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Sap flow of the southern conifer, *Agathis australis* during wet and dry summers

Cate Macinnis-Ng · Sarah Wyse · Andrew Veale ·
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Abstract

Key message **Analysis of sap flux density during drought suggests that the large sapwood and rooting volumes of larger trees provide a buffer against drying soil.**

Abstract The southern conifer *Agathis australis* is amongst the largest and longest-lived trees in the world. We measured sap flux densities (F_d) in kauri trees with a DBH range of 20–176 cm to explore differences in responses of trees of different sizes to seasonal conditions and summer drought. F_d was consistently higher in larger trees than smaller trees. Peak F_d was 20 and 8 g m^{-2} s^{-1} for trees of diameters of 176 and 20 cm, respectively, during the wet summer. Multiple regression analysis revealed photosynthetically active radiation (PAR) and vapour pressure deficit (D) were the main drivers of F_d. During drought, larger trees were more responsive to D whilst smaller trees were more responsive to soil drying. Our largest tree had a sapwood area of 3,600 cm^2. Preliminary analysis suggests stem water storage provides a buffer against drying soil in larger trees. Furthermore, F_d of smaller trees had higher R^2 values for soil moisture at 30 and 60 cm depth than soil moisture at 10 cm depth ($R^2 = 0.68$–0.97 and 0.55–0.67, respectively) suggesting that deeper soil moisture is more important for these trees. Larger trees did not show a relationship between F_d and soil moisture, suggesting they were accessing soil water deeper than 60 cm. These results suggest that larger trees may be better prepared for increasing frequency and intensity of summer droughts due to deeper roots and/or larger stem water storage capacity.

Keywords Sap flow · Plant water storage · New Zealand · Kauri · Large trees · Soil moisture

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Introduction

New Zealand has a unique native flora, 80 % of which is endemic to the country (McGlone et al. 2010). However, the tree ecophysiology literature of New Zealand has predominantly concentrated on introduced commercial forestry species (for instance, Meason and Mason 2013), and knowledge of native forest function is scant. With the frequency and intensity of summer droughts predicted to increase across much of the country (Mullan et al. 2005; IPCC 2013), there is an urgent need to understand the water relations and the threat of water scarcity to these indigenous ecosystems, including the kauri forests of the northern North Island. In the New Zealand context, droughts last for months, rather than years, however, Choat et al. (2012) note that all forest biomes are equally vulnerable to hydraulic failure irrespective of current rainfall regimes. The drought of early 2013 was amongst the most severe and widespread in decades (NIWA 2013) and as such, it provided the ideal conditions to investigate the impact of drought on sap flow of kauri.

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Kauri, *Agathis australis* (D. Don) Lindl. (Araucari-aceae), is an iconic New Zealand species due to its large size and cultural significance (Steward and Beveridge 2010). Kauri is endemic to New Zealand, and occurs naturally north of 38°07′S in the North Island (Ecroyd 1982; Fig. 1). Kauri commonly reach diameters of 1–2 m, occasionally up to 3–7 m (Allan 1961), and the maximum published age of an individual has been estimated at 1679 years (Ahmed and Ogden 1987). This makes kauri the largest and longest-lived tree species in New Zealand forests. In addition, kauri can be described as a 'foundation species' in the forests in which it occurs (Wyse et al. 2013a), as it impacts upon nutrient cycling and carbon sequestration (Silvester 2000; Silvester and Orchard 1999), and exerts significant effects on the composition of the plant communities below its crowns (Wyse et al. 2013b). These effects of kauri are likely attributable to its acidic, tannin-rich leaf litter (Wyse and Burns 2013; Verkaik et al. 2006), which results in the formation of deep layers of acidic mor humus beneath mature individuals (Silvester 2000; Silvester and Orchard 1999).

Several lines of evidence indicate that kauri are highly responsive to environmental conditions. First, kauri distri-bution has shifted over geological time. During the warmest and coolest periods of the last 100,000 years, kauri have become more restricted and scarce (Ogden et al. 1992), suggesting they are sensitive to climatic extremes.

Second, kauri feature heavily in the NZ tree ring literature since tree ring growth is correlated with the cool–dry and warm–wet fluctuations of El Niño Southern Oscillation (Fowler 2008; Fowler et al. 2008). However, tree response to these fluctuations is not consistent. For instance, tree ring climate signals are stronger in larger trees than smaller [diameter at breast height (DBH) <40 cm] trees (Wunder et al. 2013). The ecophysiological mechanisms of these observations have not been explored.

Plant water status responds to climatic conditions, particularly drought (McDowell et al. 2008), yet very little is known about water relations of kauri. We do know that kauri are highly vulnerable to xylem embolism (Pitter-mann et al. 2006), and we can infer high drought sensi-tivity from the comparatively low xylem pressures required to cause loss of conductivity. Ecroyd (1982) and Verkaik et al. (2007) suggested that kauri have shallow roots, preventing access to deeper water stores, however, kauri seedlings have been shown to be capable of en-hanced root growth in dry conditions (Bieleski 1959, Wyse et al. unpub. data) but it is unclear if this is vertical or horizontal growth. Even if rooting depth is not an issue, many of the remaining stands occur on ridge-tops (Wardle 2002) where soils are shallow and dry out quickly when water is scarce. However, there are a number of indica-tions that kauri are well-prepared for drought. Wyse et al. (2013b) recorded stomatal conductance (g_s) of seedlings

Fig. 1 The North of the North Island of New Zealand showing the study site location and the natural southern limit to the distribution of kauri (taken from Steward and Beveridge [2010])
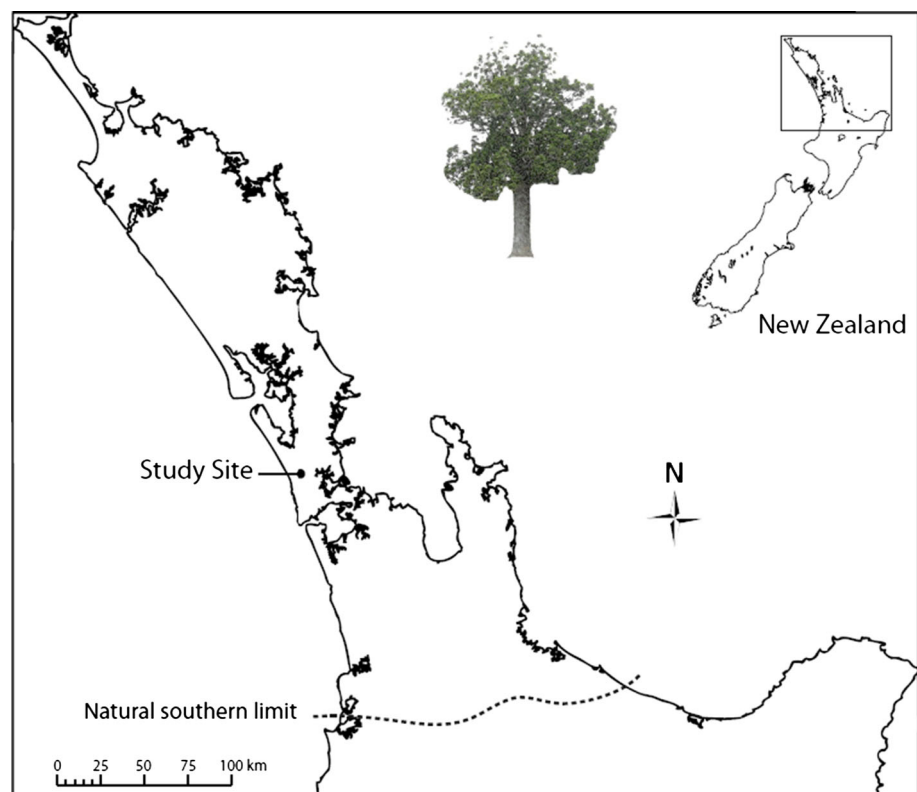
of kauri and other species from northland forests under induced drought. Kauri were found to be the best-prepared of these species under water-limited conditions because low g_s values allowed them to avoid reductions in water potential. The carbon cost of low g_s was not explored, but resources were allocated to below-ground growth under drought (Wyse unpublished data). Comparatively low g_s values have also been recorded in mature kauri in the field (Macinnis-Ng unpublished data). Recovery after xylem embolism has not been explored and the potential for peg roots to allow access to deep soil water stores is unquantified (Steward and Beveridge 2010).

