

Effects of season and frequency of harvest on browse yield and root carbohydrate reserves of willows (*Salix* spp.) in New Zealand

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Abstract Provision of large amounts of browse of willows (*Salix* spp.) for livestock in dry summers requires the selection of suitable times for coppicing the trees. The effects of time and frequency of harvest on the edible and total dry matter yield and root carbohydrate reserves of *Salix matsudana* × *alba* and *S. kinuyanagi* were measured. Trees were harvested initially in winter (WSpSuA), spring (SpSuA), or summer (SuA), and then at 10-weekly intervals until autumn, except for the winter control (WA) harvested initially in winter and then again in autumn. The greatest cumulative edible and total dry matter (DM) yields were for *S. kinuyanagi* in the WA treatment. In the WSpSuA and SpSuA treatments, the DM yields of this species were 2- to 4-fold greater than for the SuA treatment. For *S. matsudana* × *alba*, yields of the WA, WSpSuA, and SpSuA treatments were similar and exceeded

those of the SuA treatment by 4- to 6-fold. Root carbohydrate reserves in *S. matsudana* × *alba* comprised more than 90% sucrose and were highest in mid spring. Spring harvesting of *Salix* trees in coppice blocks will result in reasonable yields of accessible, edible DM for browsing by livestock in summer.

Keywords coppice; harvesting frequency; harvesting season; regrowth; silvopastoral; *Salix matsudana* × *alba*; *Salix kinuyanagi*; willows

INTRODUCTION

In New Zealand, willows (*Salix* spp.) are used for soil conservation and shelter on pastoral and horticultural farms (van Kraayenoord & Hathaway 1986a,b). Willows are also potentially useful browse species (Douglas et al. 1996; Oppong et al. 2001), but appropriate management strategies still need development if they are to be used for supplying supplementary forage during dry summers.

Regrowth, dry matter (DM) yield, and persistence of browse species are influenced markedly by the time of initial harvest and the frequency of harvest of regrowth during the growing season (Osman 1981; Blake 1983; Kays & Canham 1991). In temperate tree species such as *Eucalyptus obliqua*, *E. occidentalis*, and *Platanus occidentalis*, regrowth is maximised by harvests in winter or early spring and minimised by harvests in mid summer (Blake 1983). Hardesty et al. (1988) also found differences in regrowth yield of *Auxemma oncocalyx*, *Caesalpinia pyramidalis*, *Croton hemiargyreus*, *Mimosa acutistipula*, and *M. caesalpinifolia* harvested in different seasons. For example, harvesting late in the dry (dormant) season maximised the yield of *A. oncocalyx* whereas an earlier harvest maximised the yields of *C. pyramidalis* and *M. acutistipula*. Frequency of harvests can also greatly affect DM yields. For example, *Leucaena leucocephala* trees harvested 3 times yielded less than trees harvested once (Karim et al. 1991).

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Regrowth after defoliation has also been linked to the level of carbohydrate reserves in the roots and remaining shoot parts (George & McKell 1978; Erdmann et al. 1993). Because root reserves in deciduous tree species generally increase during the growing season, harvesting above-ground biomass during the period of active growth is likely to affect stored root reserves available for subsequent regrowth (Kays & Canham 1991). Kramer & Kozlowski (1979) showed that deciduous temperate trees have seasonal carbohydrate cycles that are different from those of evergreen trees. In deciduous trees, there are often dramatic reductions in carbohydrate reserves in spring when the growing season commences. Deposition of starch (the primary carbohydrate reserve) in the roots begins shortly after leaf expansion and reaches a peak when shoot growth ceases in *Populus* spp. and *Morus alba* (Loescher et al. 1990). Thus, in deciduous trees, maximum starch accumulation in the roots usually occurs in late summer/autumn (Kramer & Kozlowski 1979). Evergreen trees also use some reserve carbohydrates for early season growth but the changes in concentration of reserves are often relatively small compared with those in deciduous species. A common feature of deciduous and evergreen trees of the temperate zone is a late winter conversion of sugar to starch (Ryugo 1988).

