efficiency and tolerance to drought conditions (Blake et al. 1984; Marron et al. 2005; Monclus et al. 2005, 2006; Strong & Hansen 1991; Yin et al. 2005; Zhang et al. 2004).

There are consistent genotypic differences in the water-use efficiency (WUE) of poplar species and hybrids, and a lack of correlation between the WUE and productivity of poplar clones (Marron et al. 2005; Monclus et al. 2005, 2006). This indicates there is potential for the selection of poplar clones that combine high water-use efficiency and high productivity, which would be an advantage for the growth of poplar trees in moderately drought-prone areas (Bonhomme et al. 2008; Marron et al. 2005).

Table 1. Hybrid poplar clones used in the experiment and the parent clones.

Poplar clones	Female parent	Male parent
MT103 - 07-05-103	*P. maximowiczii* 87-007-04	*P. trichocarpa*
MT304 - 07-02-304	*P. maximowiczii* 87-007-01	*P. trichocarpa*
TN008 - 07-03-008	*P. trichocarpa*	*P. nigra* PN866
TN014 - 07-06-014	*P. trichocarpa*	*P. nigra* PN874 'Blanc de Garonne'
'Veronese'	*P. deltoides*	*P. nigra*

In this study, the physiological responses to drought conditions of four new experimental hybrid poplar clones of *P. maximowiczii* × *P. trichocarpa* and *P. trichocarpa* × *P. nigra* were evaluated and compared with the drought-tolerant *P. deltoides* × *P. nigra* 'Veronese' poplar clone that is widely used for soil conservation in New Zealand (Table 1). The tree growth and water-use parameters of these poplar clones were evaluated in a greenhouse water-stress experiment, to characterize the drought tolerance, biomass growth, water-use efficiency, and the capacity for drought acclimation of the poplar clones.

Materials and methods

Experiment design

A completely randomised design was used in the experiment, with five poplar clones × three water regimes (total of 15 treatments). Four replicates were used for each treatment (total of 60 pots). The three water regimes were: well-watered (90% of field capacity), moderate soil water deficit (60% field capacity), and severe soil water deficit (40% field capacity), where the field capacity was defined as the soil water content of the pots after 24 hours of drainage, following saturation of the soil.

The poplar trees were grown from cuttings in 30-L plastic pots in a greenhouse at Plant & Food Research in Palmerston North. The roof and walls of the greenhouse are enclosed with clear plastic sheeting, with the exception of the lower walls. These were covered with cloth along the two long sides of the greenhouse, to provide good ventilation and exposure to the wind. The greenhouse was ventilated by two fans that were activated when the air temperature of the greenhouse reached 22°C.

Propagation of the poplar trees

The poplar trees were propagated from cuttings of 15 to 26 mm diameter and 40 cm length. The cuttings were cut from 1-year-old shoots from nursery stools. The diameter of each cutting at the mid-point (along the length) was measured prior to soaking in water for 5 days. The cuttings were selected to provide a similar distribution of mid-point diameter for each poplar clone.

The poplar cuttings were planted on 1 October 2013, with one cutting planted in each of the 30-L plastic pots. The cuttings were planted after the soil in the pots was saturated with water, and drained for 24 hours to field capacity. The pots were positioned in a randomised block design inside the greenhouse. The pots were placed in four rows along the length of the greenhouse (Figure 1), with one pot of each poplar clone randomly assigned to each of three blocks of five pots within each row.

The pots were weighed every 2 days, and the water transpired was measured and replaced to maintain the soil at 90% of field capacity (FC). The addition of water to the trees was adjusted for the growth in the fresh weight of the shoots. The evaporation of water from the soil surface was minimised by covering the surface with plastic sheeting. The poplar trees were grown at 90% of field capacity for 70 days (10 weeks), at which time the cuttings had developed sufficient shoot biomass, and then the moderate soil water deficit (60% FC) and severe soil water deficit (40% FC) treatments were applied.

Application of the soil water deficits

The trees (pots) of each poplar clone were re-allocated to four blocks in the greenhouse based on the amount of shoot biomass (leaves + stems) after 10 weeks of growth. The three trees of each clone with the largest amount of shoot biomass were allocated to block one, and the process was repeated for blocks two, three, and four, with three trees of each clone with progressively smaller amounts of shoot biomass. The three trees of each clone, in each of the four blocks, were randomly allocated to the 90%, 60%, or 40% of field capacity treatments.

The water regimes were started on 10 December 2013 by allowing the pots to dry down to the required soil water content, and were applied to the poplar trees for 49 days (7 weeks). The water regimes were maintained by weighing each pot every 2 days, and the transpired water was measured and replaced to maintain the pots at 90%, 60%, or 40% of field capacity (FC). The addition of water to the trees was adjusted for the growth in the fresh weight of the shoots.