Measurements of sap flow under drought demonstrate changing water relations as soils dry (e.g. Meinzer et al. 2013). Depending on stomatal responses to soil moisture availability, rooting depth and other factors, sap flux density (F_d) can decline under drought (Pfautsch and Adams 2013), remain unchanged (Zeppel and Eamus 2008) or increase (Bucci et al. 2008) due to increased vapour pressure deficit (D) during dry periods. A combination of factors determines the response of F_d under drought. For example, declining F_d may be due to stomatal control of plant water loss (Stöhr and Lösch 2004; Zeppel and Eamus 2008) or shedding of leaves during severe drought (Ford et al. 2011; Pineda-Garcia et al. 2013). Leaf shedding may allow a plant to maintain its whole plant hydraulic conductance, reducing whole plant water use for a given D (Meinzer et al. 2013), but when D increases as soil dries, increased evaporative demand may drive higher whole plant water use (Bucci et al. 2008, Meinzer et al. 2013). Use of stored water in stems, roots and leaves may also interact with D and soil moisture to influence whole plant water use (Holbrook 1995; Goldstein et al. 1998; Scholz et al. 2011). There are clear relationships between stem water storage and tree size (Meinzer et al. 2004; Scholz et al. 2011). Studies of plant water storage are scarce for temperate regions (Scholz et al. 2011) and measurements of F_d in kauri represent an opportunity to explore water relations in a large, temperate conifer endemic to the southern hemisphere.

The aim of this study was to investigate the effect of drought on sap flux of kauri trees. We calibrated Granier-type sap flow probes for our study species in the laboratory using felled stems. We measured rates of water use of six trees across a range of size and canopy position classes across a 2-year period (July 2011–June 2013) including a wet and a dry summer. We compared F_d across different tree sizes and seasons (winter and two contrasting summers) and explored changes in rates of water use as the drought of summer 2013 progressed and plotted responses of sap flow as soil dried. Finally, we investigated the roles of environmental drivers in rates of sap flow and how these change when the soil is dry.

Methods

Study site

The University of Auckland (UoA) Scientific Reserve at Huapai is approximately 15 ha of forest gifted to the University in 1947 (Thomas and Ogden 1983). The land is in the northern region of the Waitakere Ranges west of Auckland (36°47.7′S, 174°29.5′E). The study stand is dominated by kauri with 770 stems per ha and a basal area of 75 m^2 ha^{-1}, equating to approximately 80 % of total basal area (Wunder et al. 2010). Many of the kauri individuals remain in a suppressed state although the forest is characterised as mature (Wunder et al. 2010) and virgin (Thomas and Ogden 1983). Silver ferns (*Cyathea dealbata*) are highly abundant, and less-numerous species are a mixture of podocarps and broadleaved species, including *Phyllocladus trichomanoides*, *Myrsine australis*, *Coprosma arborea* and *Geniostoma ligustrifolium*. Total annual rainfall at the site is approximately 2,000 mm and is winter dominant (Fig. 2). Soils are brown granular clays that are sticky when wet and hard and fragile when dry (Thomas and Ogden 1983).

Six trees were selected for the study, ranging in size from 20 to 176 cm DBH (Table 1). The tallest tree had a height of approximately 35 m (Macinnis-Ng et al. 2013). Visual inspection of increment cores held by the Tree Ring Lab at UoA indicated that the sapwood depth for most trees was approximately 12 cm, but when we confirmed this using the dye injection method (Meinzer et al. 2001), we measured sapwood depths between 8.2 and 17.8 cm (Table 1). Inspection of stored cores for sample trees indicated consistent tree ring size at different azimuthal locations so we assumed sapwood depth was also consistent around each tree. The sapwood area of the largest tree was 3,676 cm^2.

Meteorological and soil moisture data

A meteorological station was installed in an open paddock approximately 1 km from the study site. Air temperature (°C) and relative humidity (%) were collected with a Vaisala HUMICAP probe (HMP155, Vantaa, Finland) in a radiation shield, PAR (µmol m^{-2} s^{-1}) was measured with a Li-cor quantum light sensor (Li190, Lincoln, NE, USA), wind speed was measured with a cup anemometer and wind direction with a wind vane (WMS301, Measurement Engineering Australia (MEA), Magill, S.A.), whilst rainfall was measured with a tipping bucket rain gauge (RIM8020, MEA) with measurement resolution of 0.4 mm. All weather sensors were mounted on a weather station tripod (MEA) and attached to a Campbell Scientific data logger (CR10x, Logan, UT, USA) powered by a solar panel.
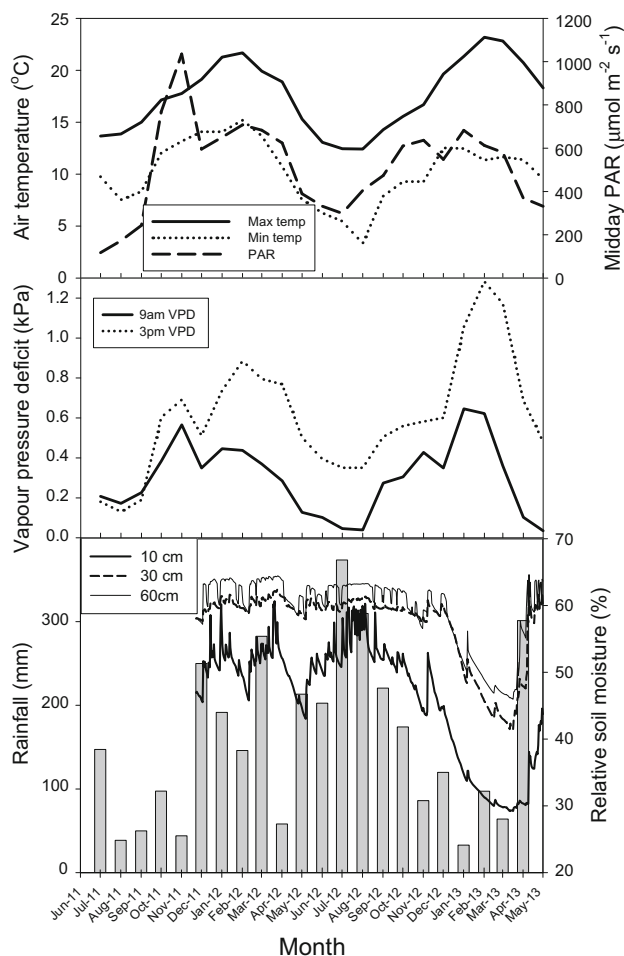
Fig. 2 Environmental and meteorological conditions at the site June 2011–May 2013. Values are mean monthly maximum and minimum temperatures (°C), mean monthly midday photosynthetically active radiation (*PAR* μmol m^{-2} s^{-1}), mean monthly 9 am and 3 pm vapour pressure deficit (*D* kPa), total monthly rainfall (mm) and volumetric soil moisture content (%) at depths of 10, 30 and 60 cm. Soil moisture in the litter layer is not shown to prevent cluttering the figure, but this *line* was similar to the 10 cm moisture content

Where power supply issues caused gaps in the dataset, data from the nearest Auckland Council station (at Kumeu, 7 km away) were used. Data from these two stations were closely correlated (*r* = 0.97 for temperature).