There is little information on the effect of time of initial harvest and frequency of harvesting on the regrowth of browse species such as the deciduous *Salix* spp. (Douglas et al. 1996). If *Salix* spp. are to be used for fodder supply during dry summers, then it is desirable to maintain adequate edible biomass on the trees until it is needed. When trees are harvested in winter and allowed to regrow until mid to late summer, nutritional value of the foliage declines (Oppong 1998), and large quantities of edible forage exceed the reach of the grazing animal (Douglas et al. 1996). These limitations could be overcome by selecting a suitable time within the growing season when the trees could be harvested and still regrow high yields of edible DM. The objectives of this experiment were to determine (1) the best time to harvest *Salix matsudana* × *alba* and *Salix kinuyanagi* to maximise regrowth of edible DM; (2) the effect of frequency of harvest on DM yields of both *Salix* species; and (3) the changes in root carbohydrate reserves after defoliation. These species of *Salix* were selected for this study because they are used on farms for shelter and soil conservation and any additional role in forage supply

would enhance their multipurpose status and encourage wider use.

MATERIALS AND METHODS

Site description

The experiment was conducted at AgResearch Grasslands, Palmerston North, on a Manawatu silt loam (Hewitt 1998), which is poorly drained. Soil sampled from the site was moderately acid (pH (1:2.5 slurry) = 5.2), and had Olsen phosphate and sulphate sulphur levels of 27 and 4 mg kg⁻¹ soil, respectively. The long-term (1935–95) mean annual rainfall recorded at a meteorological station (Palmerston North, AgResearch, Station No. E05363) within 500 m of the site is 995 mm with relatively dry months occurring from January to April. The long-term mean annual air and soil (30 cm depth) temperatures are 12.9 and 14°C (Burgess 1988), respectively.

The site was prepared by eliminating existing vegetation. A few mature trees of *Chamaecytisus palmensis* (tagasaste) were harvested to ground level and removed. Pasture, predominantly *Lolium perenne* and *Trifolium repens*, was killed with glyphosate (1.1 kg a.i. ha⁻¹).

Plant species

The species were (1) *S. matsudana* × *alba* (hybrid willow) clone 'Tangoio', a reasonably drought-tolerant hybrid tree willow developed in New Zealand and released in 1980 for farm and horticultural shelter, coded NZ1040 (Hathaway 1986; van Kraayenoord & Hathaway 1986a,b); and (2) *S. kinuyanagi* (Kinuyanagi willow), a shrub willow represented in New Zealand by a single male clone which was imported from the United Kingdom, coded PN386 (Douglas et al. 1996). Unrooted poles of each species were planted in October 1994 at 1.5 m × 2.5 m spacing. Pasture within tree rows was sprayed with glyphosate (1.1 kg a.i. ha⁻¹) every 1–3 months and that between rows was mowed monthly.

Experimental treatments and design

The experiment was a split plot design with tree species allocated to main plots and harvest frequencies to subplots in 4 randomised complete blocks. The initial harvests were in winter (W), spring (Sp), and summer (Su), followed by harvests of regrowth material at approximately 10-week intervals for 3 of the treatments and after 31 weeks for 1 treatment. All treatments were harvested in

autumn (A). The first harvests were conducted on 30 August 1996 when the trees were aged 22 months and final harvests of all treatments were on 4 April 1997. At the initial and subsequent harvests, all trees within the appropriate subplots were cut horizontally at a height of 300 mm above the ground.

The subplot treatments were:

- (1) First harvest in winter (30 August 1996) with subsequent regrowth harvested 3 times (18 November 1996, 4 February, and 4 April 1997), termed WSpSuA;
- (2) First harvest in spring (18 November 1996) with subsequent regrowth harvested twice (4 February and 4 April 1997), termed SpSuA;
- (3) First harvest in summer (4 February 1997) with subsequent regrowth harvested once (4 April 1997), termed SuA; and
- (4) Control treatment for WSpSuA harvested in winter (30 August 1996) and subsequent regrowth harvested once, in autumn (4 April 1997), termed WA.

The number of trees in each treatment depended on the number of harvests during the experiment, with treatments WSpSuA and WA comprising 8 trees in a row per subplot while treatments SpSuA and SuA, which had fewer harvests, had 6 and 4 trees per subplot, respectively.