Monitoring the growth of the poplar trees

The basal diameter, number of leaves, and height of the shoots of each tree were measured weekly. The fresh weight of the shoots (leaves + stems) was estimated for each tree using the basal diameters and heights of the shoots in the linear regression equation:

$$\mathrm{Log}_{10}\, S = \log_{10} \mathrm{a} + \mathrm{b} \log_{10} B \qquad (1)$$

where S is the fresh weight of the shoot, and B is the basal diameter multiplied by the square of the shoot height. The equation was back-transformed to the power function:

$$S = \mathrm{a}B^{\mathrm{b}} \qquad (2)$$

where the anti-log of the intercept was multiplied by a correction factor in order to account for bias inherent in fitting the model to the geometric mean rather than the arithmetic mean (Sprugel 1983). The correction factor was calculated as:

$$CF = 10^{(S^2{}_{y.x}/2)} \qquad (3)$$

where Sy.x is the standard error of the estimate (SEE) of the regression.

The regression coefficients in equation (1) were calculated using sample shoots with a wide range of basal diameter and height from nursery stools of the hybrid poplar clones. A single equation was found to give a good fit to the shoot data from all the poplar clones.

The diameter growth of the cuttings was measured at weekly intervals, from the start of the application of the water regimes. Two diameters were measured at right angles on the tree stems, using calipers and averaged.

Leaf stomatal conductance and water potential

The stomatal conductance of the leaves was measured using a cycling porometer (Delta-T porometer type AP4, Delta-T Devices Ltd, Cambridge, UK), and the water potential of the leaves was measured using a Scholander-type pressure chamber (Soil Moisture Equipment Co., Santa Barbara, California, USA). The stomatal conductance and water potential of the leaves were measured on all the poplar trees (blocks 1 to 4) at 6–7 weeks after the application of the water regimes. The measurements were made over a period of 8 days, between 13:30 and 17:30 on clear sunny days. One young fully expanded mature leaf was measured on each tree, on the first and second days of the 2-day watering cycle (total of 2 leaves per tree) to provide a wide range of water potential. The stomatal conductance was measured two to four times on the abaxial (lower) surface of each leaf, and this was followed immediately by the measurement of the water potential.

Harvesting the poplar trees

The poplar trees were harvested 49 days (7 weeks) after the application of the water regimes, on 28 January 2014. The biomass of the trees was divided for the leaves, stems, cuttings, and roots. The roots were separated from the soil by screening and washing with water the roots retained on a 2 mm size mesh. The biomass of the leaf, stem, cutting, and root partitions were measured for each tree after oven-drying at 70ºC to constant weight.

The water-use efficiency (WUE) of biomass production was determined for each tree. This was the ratio of the total biomass to the total amount of water used throughout the growing season (g biomass kg^{-1} water). The total biomass included the oven-dried leaf, stem and root weight, and the cutting weight minus the original cutting weight at the start of the experiment.

Statistical analysis

Analysis of variance (ANOVA) and covariance (ANCOVA) were used to assess the effects of the water regime, poplar clone and block (covariate), and the water regime × poplar clone interaction, on the various traits measured. The cutting diameter at the beginning of the experimental treatment period (70 days) was used as an additional covariate in the ANCOVA in order to statistically consider the effects of the initial plant size on the traits. Fisher's least-significant-difference LSD test was used to provide multiple comparisons of the poplar clone and water regime means. All the statistics were computed using the GenStat statistical software package (Version 14.2; VSN International Ltd, UK).

Results

Growth of the poplar trees prior to the soil water deficits

The poplar trees were grown at 90% of field capacity (FC) for 70 days, prior to the application of the soil water deficits of the 60% and 40% FC water regime treatments. During this period, the 'Veronese' clone had the fastest growth, with greater shoot biomass, shoot length, and leaf area (Table 2, Figure 1), while the TN008, TN014, and MT304 clones had slower growth, and the MT103 clone had the slowest growth. The number of leaves on the TN008 clone increased rapidly from 50 to 70 days (Figure 1), and it had a higher number of leaves than the other clones at 70 days. This could be attributed to the smaller size of the leaves, and to the large number of callus shoots that grew from the top of the cuttings of the TN008 clone.

Growth of the poplar trees after the application of soil water deficits

The application of the moderate and severe soil water deficits of the 60 and 40% FC water regime treatments, from 70 to 119 days, had a noticeable effect on the height growth of the poplar trees and the number of leaves.

Table 2. Shoot biomass (fresh leaf + stem weight), leaf area, number of leaves, and mean shoot height for the tallest shoot per tree, of the poplar clones at 70 days from planting. Values are the mean ± standard error, and different letters represent significant differences among the water regimes within the same clone ($P < 0.05$).