Soil volumetric moisture content (VMC) was measured at two locations in the forest at the following depths: the litter/mineral soil interface, and 10, 30 and 60 cm below the interface. Soil moisture was measured with horizontally installed water content reflectometers (CS616, Campbell Scientific, Logan UT, USA). All sensors were connected to Campbell Scientific CR10x loggers (one for each of the two locations). Data were logged at half hour time steps and the Campbell Scientific calibration equation was used to calculate volumetric water content.

Sap flow methods and analysis

Sap flow probes were constructed according to the specifications of James et al. (2002), with some modifications as described in Macinnis-Ng et al. (2013). These Granier-type probes have measuring components confined to the 1-cm aluminium tip, allowing measurement of sap flow at any depth, so are especially effective for trees with deep conducting sapwood. Each sensor consists of two probes. Chip resistors were used as the heating element for the downstream heated probe, instead of nichrome wire. Four 1.6 × 0.8 × 0.5 mm chip resistors (Kamaya, Kanagawa, Japan) were soldered end to end to give a heating element with a total resistance of 660 Ω. This type of heating element was easier to assemble into the final probe tip than the nichrome wire, and the higher resistance values that can be achieved with resistors reduced the drop-out voltage and power loss associated with the regulated voltage power supply. Specifications of thermocouples in each probe, casings and wiring were identical to those of James et al. (2002).

In July 2011, we inserted five sensor sets in our largest sample tree to depths of 1.5, 3.5, 5.5, 7.5 and 9.5 cm, therefore, our sampled sapwood depths were 0.5–1.5, 2.5–3.5, 4.5–5.5, 6.7–7.5 and 8.5–9.5 cm. Sensor depths for other trees are listed in Table 1. Pairs of holes with a vertical separation of 10 cm were drilled with a 2.45 mm diameter drill bit at approximately 1.5 m height. Bark was carefully removed with a chisel prior to drilling to ensure correct insertion depth (typically 1–2 cm deep). Kauri trees produce protective resin when damage occurs, so sensors were quickly inserted into drill holes before they could fill up with resin. We were unable to move sensors once they were inserted because of the resin. Sensors were placed in an upward spiral around the tree at least 5 cm apart to prevent interference between adjacent probes (James et al. 2002). Sensors were protected from sunlight with foil bubble-wrap insulation attached to the bark of the tree. Temperature difference between the two probes was converted from differential voltage measurements of the thermocouple leads. Every 15 min, the mean of the one minute temperature differences was recorded with a Campbell CR10x logger (Campbell Scientific, Logan, UT, USA) equipped with a 32-channel multiplexer (AM416, Campbell Scientific). A constant 0.15 W was dissipated from each of the heated probes, supplied by three 12 V, 40 Ah batteries recharged every fortnight.

A test of the sap flow probes was carried out in the laboratory using a felled kauri stem with a DBH of 19 cm. A length of 40 cm was cut from the stem using a hand saw and clamped between two clear acrylic plates, with o-rings positioned at each end to form a seal between the bark and plate. A hole and pipe fitting at the centre of each plate allowed water to pass into and out of the cut ends of the

Table 1 Specifications of sample trees

Tree ID	DBH (cm)	Height (m)	Sensor depths (cm)	Sapwood depth (cm)	Sapwood area (cm^2)	Wood density (g cm^{-3})	Canopy position
D024	176	25	1.5, 3.5, 5.5, 7.5, 9.5	17.8	3,676	0.54	Canopy dominant
C022[a]	128	25	1.5, 3.5, 5.5, 7.5	17.8	2,776	0.63	Canopy dominant
A050[a]	79	23	1.5, 3.5, 5.5	14.5	1,405	0.57	Canopy dominant
A046	40	24	1.5, 3.5	14.0	601	0.55	Co-dominant
B079	20	20	1.5, 3.5	8.2	188	0.59	Intermediate
A109	47	24	1.5, 3.5	12.5	651	0.57	Co-dominant
A053[a]	34	18	None				Intermediate
A054[a]	34	19	None				Intermediate

Bark depth varied between 2.0 and 0.4 cm

Canopy position taken from Wunder et al. (2010)

[a] Water potential measurements were conducted on trees marked with an asterisk

stem. A 20 L reservoir of water was positioned between 0.5 and 2.0 m above the stem to create a pressure head and water passing out the other end was collected into a reservoir on an electronic balance (MS304S, Mettler-Toledo, Columbus, Ohio) connected to a computer, with mass recorded at 60-s intervals and converted to a rate of flow. The reservoir was sealed with foil to prevent evaporation of water. Three sap flow probe sets were installed in the stem with sufficient spatial separation to prevent cross-heating between probes and connected to a datalogger (CR10X, Campbell Scientific, Utah). Only small amounts of resin oozed from the cut stem when sensors were installed. The height of the water reservoir was changed periodically to generate a range of flow rates, then one of the three probes was twice re-installed at new locations on the stem, with the flow rate varied again after each installation.

Probe-measured flow rates were found to vary with circumferential position in the calibration stem, but the overall calibration relationship between measured sap flux density and probe temperature was not significantly different to that originally described by Granier (1985) (linear regression between gravimetric and probe-measured velocity, assuming the original relationship, $R^2 = 0.57$, slope $= 0.99 \pm 0.07$, $p < 0.001$). Therefore, sap flux density (F_d: g m^{-2} s^{-1}) in the living trees was calculated according to the original equation

$$F_d = 119 \left((\Delta T_m - \Delta T)/\Delta T \right)^{1.231}$$

(Granier 1985), where ΔT is the temperature difference between the heated and unheated probe, and ΔT_m is the temperature difference when F_d is zero. We identified zero F_d periods as times when several consecutive days of rain combined with high relative humidity caused little or no flow.

Water potential data

Water potentials (Ψ) of terminal shoots were measured across the day on 17th and 18th January 2012 and 5th and 6th March 2013 for three trees of different sizes (indicated in Table 1). Due to the height of the canopy, steep topography, density of surrounding bush and safety requirements, access to leaves was complicated. Professional tree climbers were employed to collect sunlit terminal shoots using secateurs. Samples were bagged and dropped to the ground. The cut ends were stripped of bark (to prevent resin covering the cut xylem), freshly sliced with a razor blade and immediately placed in a custom built Scholander-type pressure bomb for measurement of xylem pressure potential. Measurements were conducted continuously throughout the day with three terminal shoots (about 15 cm long) from each of the three trees sampled each hour. Two small trees were sampled alternately to avoid removing a large proportion of their total leaf area. We were not able to access the canopy prior to dawn due to safety regulations for climbers so on the day before sampling, small branches on each of the trees were wrapped in foil and sealed in plastic bags for morning sampling. These bagged samples were the first measured each day (usually about an hour after dawn) and used as a surrogate for predawn water potential (O'Grady et al. 2006; Zeppel et al. 2008).