Measurements

Rainfall and air temperature were recorded at a meteorological station within 500 m of the site. The number of regrowth shoots and the length and basal diameter of the longest regrowth shoot of each tree in a subplot were recorded. From all trees within a subplot, two were randomly selected and harvested destructively each time to measure above- and below-ground attributes. Regrowth shoots harvested from each of these trees were subsampled, dissected into leaf, edible stem (<5 mm diameter), and woody stem, and the dry weight (80°C for 24 h) of each component was determined. Leaf to stem ratio was calculated by dividing leaf DM by total (edible plus woody) stem DM. Samples of the lateral roots (6–8 mm diameter) from the harvested stumps of each tree were washed, excised, and stored within 8 h of harvesting at –20°C.

Carbohydrate analyses

Root samples were prepared for analysis by freeze-drying (drum freeze dryer, Cuddon Ltd, New

Zealand) and grinding with a Wiley mill to pass through a 1 mm sieve. Due to resource limitations, only samples of *S. matsudana* × *alba* were analysed, because it is the most widely planted species (Hathaway 1986). Single samples (bulked across replicates) for WA and WSpSuA harvested trees were analysed for sucrose, fructose, and glucose using high performance liquid chromatography (Sturgeon 1990). This method is used routinely in the analytical laboratory and enabled rapid processing of samples. Starch concentration was calculated by multiplying the glucose concentration of the starch fraction by 0.9 (Moore & Hatfield 1994). Samples of the WA and WSpSuA treatments were analysed because they represented the extremes in the range of treatments evaluated.

Data analyses

Split plot analysis of variance was performed on the regrowth harvest data for the first 10 weeks after the initial harvest to determine the effect of season of initial harvest on subsequent regrowth. Analyses were conducted using PROC GLM (SAS 1994) and variables analysed were number of regrowth shoots, length and basal diameter of longest regrowth shoot, leaf DM, edible stem DM, woody stem DM, total and edible DM, and leaf to stem ratio. Split plot analyses were also conducted on the leaf, edible stem, woody stem, and total and edible DM yields for all the treatments over the experimental period. Root reserve carbohydrate concentrations for WA and WSpSuA harvested trees of *S. matsudana* × *alba* were graphed to show trends.

Relationships between the yield components (number of regrowth shoots, length of longest regrowth shoot, and basal diameter of longest regrowth shoot) and edible DM yields for the first regrowth harvest of each *Salix* species were determined using multiple regression analysis (SAS 1994) on log-transformed data. Standardised partial regression coefficients were estimated for the yield components to determine their relative importance in contributing to yield.

RESULTS

Weather

In the 2 months before the November harvest, the weather was wetter (100 versus 82 mm rainfall) and warmer (13.0 versus 11.6°C air temperature) than the 60-year average (Table 1). Over a similar period preceding the February harvest, rainfall (80 versus

87 mm) and temperature (15.9 versus 16.8°C) were slightly less than average. For the 2 months before the final harvest in early April 1997, rainfall (63 versus 68 mm) and temperature (17.2 versus 17.0°C) were similar to average conditions experienced at the site. February was the driest and hottest month during the experimental period.

Effect of season of initial harvest on regrowth

The number of regrowth shoots of *S. matsudana* × *alba* and *S. kinuyanagi* did not differ significantly with the season of first harvest (Table 2). Ten weeks after an initial spring harvest, *S. matsudana* × *alba* regrowth had 40% longer and 30% thicker shoots than those of *S. kinuyanagi*, whereas winter harvested trees of *S. kinuyanagi* had 20% thicker shoots than those of *S. matsudana* × *alba* (Table 2). When first harvested in spring, the regrowth after

10 weeks for *S. matsudana* × *alba* outyielded *S. kinuyanagi* in leaf (+55%), edible stem (+150%), woody stem (+52%), and total (+62%) and edible (+64%) DM ($P < 0.05$; Table 2).

Salix kinuyanagi had similar biomass regrowth 10 weeks after initial harvesting in winter and spring apart from edible stem DM which for the spring harvest was twice ($P < 0.05$) that from trees harvested in winter. The total DM for regrowth after 10 weeks for *S. kinuyanagi* was less for the initial harvest in summer than in winter and spring ($P < 0.05$; Table 2). In contrast, the biomass regrowth of trees of *S. matsudana* × *alba* harvested in spring was 3- to 5-fold greater than that from winter or summer harvested trees ($P < 0.05$; Table 2). The season of initial harvest altered the leaf to stem ratio only of *S. kinuyanagi*. Both species had a similar leaf to stem ratio for spring regrowth, but the ratios for *S. kinuyanagi* were significantly higher ($P < 0.05$) than those for *S. matsudana* × *alba* following winter and summer harvests (Table 2).