Clone	Shoot biomass Leaf + stem g	Leaf area cm^2	Number of leaves	Mean shoot height cm
MT103	130 ± 12 a	265 ± 33 a	73 ± 4 a	75 ± 5 a
MT304	212 ± 40 b	387 ± 89 a	101 ± 7 ab	82 ± 10 a
TN008	195 ± 30 ab	397 ± 46 a	265 ± 20 c	81 ± 6 a
TN014	230 ± 23 bc	344 ± 30 a	111 ± 12 b	89 ± 4 ab
'Veronese'	294 ± 13 c	546 ± 32 b	130 ± 11 b	101 ± 2 b

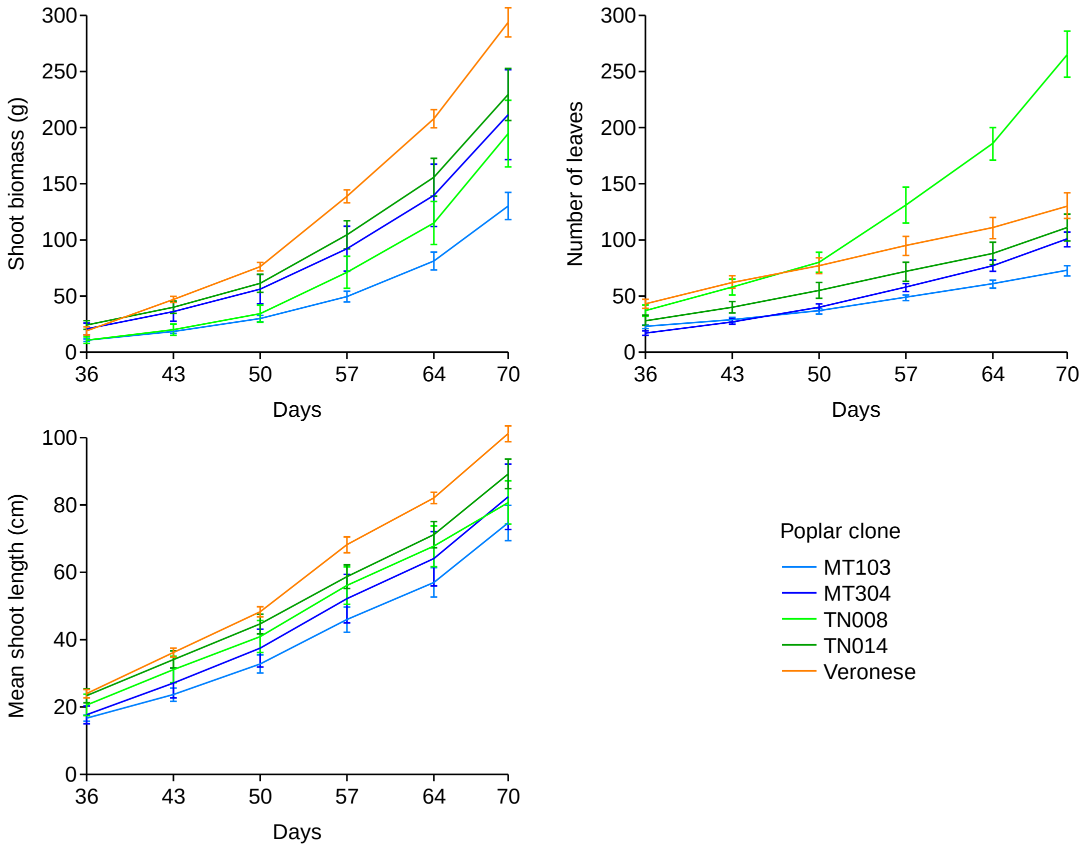

Figure 1. Growth to 70 days of the fresh shoot biomass (leaf + stem), number of leaves (per tree), and mean shoot height (for the tallest shoot per tree) of the poplar clones, prior to the application of the water regimes. The error bars are the standard errors of the means.

The height growth of the shoots was slower for the 60 and 40% FC water regime treatments (P < 0.001), compared with the 90% FC treatment (Figure 2). This was particularly noticeable for the 'Veronese', TN008 and TN014 clones, which had dropped their lower leaves in response to the moderate and severe soil water deficits. These clones had slower height growth than the MT103 and MT304 clones at 60 and 40% FC, and the 'Veronese' and TN008 clones also had slower height growth at 90% FC. The height growth of some of the 'Veronese' and TN014 trees stopped at 60% and 40% FC, and some shoot tip die-back was observed during the last 3 weeks.

The 'Veronese', TN008 and TN014 clones showed leaf senescence and abscission on the lower parts of the stems within 8 days of the commencement of the water regime treatments (Figure 3). The number of leaves on the 'Veronese' 40% and 60% FC trees declined and remained at reduced levels on the 40% FC trees, and increased only slightly for the 60% FC trees, while the 'Veronese' 90% FC trees showed a large and continued increase in the number of leaves. The TN008 and TN014 clones showed a decline in the number of leaves on the 40% FC trees, but these and the 60% FC trees then showed a slow increase in the number of leaves that was less than for the 90% FC trees. The MT103 and MT304 clones showed no leaf abscission in response to the soil water deficits of the water regimes, but the number of leaves increased more slowly for the 60% and 40% FC trees, compared with 90% FC trees.