Statistical analysis

In this paper, we present data for the period 1st July 2012 to 15th May 2013. A lag time between leaf-level transpiration and sap flow at 1.3 m can occur because of hydraulic capacitance and resistance in the stem (Phillips and Oren

1998; Vergeynst et al. 2015). Due to the large sapwood volumes of our trees, we assumed a lag time would arise (Meinzer et al. 2004). Lag time can also change due to drought conditions (e.g. Zeppel and Eamus 2008). To estimate the lag period, we performed a series of regression analyses between F_d values at 1.5 and 3.5 cm deep for each tree and PAR for data from cloud-free days in January 2012, July 2012 and January 2013. Time differences of −1, 0, 1, 2, 3 and 4 h were used. The regression with the highest R^2 was deemed to be the time lag (Oren et al. 1999; Phillips and Oren 1998; Zeppel and Eamus 2008) and this offset was used to explore the relationship between environmental drivers and F_d.

Multiple regression analysis was used to identify the contributions of a number of predictors in explaining the variance of F_d across changing seasons and soil moisture conditions. The dataset was first separated into low and high soil moisture (above and below 32 % at 10 cm depth). The predictors assessed were VMC (at four depths), air temperature, PAR, wind direction and speed, rainfall and D. Examination of the variance inflation factors (VIF) indicated that there was strong collinearity amongst soil moisture at different depths and between D and air temperature. We removed soil moisture values from the litter, 10 and 60 cm depths (leaving 30 depth as the most representative) and removed air temperature from the final analysis. In all instances, there was no collinearity detected amongst predictor variables. Quinn and Keough (2002) suggest a threshold of ten and all of our VIF values were less than four. The relationships of each predictor and F_d were determined from the partial slope and the partial R^2 value. The partial R^2 value describes the unique contribution of a predictor variable in explaining the variance of the dependent variable (F_d), once the other predictor variables in the model have been controlled (Quinn and Keough 2002). The predictor variables were offset by 3 h for low soil moisture and 2 h for high soil moisture following the results of the lag time analysis to account for the time lapse between canopy processes and F_d at the base of the stem. Regression analysis was also used to explore the relationship between soil volumetric moisture content and total daily F_d for sensors at 3.5 cm (trees D024 and C022) and 1.5 cm (trees A050 and A109) depths during the summer 2013 drought. Rainy, cloudy days were removed from the dataset before analysis and linear or curvilinear regressions were fitted for each soil depth. Only four trees were used in this analysis due to sensor failure in the other trees at some point during the sample period.

Analysis of variance and a Tukey's pairwise comparison were used to identify significant differences between water potentials of terminal branches of sample trees, after tests for normality and homogeneity of variance. All statistics were carried out using IBM SPSS Statistics (v. 20) except

for the multiple regression, which was done using R v. 2.13.0 (R Development Core Team 2011).

Results

Meteorological conditions varied seasonally and between summers (Fig. 2). Maximum air temperatures were approximately 13 °C in winter and over 20 °C in summer. Vapour pressure deficit (D) was higher at 3 pm in summer 2013 (1.2 ± 0.1 kPa) than summer 2012 (0.8 ± 0.1 kPa). Volumetric soil moisture content declined from almost 60 % to less than 30 % at 10 cm depth during the dry months of summer 2013. Deeper soil moisture (at 30 and 60 cm depth) did not deplete below 42 % during the dry period. Despite the dry summer in 2013, total annual rainfall was higher during the period August 2012–July 2013 than August 2011–July 2012 (2,423 and 1,947 mm, respectively) due to large amounts of rainfall in May and June 2013.

Sap flux densities varied with tree size, sensor depth and season (Fig. 3) on cloudless days. In general, summer F_d values were higher than winter and larger trees had higher F_d. For larger trees, the sensor centred around 3 cm depth had higher F_d than the sensor centred around 1 cm depth, whilst for smaller trees, F_d values for the two depths were equal or the reverse was true. See Macinnis-Ng et al. (2013) for more detailed analysis of radial variation in F_d. F_d peaked at around 1,600 h throughout the sample period and there was evidence for nocturnal flow. Nocturnal F_d declined during wet periods of several days of rain (data not shown). Peak F_d declined in January 2013 compared to January 2012 for the largest tree (D024), but summer F_d remained high for the next largest tree (C022).

Analysis of time lags between PAR and F_d showed that larger trees had a shorter time lag of two to three h compared to smaller trees (three to four h) (Fig. 3). Time lags were significantly lower ($p < 0.01$) in the wet summer than the dry summer or winter with all trees having longer time lags in July 2012 and January 2013 compared to January 2012. Mean time lags were 2.1, 3.2 and 3.3 h for January 2012, July 2012 and January 2013, respectively.

Rates of F_d were higher for D024 and C022 than other trees, for a given D (Fig. 3). The slope of the relationship between F_d and D is also steeper for larger trees (Table 2). During the summer drought of 2013 (January to mid-April), F_d values declined on cloud-free days as the drought progressed, irrespective of tree size (Figs. 4, 5). Smaller trees were more sensitive to soil drying than larger trees (Fig. 4). Tree C022 (DBH 128 cm) showed no significant relationship between soil moisture and F_d whilst for tree D024 (DBH 176 cm), soil drying explained less than 31 % of the variation in F_d. The strongest relationship