Table 1 Monthly rainfall (mm) and mean monthly air temperature (°C) from September 1996 to April 1997, and long-term averages from a meteorological station within 500 m of the experimental site.

Month	Rainfall (mm)		Temperature (°C)	
	1996/97	1935–95	1996/97	1935–95
Sep	103	75	12.4	10.7
Oct	96	88	13.1	12.5
Nov	101	78	13.2	14.2
Dec	91	94	15.9	16.1
Jan	68	79	15.9	17.4
Feb	58	67	18.2	17.6
Mar	68	69	16.2	16.3
Apr	145	81	12.4	11.4

Effects of season and frequency of harvest on dry matter yield

The cumulative DM for the treatments was compared for the regrowth periods after the initial season of harvest. The total regrowth periods for the WA, WSpSuA, SpSuA, and SuA treatments were 217, 217, 137, and 59 days, respectively. The mean daily production of total edible DM over both *Salix* species was 2.86, 2.12, 2.45, and 1.95 g DM tree⁻¹ day⁻¹ for the WA, WSpSuA, SpSuA, and SuA treatments, respectively. In both *Salix* species, 3 (WSpSuA) and 2 (SpSuA) harvests over the

Table 2 Effect of season of initial harvest on the first 10 weeks of regrowth (g DM (dry matter) tree⁻¹) above 300 mm above ground of two *Salix* species growing at Palmerston North in 1996/97. Means with the same letters in a column are not significantly different at 5% significance level; SEM = standard error of the mean; $n = 24$.

Species	Initial harvest season	Yield components			Regrowth biomass (g DM tree ⁻¹)					
		No. of shoots	Longest shoot length	Longest shoot diameter	Leaf DM	Edible stem DM	Woody stem DM	Total edible DM	Total DM	Leaf:stem ratio
			(m)	(mm)						
<i>Salix matsudana</i> × <i>alba</i>	winter 1996	38 ^a	1.0 ^c	8.9 ^c	66.3 ^c	15.0 ^c	77.2 ^c	81.3 ^c	158.5 ^c	0.8 ^b
	spring 1996	48 ^a	1.8 ^a	13.6 ^a	261.3 ^a	87.7 ^a	275.4 ^a	349.0 ^a	624.4 ^a	0.7 ^b
	summer 1997	39 ^a	1.1 ^c	7.9 ^c	77.8 ^c	20.4 ^b	75.4 ^c	98.2 ^c	173.6 ^c	0.8 ^b
<i>Salix kinuyanagi</i>	winter 1996	32 ^a	1.0 ^c	10.6 ^b	163.4 ^b	19.0 ^c	127.7 ^{bc}	182.7 ^b	310.1 ^b	1.1 ^a
	spring 1996	35 ^a	1.3 ^b	10.6 ^b	171.1 ^b	36.7 ^b	174.6 ^b	207.8 ^b	382.5 ^b	0.8 ^b
	summer 1997	40 ^a	0.9 ^c	7.4 ^c	118.7 ^b	11.3 ^c	71.6 ^c	129.9 ^{bc}	201.5 ^c	1.5 ^a
SEM		4	0.1	0.6	23.9	5.5	26.9	28.9	53.8	0.1

growing season produced similar cumulative DM yields for all fractions but 1 (SuA) harvest yielded 60–80% less DM than for the more frequently harvested trees ($P < 0.05$; Table 3).

The WA treatment of *S. kinuyanagi* yielded more leaf, woody stem, and edible DM than the WSpSuA, SpSuA, and SuA treatments (Table 3). For *S. matsudana* × *alba*, the WA, WSpSuA, and SpSuA treatments were similar and resulted in greater cumulative total and total edible DM yields than the SuA treatment. In contrast, the WA treatment of *S. matsudana* × *alba* produced slightly less leaf mass than the WSpSuA and SpSuA treatments but more than 3 times the mass of the SuA treatment ($P < 0.05$; Table 3). Woody stem yield of the WA treatment was at least twice that of the 3 treatments harvested during the growing season. Trees in the WA treatment for both *Salix* species had the lowest leaf to stem ratio, except for the WA and SpSuA treatments for *S. kinuyanagi* (Table 3), which were similar ($P > 0.05$).