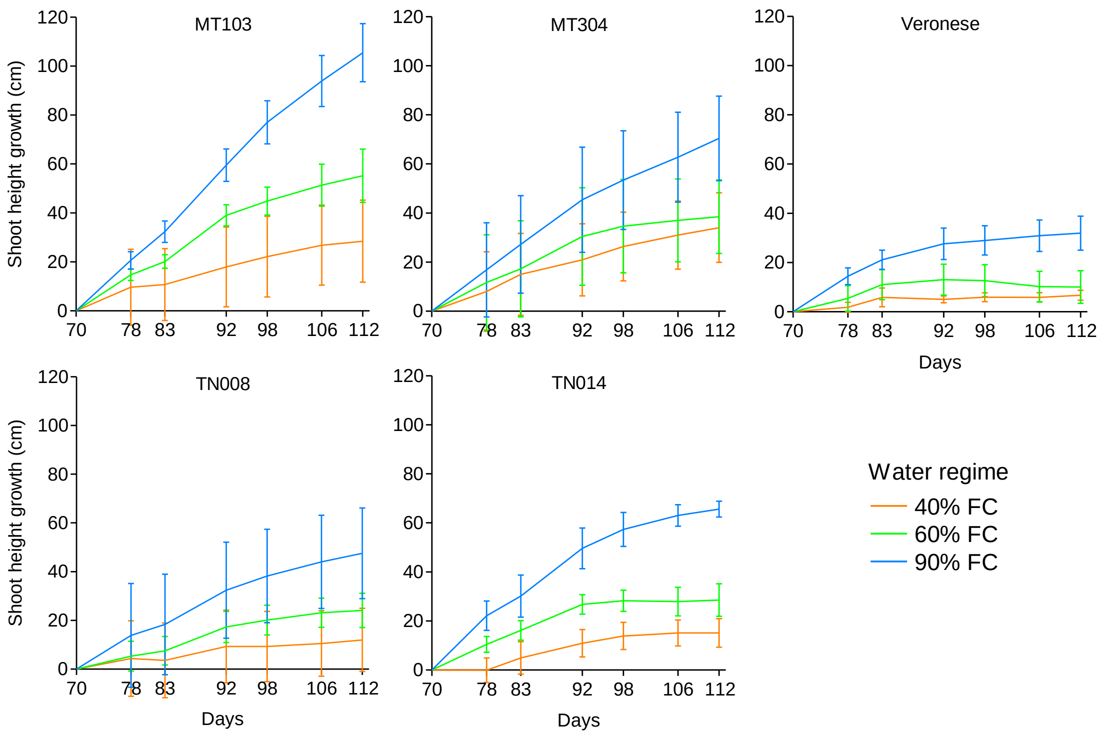

Figure 2. Growth of the mean shoot height (tallest shoot per tree) for the poplar clones, following the application of the water regimes at 70 days. The water regimes were 40, 60, and 90% of field capacity (FC). The error bars are the standard errors of the means.

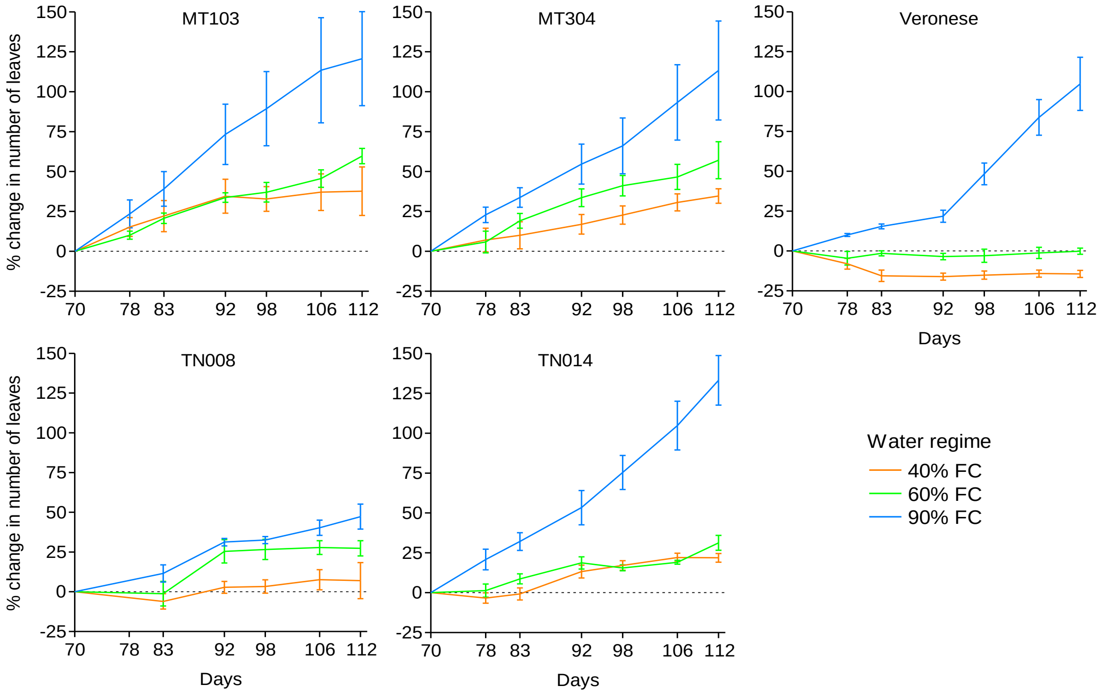

Figure 3. Change in the number of leaves on the trees of the poplar clones, following the application of the water regimes from 70 days. The water regimes were 40, 60, and 90% of field capacity (FC). The error bars are the standard errors of the means.