Fig. 3 Sap flux density for cloudless days during January 2012 (wet summer), July 2012 (winter) and January 2013 (dry summer) for sensors centred around 1 and 3 cm depth for five sample trees (labelled with tree id and DBH in brackets). Midday is indicated with the *dashed line*. Tree details are listed in Table 1. Due to sensor failure, tree A109 was not included in this comparison and data are missing for tree A050 for July 2012. For each sensor depth at each sampling time, the time lag (h) was determined by choosing the highest R^2 in regression analysis between PAR and F_d for time shifts of -1, 0, 1, 2, 3 and 4 h. This is listed in the *upper right*-hand corner of each panel
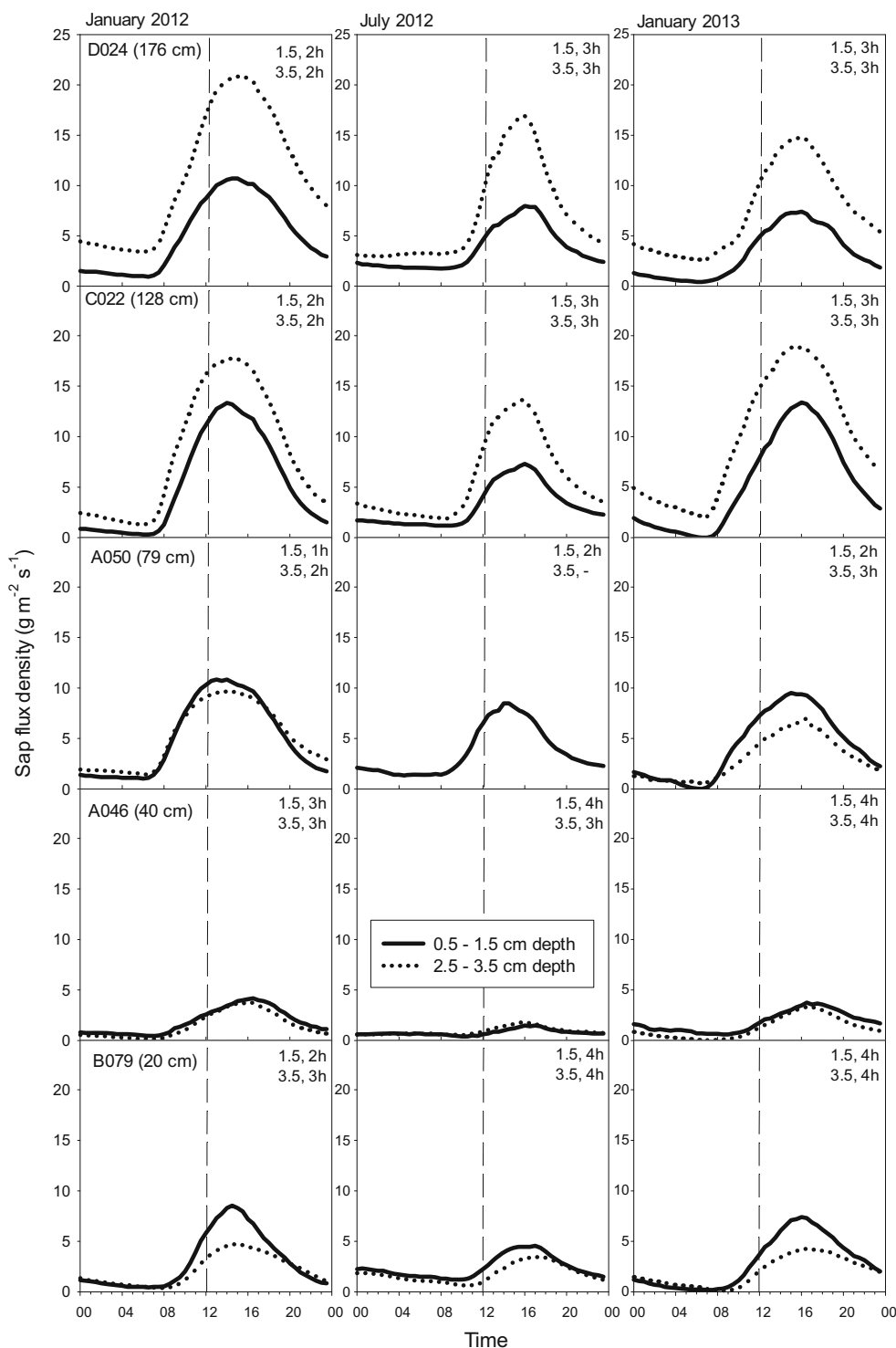
between soil moisture and F_d was for tree A109 (DBH 47 cm) at soil depths of 30 and 60 cm whilst tree A050 (DBH 79 cm) had equally strong connectivity with all soil layers (Fig. 4). On cloud-free days, peak F_d declined as the drought progressed, but increased again once rain replenished soil moisture in late April (Fig. 5). Changes in peak F_d were smallest in tree C022.

Lowest half-hourly F_d values were recorded in mid-April, even though soil moisture was higher than mid-Feb (Figs. 2, 5). Values of F_d were declining in March, but had recovered by May after the heavy rainfall in April replenished soil water stores (Fig. 2). Multiple regression analysis revealed higher R^2 values when soil was moist compared to dry soils (Table 2). The two top contributors

Table 2 Results of multiple regression analysis of half-hourly sap flux density data for the period 1st July 2012–15th May 2013 for trees D024, C022, A109 and A050 at probe depths of 3.5 cm for the first two trees and 1.5 cm for the second two trees (representing maximum flow rate)

	VMC < 32 %			VMC > 32 %		
	Partial slope	P value	Variation explained (%)	Partial slope	P value	Variation explained (%)
D024 3.5			$R^2 = 0.620$			$R^2 = 0.742$
VMC 30 cm	0.144	<0.001	1.043	0.188	<0.001	1.454
PAR	0.012	<0.001	35.108	0.009	<0.001	35.157
Wind dir.	0.002	<0.001	0.415	0.000	0.037	0.030
Wind speed	−0.119	0.167	3.406	0.112	<0.001	7.239
Rainfall	−0.178	<0.001	0.539	−0.362	<0.001	0.953
D	1.554	<0.001	21.448	5.746	<0.001	29.324
C022 3.5		$R^2 = 0.735$				$R^2 = 0.837$
VMC 30 cm	−0.087	<0.001	0.617	−0.144	<0.001	1.985
PAR	0.016	<0.001	38.036	0.011	<0.001	34.646
Wind dir.	0.000	0.983	0.024	0.001	0.017	0.076
Wind speed	−1.062	<0.001	3.077	−0.556	<0.001	10.830
Rainfall	−0.171	<0.001	0.646	−0.400	<0.001	0.590
D	4.689	<0.001	31.141	6.680	<0.001	35.606
A109 1.5		$R^2 = 0.578$				$R^2 = 0.793$
VMC 30 cm	0.129	<0.001	0.789	0.030	<0.001	0.922
PAR	0.014	<0.001	36.42	0.014	<0.001	45.634
Wind dir.	0.001	0.177	0.089	−0.001	0.001	0.043
Wind speed	−0.302	0.001	2.639	0.145	<0.001	7.156
Rainfall	−0.144	<0.001	0.375	−0.141	<0.001	0.407
D	0.557	0.001	17.507	3.220	<0.001	25.163
A050 1.5		$R^2 = 0.600$				$R^2 = 0.769$
VMC 30 cm	0.095	<0.001	1.148	−0.016	<0.001	6.503
PAR	0.010	<0.001	37.410	0.008	<0.001	34.933
Wind dir.	0.000	0.812	0.034	−0.001	<0.001	0.053
Wind speed	0.255	<0.001	4.648	−0.443	<0.001	3.955
Rainfall	0.072	0.004	0.125	0.295	<0.001	0.228
D	0.045	0.685	16.641	4.211	<0.001	31.181

The dataset was split into two according to volumetric moisture content (VMC) of soil at 10 cm depth with low (<32 %) and high (>32 %) soil moistures. The model included soil VMC of litter and at a depth of 30 cm, PAR, wind direction, wind speed, rainfall and vapour pressure deficit (D). A lag period of 3 h was applied for low soil moisture and an offset of 2 h was applied for high soil moisture to all environmental drivers, consistent with the results of Fig. 3

to variation in F_d were PAR and D. In all other cases, PAR was the strongest driver of F_d, explaining between 35 and 46 % of the variation in F_d whilst D explained between 17 and 36 % of variation in F_d. The influence of D was smaller in the smaller trees (A109 and A050). The two next highest drivers of F_d were wind speed (3–11 % of variation) and soil moisture at 30 cm (1–7 %).

Daily course of water potential (Ψ) of terminal branches was generally lower for the medium tree and for March 2013 than January 2012 (Fig. 6), when atmospheric conditions were similar, but soil water content changed due to the drought (Table 3). Predawn values (Ψ_{pd}) were lowest

for March 2013 and minimum values (Ψ_{min}) were lower in March 2013 and lower in the medium tree compared to the large and small trees (Fig. 7). Plotting Ψ_{pd} against Ψ_{min} showed a clear distinction between the two sampling events (Fig. 8) in the early wet (2012) and late dry (2013) summers.