Salix kinuyanagi outyielded *S. matsudana* × *alba* in the WA treatment with respect to all DM measurements except edible stem DM yield, which was similar for both species (Table 3). Furthermore, in the WA treatment, *S. kinuyanagi* produced approximately twice as much leaf, woody stem, and total edible and total DM as *S. matsudana* × *alba*, and had a 50% higher leaf to stem ratio (Table 3). Both species had similar cumulative DM yields for all the measurements for the WSpSuA, SpSuA, and SuA treatments, except for total edible DM yield

of SuA trees where *S. kinuyanagi* yielded 30% more than *S. matsudana* × *alba*. Leaf to stem ratios of WSpSuA and SuA trees of *S. kinuyanagi* were also higher than those of *S. matsudana* × *alba* (Table 3).

In the WA treatment, total edible yield was 38 and 42% of total DM for *S. matsudana* × *alba* and *S. kinuyanagi*, respectively. Within the WSpSuA, SpSuA, and SuA treatments, this proportion was 56–59% for *S. matsudana* × *alba* and 56–65% for *S. kinuyanagi* (Table 3).

Reserve carbohydrate changes with season

Sucrose concentration was much higher than the concentration of each of the other carbohydrate components in the tree roots in both the WA and the WSpSuA treatments, and comprised over 90% of total carbohydrate concentration (Fig. 1). Starch, glucose, and sucrose concentrations in the WA trees increased from late winter to mid spring then declined over summer and early autumn. In contrast, the concentrations of these sugars in the WSpSuA tree roots declined from winter to mid spring, increased in mid summer, and declined slightly in early autumn (Fig. 1). Concentration of fructose in roots of the WSpSuA trees varied much less over the study period than in those of the WA trees.

Relationships between yield components and DM yield

The standardised partial regression equations derived for the edible DM yields were:

Table 3 Effects of initial harvest season (winter (W), spring (Sp), and summer (Su)) and harvest frequency (spring (Sp), summer (Su), and autumn (A)) on cumulative dry matter (DM) yield (kg DM tree⁻¹) of two *Salix* species growing at Palmerston North in 1996/97. Means with the same letters in a column are not significantly different at 5% significance level; SEM = standard error of the mean; $n = 32$.

Species	Harvest treatment	Dry matter yield (kg DM tree ⁻¹)					
		Leaf DM	Edible stem DM	Woody stem DM	Total edible DM	Total DM	Leaf:stem ratio
<i>Salix matsudana</i> × <i>alba</i>	WA	0.29 ^c	0.13 ^a	0.70 ^b	0.42 ^b	1.11 ^b	0.4 ^d
	WSpSuA	0.31 ^b	0.11 ^a	0.31 ^c	0.42 ^b	0.73 ^b	0.7 ^c
	SpSuA	0.30 ^b	0.09 ^a	0.31 ^c	0.39 ^{bc}	0.70 ^b	0.8 ^c
	SuA	0.08 ^d	0.02 ^a	0.08 ^d	0.10 ^d	0.17 ^c	0.8 ^c
<i>Salix kinuyanagi</i>	WA	0.75 ^a	0.07 ^a	1.16 ^a	0.82 ^a	1.97 ^a	0.6 ^c
	WSpSuA	0.43 ^b	0.08 ^a	0.38 ^c	0.50 ^b	0.89 ^b	1.0 ^b
	SpSuA	0.23 ^b	0.05 ^a	0.21 ^c	0.28 ^{bc}	0.49 ^{bc}	0.9 ^{bc}
	SuA	0.12 ^d	0.01 ^a	0.07 ^d	0.13 ^c	0.20 ^c	1.5 ^a
SEM		0.05	0.02	0.08	0.06	0.13	0.1