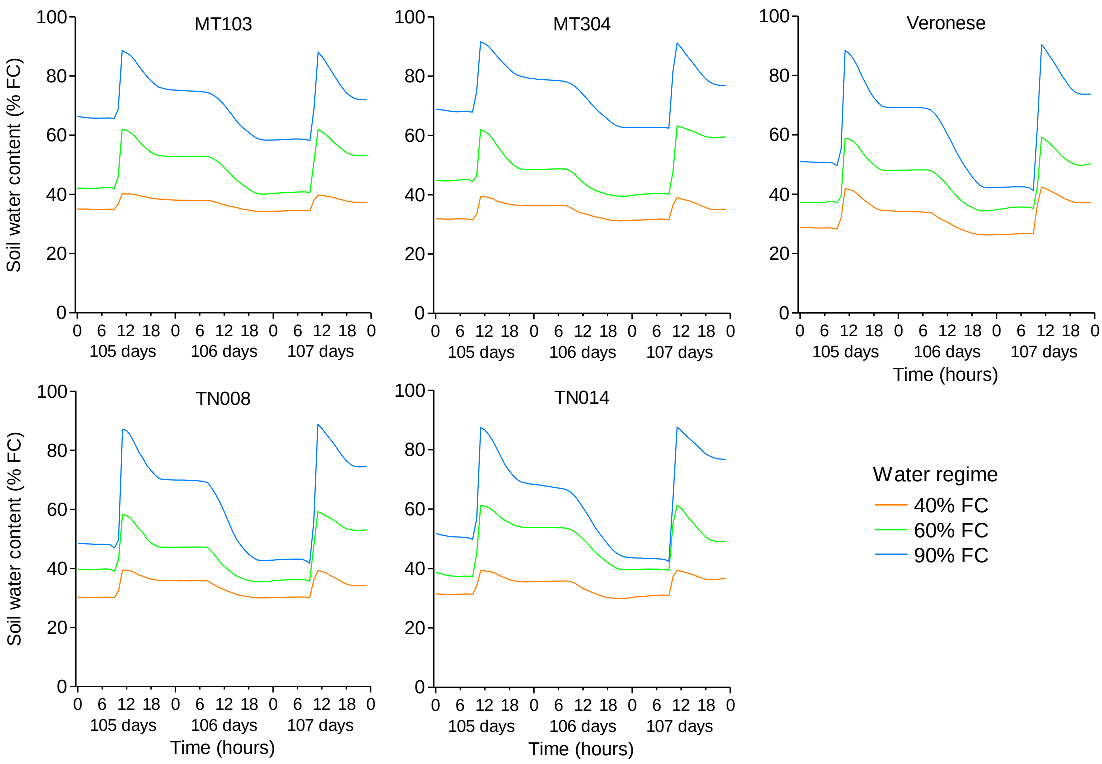

Figure 4. Water content of the soil of the poplar clones and water regimes, between watering cycles on days 105 to 107. Hourly average values of soil water content, as a percent of the field capacity. The water regimes were 40, 60, and 90% of field capacity (FC).

Water content of the soil after the application of soil water deficits

There was no significant difference in the soil water content of the 40% FC water regime treatment for the poplar clones, but there were significant differences between the clones for the 90% and 60% FC treatments (P = 0.007). The trees of the TN008, TN014, and 'Veronese' clones, reduced the soil water content to lower levels, compared with the MT103 and MT304 clones (Figure 4). The differences between the clones were larger for the 90% FC treatment, than for the 60% FC treatment, with much of the difference occurring on the second day of the 2-day watering cycle.

Biomass of the poplar trees at harvest

The soil water deficits of the water regime treatments and the poplar clones had a large effect on the biomass of the poplar trees at harvest, and on the water use efficiency of the trees, after 17 weeks of growth.

The amount of water used and the dry weight (DW) gain of biomass by the poplar trees was lower and the water-use efficiency (WUE) and root-to-shoot ratio was higher for the 60% and 40% FC water regime treatments than the 90% FC treatment (Tables 3 and 4). There was a progressive decrease in the amount of water used and in the DW gained, and a progressive increase in the water-use efficiency (WUE) of the trees, with the increasing severity of the soil water deficits. In contrast, the increase in the root-to-shoot ratio was similar for the 60% and 40% FC treatments.

The poplar clones showed significant differences in the water-use efficiency (WUE) of the water regime treatments (Tables 3 and 4). The differences were larger for the 60% and 40% FC water regime treatments, with the MT103, MT304, and TN008 clones having higher water-use efficiency (WUE) than the TN014 and 'Veronese' clones.

Leaf stomatal conductance and density, and water potential

The soil water deficits of the 60% and 40% FC water regimes had a large effect on the leaf stomatal conductance and water potential of the poplar trees (Tables 3 and 4). The stomatal conductance of the abaxial (lower) surface of the leaves, and the water potential of the leaves, decreased with the increasing severity of the soil water deficits. The leaves of the trees of the 60% and 40% FC water regime treatments had lower stomatal conductance and water potential than the 90% FC treatment. An exception was the TN008 clone, where the water potential of the trees did not decrease with lower stomatal conductance at 60% and 40% FC. The stomatal conductance of this clone was low, with the 60% and 40% FC treatments having the lowest stomatal conductance values of all the poplar clones.