Discussion

The drought of 2012–13 was one of the most extensive and severe for decades in New Zealand with the whole country

Fig. 4 Daily sap flux
density for cloud-free, rain-free days
with high D as summer drought
progressed in four of the sample
trees with soil water content at
four depths in the soil for each
date. Probe depths were 3.5 cm
for trees D024 and C022 and
1.5 cm for trees A050 and
A109, representing the
maximum flow rate for each
tree. R^2 values are shown for
each soil depth in brackets in
the key. In all cases, $p < 0.01$
except for regressions for tree
C022 which were not significant
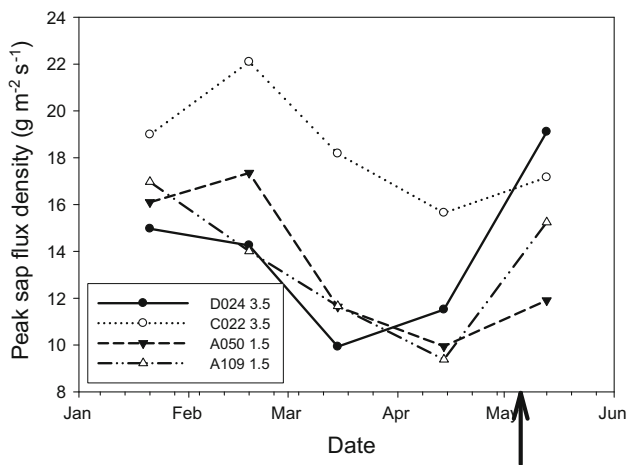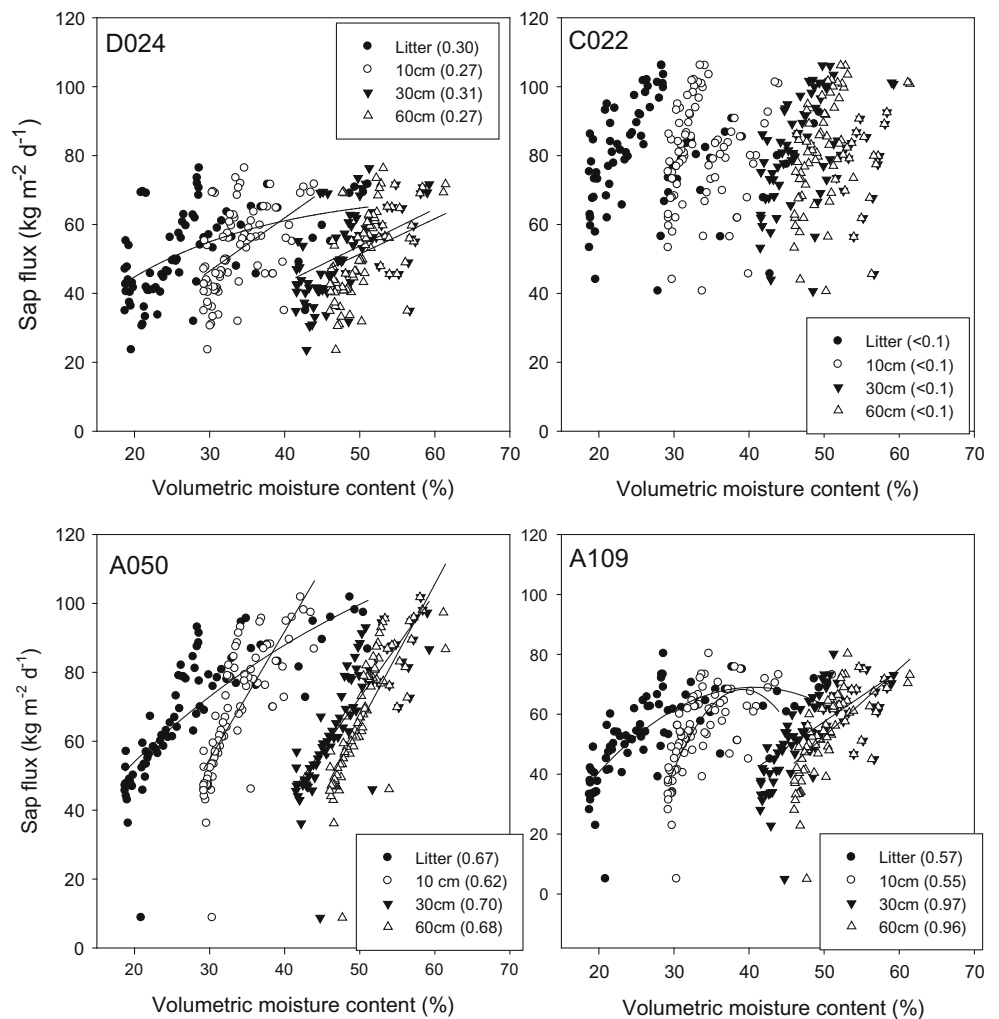
Fig. 5 Peak sap flux density on cloud-free days as the drought
progressed from January 2013. *Arrow* indicates date of the start of
rainfall. *Key tree* identification and sensor depth at maximum F_d

declared under drought in March 2013 (NIWA 2013).
Overall, we observed lower F_d values in smaller trees,
lower F_d values in winter than the wet summer and lower

F_d values during the dry summer compared to the wet
summer. Differences in responses to climatic and soil
conditions are consistent with variation in growth–climate
relationships for trees of different sizes (Wunder et al.
2013). Here, we explore the environmental and physio-
logical reasons for these differences and identify knowl-
edge gaps in our understanding of water relations in kauri.

Tree size and plant–water relations

Three factors may account for the lower F_d in smaller trees.
First, canopy position may reduce effective evaporative
demand for smaller trees (Kelliher et al. 1992). All sample
trees were independently classified as canopy dominant,
co-dominant or intermediate by Wunder et al. (2010). The
two largest trees (D024 and C022) had the distinctive
dominant growth forms of kauri (Burns and Smale 1990)
with large, imposing canopies dominating the leaf area of
the stand. Tree A050 was somewhat smaller in size, but
still occupied a substantial proportion of the canopy