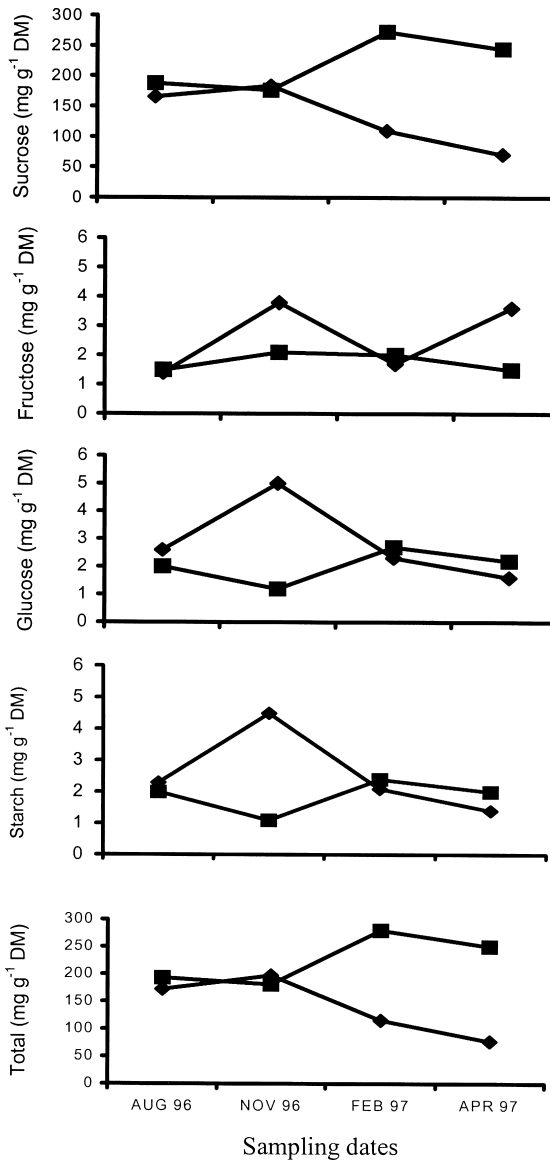


Fig. 1 Comparison of root reserve carbohydrates in *Salix matsudana* × *alba* trees when harvested initially in winter and then again in the following autumn (WA) (◆), and when harvested initially in winter and then again in spring, summer, and autumn (WSpSuA) (■), during 1996/97.

Salix matsudana × *alba*

$$\text{Log edible DM (g DM tree}^{-1}\text{)} = 0.62\text{log S} + 1.37\text{log L} + 0.73\text{log D} + 0.63 \quad (1)$$

$$R^2 = 90\%, P < 0.0002$$

Salix kinuyanagi

$$\text{Log edible DM (g DM tree}^{-1}\text{)} = 1.01\text{log S} - 0.15\text{log L} + 1.39\text{log D} + 1.59 \quad (2)$$

$$R^2 = 64\%, P < 0.04$$

where S = number of coppice shoots, L = length of longest shoot, D = diameter of longest shoot.

Equation 1 shows that shoot length was about twice as important as the other attributes in determining edible DM of *S. matsudana* × *alba*, but the number of coppice shoots and diameter of the longest shoot were also influential and to a similar extent. Conversely, for *S. kinuyanagi* (Equation 2), diameter of the longest shoot and number of coppice shoots were important in determining edible DM, with diameter being the most important.

DISCUSSION

Edible and total DM yield

The cumulative edible and total DM yields of *S. matsudana* × *alba* over a growing season were similar after 2 or 3 harvests following an initial harvest in winter (WSpSuA treatment) or spring (SpSuA), and with an initial harvest in winter and a harvest in autumn (WA). In contrast, the cumulative edible and total DM yields of *S. kinuyanagi* were decreased by periodic harvesting during the growing season. *Salix matsudana* × *alba* was better suited to a harvesting frequency of 10 weeks than was *S. kinuyanagi*, the latter having greater edible DM production when harvested only at the end of the season (WA treatment). The tree spacing used equated to a tree density of 2670 ha⁻¹. On this basis, *S. matsudana* × *alba* in the WA treatment produced 1.1 t edible DM ha⁻¹ and 3.0 t total DM ha⁻¹, and *S. kinuyanagi* yielded 2.2 t edible DM ha⁻¹ and 5.3 t total DM ha⁻¹ over 217 days. For both species, the greatest regrowth after 10 weeks followed initial harvesting in spring, being 0.9 t edible DM ha⁻¹ and 1.7 t total DM ha⁻¹ for *S. matsudana* × *alba*, and 0.6 t edible DM ha⁻¹ and 1.0 t total DM ha⁻¹ for *S. kinuyanagi*.