Table 3. *P* values of the analysis of covariance for the fixed effects of poplar clone and water regime, and the interactions between them, on the dry weight (DW) gain, water use, water-use efficiency (WUE), root-to-shoot ratio (RSR), leaf stomatal conductance and water potential of the poplar clones.

Source of variation	Degrees of freedom	DW gain	Water use	WUE	RSR	Stomatal conductance	Water potential
Block	3	<.001	<.001	0.124	0.610	0.078	<.001
Initial cutting diameter	1	<.001	<.001	0.043	—	—	—
Clone	4	<.001	<.001	<.001	<.001	<.001	0.190
Water regime	2	<.001	<.001	<.001	<.001	<.001	<.001
Clone x water regime	8	0.042	0.080	0.615	0.032	0.048	0.361

Table 4. Dry weight (DW) gain, water use, water-use efficiency (WUE), root-to-shoot ratio (RSR), leaf stomatal conductance and water potential of the poplar clones. Values are the mean ± standard error, and different letters represent significant differences among the water regimes within the same clone (P < 0.05).

Clone	Water regime	DW gain g	Water use kg	WUE g DW kg^{-1} water	RSR	Stomatal conductance mmol m^{-2} s^{-1}	Water potential MPa
MT103	40% FC	124 ± 7 a	23 ± 4 a	5.5 ± 0.3 c	0.22 ± 0.02 b	164 ± 57 a	-1.03 ± 0.12 a
	60% FC	201 ± 15 b	44 ± 3 b	4.6 ± 0.1 b	0.24 ± 0.02 b	308 ± 61 a	-0.90 ± 0.10 a
	90% FC	246 ± 12 c	64 ± 4 c	3.9 ± 0.2 a	0.16 ± 0.01 a	1048 ± 173 b	-0.71 ± 0.05 a
MT304	40% FC	157 ± 43 a	29 ± 7 a	5.3 ± 0.1 c	0.22 ± 0.02 b	129 ± 67 a	-1.15 ± 0.13 b
	60% FC	270 ± 6 b	52 ± 8 b	4.8 ± 0.0 b	0.23 ± 0.01 b	283 ± 99 a	-0.94 ± 0.13 ab
	90% FC	334 ± 21 c	77 ± 9 c	4.1 ± 0.0 a	0.15 ± 0.01 a	849 ± 240 b	-0.64 ± 0.07 a
TN008	40% FC	173 ± 17 a	33 ± 4 a	5.3 ± 0.3 c	0.20 ± 0.00 b	28 ± 9 a	-0.76 ± 0.18 a
	60% FC	261 ± 39 b	56 ± 7 a	4.6 ± 0.2 b	0.19 ± 0.01 b	90 ± 36 a	-0.64 ± 0.15 a
	90% FC	351 ± 36 c	89 ± 9 b	4.0 ± 0.1 a	0.14 ± 0.01 a	480 ± 238 b	-0.82 ± 0.11 a
TN014	40% FC	176 ± 11 a	38 ± 3 c	4.6 ± 0.2 b	0.22 ± 0.02 b	57 ± 16 a	-1.09 ± 0.19 b
	60% FC	211 ± 28 a	55 ± 6 a	3.7 ± 0.1 a	0.24 ± 0.01 b	332 ± 105 a	-0.94 ± 0.16 ab
	90% FC	345 ± 25 b	98 ± 4 b	3.5 ± 0.1 a	0.14 ± 0.01 a	797 ± 116 b	-0.74 ± 0.07 a
'Veronese'	40% FC	194 ± 15 a	49 ± 2 a	3.9 ± 0.3 b	0.21 ± 0.01 a	62 ± 18 a	-1.20 ± 0.15 b
	60% FC	246 ± 17 b	72 ± 1 b	3.4 ± 0.2 a	0.26 ± 0.01 b	155 ± 28 a	-0.96 ± 0.11 ab
	90% FC	312 ± 46 c	99 ± 10 c	3.1 ± 0.2 a	0.21 ± 0.01 a	219 ± 31 a	-0.72 ± 0.03 a

Discussion

Drought tolerance, the capacity to endure at least modest meterological droughts, is generally achieved in poplars by dehydration avoidance adaptations, such as stomatal closure, leaf abscission and high root-to-shoot ratios that reduce the shoot water loss (Pallardy and Rhoads 1997). Poplars are very sensitive to dehydration, with little leaf dehydration tolerance (Braatne et al. 1992), and show stomatal closure at high values of leaf water potential (Ψ_L) (Regehr et al. 1975, Rhodenbaugh and Pallardy 1993), and leaf abscission, and higher root-to-shoot ratios under water stress (Pallardy and Rhoads 1997, Guo et al. 2010; Yin et al. 2005; Zang et al. 2004).