Fig. 6 Water potential (Ψ) of terminal branches of *A. australis* on 17th and 18th January 2012 (*top panels*) and 5th and 6th March 2013 (*bottom panels*). *Large tree* is C022, *medium tree* is A050 and *small tree* is A053 or A054 (see Table 1 for further details)
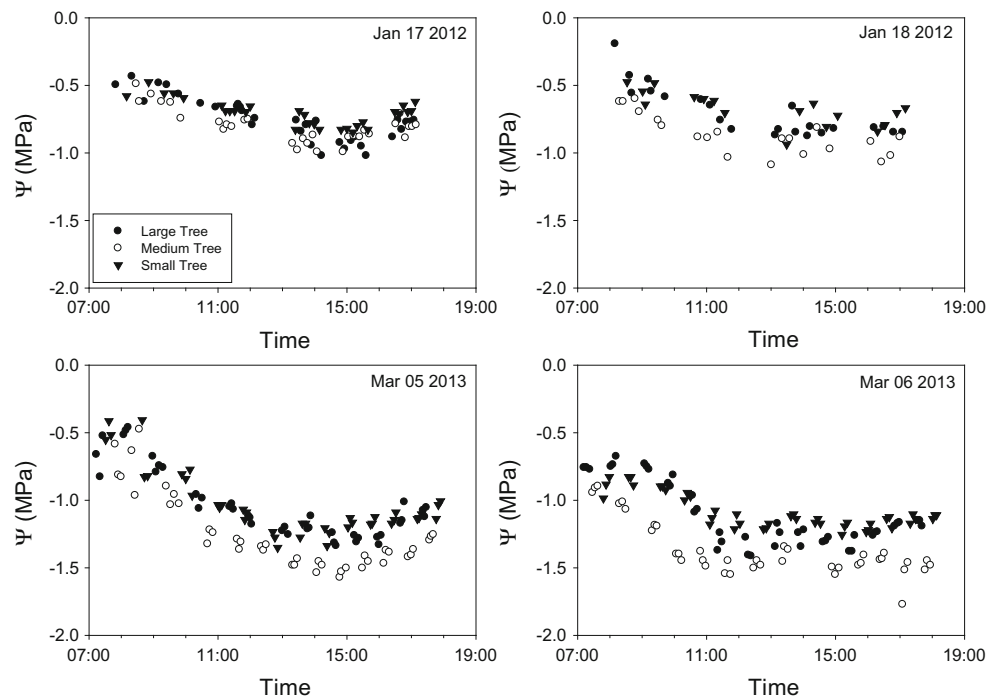
Table 3 Meteorological and soil conditions for water potential sampling days

| Date	9 am D (kPa)	3 pm D (kPa)	Max temp (°C)	Min temp (°C)	Max PAR (μmol m^{-2} s^{-1})	Soil moisture (%) at 10 cm	Soil moisture (%) at 60 cm
17th Jan 2012	0.4	0.6	22	11	1,100	52.0	63.9
18th Jan 2012	0.7	1.0	25	11	1,200	51.7	63.7
5th Mar 2013	0.6	1.0	24	13	870	29.8	46.7
6th Mar 2013	0.6	1.0	24	9	920	29.8	46.6

(Table 1). In contrast, the smaller trees (particularly A046, B079 and A109) did not emerge from the canopy or occupy substantial canopy footprint and as such, the canopy environment experienced by leaves of these species was more shaded and probably more humid, reducing water loss from leaves and in turn reducing F_d.

Second, lower leaf area in smaller trees may reduce whole plant water use (Zeppel and Eamus 2008; Zeppel 2013). We are yet to properly quantify leaf area per unit sapwood for our sample trees, but generally, suppressed trees have limited crown and leaf areas (Sterck and Bongers 2001). Third, differences in below-ground activity may influence differences in F_d for trees of different size. For instance, variation in rooting depth and biomass controls access to soil water stores, particularly during drought

(Katul et al. 1997; McDowell et al. 2008). Below-ground factors remain unquantified for kauri. Based on evidence presented here, canopy position appears to be an important factor influencing the sap flux density of trees in our stand.

Seasonal patterns in F_d

Frequently, the main factors driving seasonal variation in F_d are D, solar radiation and relative soil moisture (Jarvis 1976; Oren and Pataki 2001; Ford et al. 2004; Stöhr and Lösch 2004; Whitley et al. 2011). Similarly, we found that D and PAR were the strongest drivers for kauri (Table 2), but the importance of volumetric moisture of soil (on clear days) was greater for smaller trees than larger trees (Fig. 4). Whitley et al. (2013) found patterns held across
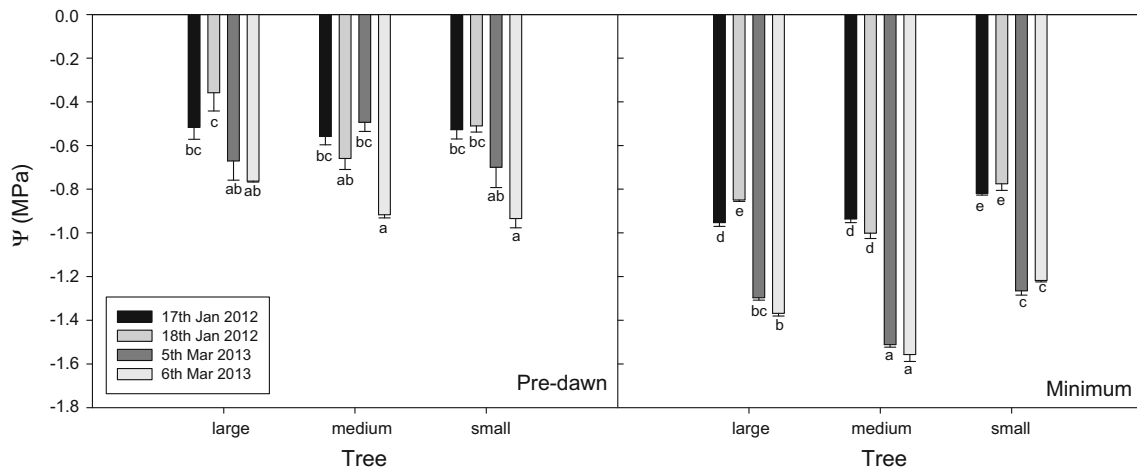
Fig. 7 Pre-dawn and minimum water potentials of terminal branches of three trees of varying sizes during January 2012 (wet conditions) and March 2013 (dry conditions). *Large tree* is C022, *medium tree* is A050 and *small tree* is A053 or A054 (see Table 1 for further details). *Columns* with *different letters* within a panel are statistically different
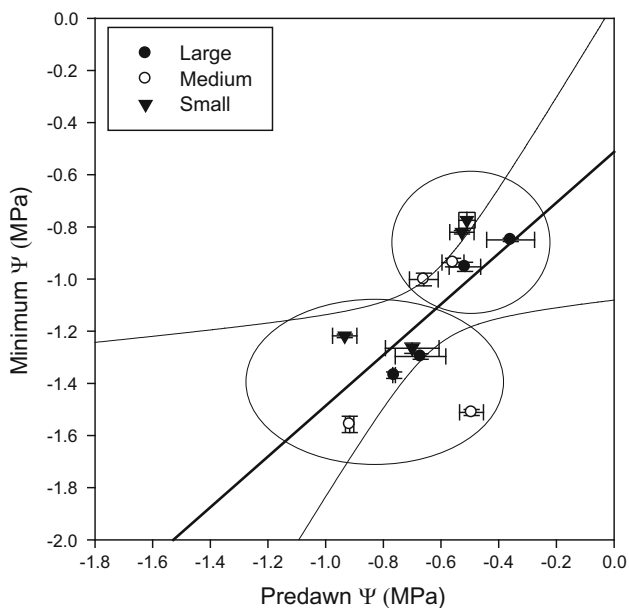
Fig. 8 Relationship between predawn and minimum water potentials of terminals twigs for three trees. *Each point* represents a tree sampled on each of four days during summer 2012 (*upper* cluster) and 2013 (*lower* cluster). The *trend line* shows a linear regression with 95 % confidence intervals ($R^2 = 0.385$ and $p = 0.03$)

five sites, but E was more responsive to R_n and D than soil moisture. Similarly, the multiple regression analysis for kauri indicated the importance of PAR and D over soil moisture during the measurement period (Table 2). There is evidence that the canopy is decoupled from the bulk air because a higher percentage of variance in F_d was explained by PAR than D (Wullschleger et al. 2000). The sole exception was for tree C022 when the soil was wetter and more variance in F_d was explained by D. Tighter stomatal

control of transpiration is associated with a stronger relationship between F_d and D over F_d and PAR (Wullschleger et al. 2000). This result when the soil is wetter is, therefore, unexpected.

Stomatal responses to D, PAR and soil moisture are pivotal to daily patterns in sap flow (Whitley et al. 2008; Zeppel et al. 2008), particularly during drought. Sap flow was highest shortly after sunrise in drought stressed European Ash saplings and this was attributed to reductions in g_s throughout the day (Stöhr and Lösch 2004). In contrast, peak sap flow in kauri occurred around 1,500 or 1,600 h even during drought due to the long lag periods in large kauri stems. We have measured diurnal leaf gas exchange values in kauri at another site and found g_s peaked before 0900 h (Macinnis-Ng unpublished). The large offset between peak g_s and peak sap flow for kauri is a result of the large stems (length and volume).

Our previous analysis of radial variation in F_d did not identify seasonal changes in relative flow rates at different sapwood depths (Macinnis-Ng et al. 2013). This is in contrast to the results of Saveyn et al. (2008) who found differences in F_d at different depths throughout the day. They attributed this to surface soil drying out as outer sapwood being hydraulically connected to surface roots whilst inner sapwood is associated with deeper roots. Our system appears to be much simpler.

F_d response to drought

Change in response of F_d to D and PAR as soil dries is common, e.g. Martínez-Vilalta et al. (2003), Zeppel and Eamus (2008). For a given D, F_d declines when soil moisture is dry. Reductions in F_d under drought varied between trees (Figs. 3, 4, 5; Table 2). For instance, tree

C022 (DBH 128 cm) had only a small reduction in F_d in the wet and dry summers (Fig. 3) and a small decline in maximum flow rates in the dry summer (Fig. 5), whilst tree D024 (DBH 176 cm) had a greater reduction in F_d (Fig. 3) and a greater reduction of peak flow rates as the drought progressed (Fig. 5). Potential reasons for these differences include tree size effects (such as differences in sapwood area), rooting depths and topographical factors. Tree D024 is located adjacent to a steep slope, this would limit available soil area and potential root biomass. Smaller trees appear to be more vulnerable to reductions in soil moisture indicated by greater reductions in relative peak sap flow, especially during March and April (Fig. 5). Smaller trees may have less rooting depth making them more vulnerable to declines in moisture in the top metre of soil. Furthermore, small sap wood areas may reduce availability of stem capacitance as a buffer to drought (Meinzer et al. 2004; Scholz et al. 2011). We have not yet measured capacitance for different-sized trees, but our lag time analysis does provide some indication of relative capacitance as described below.

Interactions between hydraulic resistance and capacitance mean that computing lag times is not the best method for quantifying stored water (Schulze et al. 1985; Phillips and Oren 1998; Vergeynst et al. 2015) and calculating leaf specific hydraulic conductance is a more informative approach (Phillips et al. 2002). However, we have not yet scaled our F_d values to whole tree water use because we need to measure sap flow in sap wood deeper than 9.5 cm to accurately account for flow rates across the radial profile (see Table 1 for sapwood depths). Sensors for deeper installation are under construction. Whilst time lag analysis is a reasonably crude method, it does provide useful indications for further research because stem capacitance is likely changing with season and soil moisture. Longer lag times in July 2012 and January 2013 compared to January 2012 are for different reasons including canopy microclimate, stomatal conductance, stem capacitance and soil moisture. We assume that the consistently longer lag time observed in January 2013 was due to drier soils as lower soil water potentials caused increased withdrawal of stored stem water. Zeppel and Eamus (2008) found a reduction in lag time when there was a large rainfall event prior to sampling. Further analysis of whole plant hydraulic conductance and installation of sap flow sensors in the canopy are needed to quantify stem capacitance properly.

Common linear relationships between basal sapwood area and diurnal storage capacity across five species (Golstein et al. 1998) along with tree diameter and stored water use across 16 species (Scholz et al. 2011) indicate stem capacitance increases with stem diameter. Therefore, we might expect our larger trees to have greater storage

capacity, in conflict with shorter lag times measured for larger trees. More limited access to soil moisture in smaller trees may account for longer lag times in these individuals. Whilst we have not yet quantified stem water storage for our trees, the importance of capacitance in avoiding drought mortality was highlighted by Scholz et al. (2011) because a tree with substantial water storage can buffer daily fluctuations in tension, thereby overriding vulnerability to embolism. In this regard, high vulnerability to xylem embolism reported in kauri (Pittermann et al. 2006) may be inconsequential for very large trees. Pineda-García et al. (2013) found soil drying effects were delayed where trees had high sapwood water reserves. In continuing research, we will instal stem dendrometers to measure daily stem diameter variation at different stem heights.

Drought tolerance and avoidance mechanisms available to kauri are summarised in Table 4. Some of these are indicated by previous studies on kauri, some are indicated by our own results and others are indicated in the literature for species other than kauri (see McDowell et al. (2008) for a review). Whilst we are still collecting data to properly quantify the relative importance of these different strategies, we do have clear indications of the physiological mechanisms for kauri responses to drought and directions for future research. Besides the sap flux processes described here, leaf loss during drought is another strategy used by kauri. Leaf litter fall increased threefold in summer 2013 compared to summer 2012 (Macinnis-Ng and Schwendenmann 2015), therefore, shedding of leaves to reduce leaf area is a clear strategy for avoiding drought, but low g_s values (Wyse et al. 2013b) should be explored as a mechanism for postponing drought in mature trees.

Conclusions

Kauri rates of F_d vary according to the size of the tree, the season and the moisture of the soil. Smaller trees have lower flow rates and flow rates decline in winter due to lower evaporative demands. For most trees, F_d declined during the summer drought of 2013, but access to deeper soil water stores (or better use of stem water stores) appeared to buffer one of our larger trees from drought. Further research is required to explore the relative importance of root biomass and depth and stem capacitance for drought survival in different-sized trees. With the prediction of increased frequency and severity of droughts in the north of New Zealand, periods of low water availability may impact on some ages of trees more severely than others. Our results indicate that large trees have the ability to survive droughts. All of our study trees survived one of the most severe and widespread droughts in decades.

Table 4 Drought avoidance strategies and adaptations potentially available to kauri (with reference to McDowell et al. 2008)

Drought adaptation	Knowledge for kauri
Stomatal regulation of water loss	Low g_s values measured for seedlings (Wyse et al. 2015, needs to be quantified for mature trees)
Comparatively high water use efficiency	Isotopic comparison with kahikatea shows higher WUE for kauri (Stephens et al. 1999)
Deep rooting	Deep tap roots with fine roots 2.5–3 m deep (Andrew Lorrey, pers. comm.)
Stem capacitance providing water store	Large conducting sapwood area offers potential water store, further study required to quantify this
Shedding of leaves	Litter fall (mostly kauri leaves and terminal twigs) 3 times greater during dry summer than wet summer (Macinnis-Ng and Schwendenmann 2015)
Carbohydrate storage and partitioning (roots, stem, leaves, reproduction)	Unknown
Recovery after xylem embolism	Unknown
Osmotic regulation of leaf turgor	Unknown

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