The poplar clones in this study showed a decline in the leaf stomatal conductance (g_L) for the moderate and severe soil water deficits. The decline in g_L was associated with more negative values of leaf water potential (Ψ_L). This was not observed for the TN008 clone, which had similar values of Ψ_L for the water-watered, moderate and severe soil water deficits. The TN008 clone appeared to be sensitive to Ψ_L, and to have a high Ψ_L threshold for stomatal closure, and low g_L at moderate and severe soil water deficits. The stomatal regulation of water loss under conditions of limited water supply is an important factor in drought tolerance, with low g_L in response to water stress providing a way for plants to survive drought (Jones 1974, 1987).

Leaf abscission occurred in the 'Veronese' clone, and to a lesser extent in the TN008 and TN014 clones, in response to the onset of the moderate and severe soil water deficits. The extent of leaf abscission reflects the severity of the water stress in the poplar trees (Monclus et al. 2006; Giovannelli et al. 2007), and has been observed to increase significantly in poplar clones as the pre-dawn leaf water potential (Ψ_{PD}) declines with the onset of drought conditions (Pallardy and Rhoads 1997). The 'Veronese', TN008 and TN014 clones had greater water use, which will have contributed to more severe water stress during the onset of the moderate and severe soil water deficits. The 'Veronese' clone was sensitive to water stress, and showed greater leaf loss and suppression of new leaf development at moderate and severe soil water deficits. In contrast, the MT103 and MT304 clones had lower water use, and were able to sustain continued leaf development without leaf abscission at the moderate and severe soil water deficits. Leaf abscission is an effective mechanism of drought tolerance, but it can limit potential productivity (Ludlow 1989).

Dry weight (DW) gain of the 'Veronese' clone was lower than the TN008 and MT304 clones for the well-watered and moderate soil water deficits, despite the higher shoot biomass of the 'Veronese' clone at the start of the soil water deficits. The 'Veronese' clone allocated more of the biomass to the roots, and less to the shoots, with higher root-to-shoot (RSR) ratios for the well-watered and moderate soil water deficits. Higher RSR's were not seen in the well-watered trees of the other poplar clones, which suggests the 'Veronese' clone was more sensitive to the water stress experienced by the well-watered treatment. Drought tolerance by increased investment in root growth has a cost in terms of reduced above-ground growth (Jones 1993), and this appears to have contributed to the lower biomass growth seen in the 'Veronese' clone in the well-watered and moderate soil water deficit treatments.

Water-use efficiency (WUE) was higher for the MT103, MT304, and TN008 clones, and lower for the TN014 and 'Veronese' clones. This reflects the differences observed in the water use and the drought tolerance strategies of the poplar clones. Lower water use contributed to the higher WUE of the MT103 and MT304 clones, while the sensitive response of the stomata to Ψ_L and the low g_L are likely to have contributed to the higher WUE of the

TN008 clone (Jones 1976). Higher water use contributed to the lower WUE of the TN014 clone, while higher water use and leaf abscission and the suppression of new leaf development contributed to the low WUE of the 'Veronese' clone.

Conclusions

The four new experimental hybrid poplar clones and the 'Veronese' poplar clone varied in their physiological responses and drought tolerance to the 90, 60 and 40% of field capacity (FC) soil water deficits. The drought tolerance of the 'Veronese', TN008 and TN014 clones was associated with leaf abscission and suppression of new leaf development, and higher root-to-shoot ratios, and for the TN008 clone sensitive stomatal regulation in response to water stress, and higher water-use efficiency. The drought tolerance of the MT103 and MT304 clones was associated with lower water use, higher water-use efficiency, and higher root-to-shoot ratios.

The MT304 and TN008 clones combined high water-use efficiency and high dry weight (DW) gain, which will be an advantage for the growth of these poplar clones in moderately drought-prone areas. The high water-use efficiency of the MT103 clone will adapt it for moderately drought-prone areas, but its slower growth will limit its productivity. The high water use and lower water-use efficiency of the TN014 and 'Veronese' clones are likely to limit their productivity in drought-prone areas, but the sensitive response of the 'Veronese' clone to water stress will give it good drought tolerance.

Acknowledgements
We thank Emily Smith (Massey University) for help with the tree watering, leaf stomatal conductance and water potential measurements, and the tree harvest; Jason Wargent and Chris Rawlingson (Massey University) for the use of the pressure bomb equipment; and Duncan Hedderley (Plant & Food Research) for advice on the experimental design and statistical analysis of the data.

References

Blake TJ, Tschaplinski TJ, Eastham A 1984. Stomatal control of water use efficiency in poplar clones and hybrids. Can. J. Bot. 62: 1344-1351.

Bonhomme L, Barbaroux C, Monclus R, Morabito D, Berthelot A, Villar M, Dreyer E, Brignolas F 2008. Genetic variation in productivity, leaf traits and carbon isotope discrimination in hybrid poplars cultivated on contrasting sites. Ann. For. Sci. 65: 503.

Braatne JH, Hinckley TM, Stettler RF 1992. Influence of soil water on the physiological and morphological components of plant water balance in *Populus trichocarpa*, *Populus deltoides* and their F1 hybrids. Tree Physiol. 11: 325-339.

Garnier BJ 1958. The climate of New Zealand. A Geographic Survey. Edward Arnold, London.

Ceulemans R, Deraedt, W 1999. Production physiology and growth potential of poplars under short-rotation forestry culture. Forest Ecol. Manag. 121: 9-23.

Gebre GM, Kuhns MR 1991. Seasonal and clonal variations in drought tolerance of *Populus deltoides*. Can. J. For. Res. 21: 910-916.

Giovannelli A, Deslauriers A, Fragnelli G, Scaletti L, Castro G, Rossi S, Crivellaro A 2007. Evaluation of drought response of two poplar clones (*Populus* × *Canadensis* Mönch 'I-214' and *P. deltoides* Marsh. 'Dvina') through high resolution analysis of stem growth. J. Exp. Bot. 58(10): 2673–2683.

Guo XY, Zhang XS, Huang ZY 2010. Drought tolerance in three hybrid poplar clones submitted to different watering regimes. J. Plant Ecology 3(2): 79-87.

Hinckley TM, Ceulemans R, Dunlap JM, Figliola A, Heilman PE, Isebrands JG, Scarascia-Mugnozza G, Schulte PJ, Smit B, Stettler RF, Van Volkenburgh E, Wiard B 1989. Physiological, morphological and anatomical components of hybrid vigor in *Populus*. In: Kreeb KH, Richter H, Hinckley TM eds. Structural and functional responses to environmental stresses. The Hague, The Netherlands, SPB Academic Publ., 199-217.

Jones HG 1974. Assessment of stomatal control of plant water status. New Phytol. 73: 851-859.

Jones HG 1976. Crop characteristics and the ratio between assimilation and transpiration. J. Appl. Ecol. 13: 605-622.

Jones HG 1987. Breeding for stomatal characters. In: Zeiger E, Farquar G, eds. Stomatal function. Standford, CA: Standford University Press, 431-443.

Jones HG 1993. Drought tolerance and water-use efficiency. In: Smith JAC, Griffiths, H eds. Water deficits: plant responses from cell to community. Bios Scientific Publishers, Oxford, UK, 193-203.

Kelliher FM, Tauer CG 1980. Stomatal resistance and growth of drought stressed eastern cottonwood from wet and dry site. Silvae Genet. 29: 166-171.

Ludlow MM 1989. Strategies of response to water stress. In: Kreeb KH, Richter H, Hinckley, TM eds. Structural and functional responses to environmental stress: water shortage. SPB Publishers, The Hague, Netherlands, 269-281.

Marron N, Villar M, Dreyer E, Delay D, Boudouresque E, Petit JM, Delmotte FM, Guehl JM, Brignolas F 2005. Diversity of leaf traits related to productivity in 31 *Populus deltoides* × *Populus nigra* clones. Tree Physiol. 25: 425-435.

Monclus R, Dreyer E, Delmotte FM, Villar M, Delay D, Boudouresque E, Petit JM, Marron N, Bréchet C, Brignolas F 2005. Productivity, leaf traits and carbon isotope discrimination in 29 *Populus deltoides* × *P nigra* clones. New Phytol. 167: 53-62.

Monclus R, Dreyer E, Villar M, Delmotte FM, Delay D, Petit JM, Barbaroux C, Le Thiec D, Bréchet C, Brignolas F 2006. Impact of drought on productivity and water use efficiency in 29 genotypes of *Populus deltoides* × *Populus nigra*. New Phytol. 169: 765-777.

Pallardy SG, Rhoads JL 1997. Drought effects on leaf abscission and leaf production in *Populus* clones. In: Pallardy SG, Cecich RA, Garrett HE, Johnson PS, eds. Proceedings 11th central hardwood forest conference. North Central Forest Experiment Station, general technical report, NC-188. Washington, DC, USA: US Department of Agriculture, Forest Service, 374–384.

Pallardy SG, Kozlowski TT 1981. Water relations in *Populus* clones. Ecology 62: 159–169.

Regehr DL, Bazzaz FA, Boggess AR 1975. Photosynthesis, transpiration and leaf conductance of *Populus deltoides* in relation to flooding and drought. Photosynthetica 9: 52-61.

Rhodenbaugh EJ, Pallardy SG 1993. Water stress, photosynthesis and early growth patterns of cuttings of three *Populus* clones. Tree Physiol. 13: 213-226.

Sprugel DG 1983. Correcting for bias in log-transformed allometric equations. Ecology 64: 209-210.

Strong T, Hansen EA 1991. Response of three *Populus* species to drought. USDA-FS Research Paper NC-302, 9 p.

Yang F, Wang Y, Miao LF 2010. Comparative physiological and proteomic responses to drought stress in two poplar species originating from different altitudes. Physiol. Plant. 139: 388-400.

Yin C, Wang X, Duan B, Luo J, Li C 2005. Early growth, dry matter allocation and water use efficiency of two sympatric *Populus* species as affected by water stress. Environ. Exp. Bot. 53: 315-322.

Zhang X, Zang R, Li C 2004. Population differences in physiological and morphological adaptations of *Populus davidiana* seedlings in response to progressive drought stress. Plant Sci. 166: 791–797.