At a nearby site, Douglas et al. (1996) found that *S. kinuyanagi* yielded 50% more edible DM than *S. matsudana* × *alba* under a range of cutting treatments in the second year of growth, but *S. matsudana* × *alba* yielded more than *S. kinuyanagi* in the fourth year of growth (Oppong et al. 1996). Douglas et al. (1996) also showed that cumulative edible DM yield of both species varied with cutting

frequency, particularly between 1-cut and 3-cut treatments. For example, for *S. kinuyanagi*, a single cut to 300 mm above ground at the end of the growing season (April) yielded 2.5 t edible DM ha⁻¹, whereas 3 cuts (December, February, April) reduced cumulative yield by 75% to 0.6 t edible DM ha⁻¹. For *S. matsudana* × *alba*, cumulative yield was reduced 56% from 1.6 (1-cut) to 0.7 (3-cut) t edible DM ha⁻¹.

The results for *S. kinuyanagi* in this study are in agreement with those found earlier (Douglas et al. 1996) in showing that the species is not well suited to multiple harvests during the growing season. For *S. matsudana* × *alba*, the similar cumulative edible DM yields obtained under single or multiple cuts contrasted with the findings of Douglas et al. (1996), where yields were reduced under more frequent cutting. Differences in weather likely accounted for these variable responses; from October to April, monthly rainfall and air temperature in this study averaged 90 mm and 15.0°C, respectively, compared with 78 mm and 14.4°C, respectively, in the earlier study (Douglas et al. 1996). Plants were of similar age in both studies and they were cut at similar times to the same height of 300 mm above ground.

Guevarra et al. (1978) found that less frequent harvesting resulted in the highest DM yield for *Leucaena leucocephala*, but the proportion of woody stem increased. The higher leaf to stem ratio and the lower woody stem yield found for the *Salix* species studied here in the WSpSuA and SpSuA treatments compared with the WA treatment, suggests that livestock browsing the frequently harvested trees would find the browse more available and palatable because of the greater density of leaves.

Edible DM in this study was defined as that comprising leaf and edible stem (<5 mm diameter). During summer drought, the nutritive value of this material is often equal to or higher than that of pasture. For example, on sandy soils in February, the nitrogen (N) concentration of edible DM of *S. kinuyanagi* and *S. matsudana* × *alba* was 21 and 22 g N kg DM⁻¹, respectively, compared with 14 g N kg DM⁻¹ for pasture (Douglas et al. 1996). Metabolisable energy (ME) of edible DM of willow during summer is 8.7–10.5 MJ ME kg DM⁻¹ (Kemp et al. 2001), whereas pasture at that time usually has a high proportion of dead matter, which has <8 MJ ME kg DM⁻¹ (Lambert & Litherland 2000). In edible DM of both *Salix* species, Oppong et al. (2001) found that N concentration of leaf material

was 2–4 times that in edible stem, and organic matter digestibility of leaf exceeded that in edible stem by 10–50 percentage units.

Regrowth and carbohydrate reserves

The *Salix* species differed in their regrowth over the first 10 weeks after the initial harvest in each season. For *S. kinuyanagi* the edible regrowth over this period was similar for each season, but edible regrowth of *S. matsudana* × *alba* was sensitive to the season of first harvest. However, as the cumulative edible DM yield of *S. matsudana* × *alba* was similar when first harvested in winter or spring, it has the potential to be coppiced or browsed in spring and then again in summer. This type of management would enable spring pasture under the trees to be grazed without concern for the effect on summer browse if the trees were defoliated. Spring defoliation of the trees would also decrease the shading of the understorey pasture. In New Zealand, browse fodder is best utilised as a supplement to pasture in mid to late summer and the standing green feed should be of an appropriate nutritive value and quantity, and at browsing height.

The high edible and total DM regrowth of *S. matsudana* × *alba* harvested in spring coincided with its highest measured concentration of total non-structural carbohydrates stored in the roots. This suggests that the rate of regrowth of *S. matsudana* × *alba* after harvesting was affected by the level of root carbohydrates, but insufficient data were available to be conclusive. Regrowth is usually maximised when trees are harvested during the dormant period and minimised when harvested between early and mid summer when tree canopies have developed fully and carbohydrate reserves are low (Blake 1983; Kozłowski & Pallardy 1997). The higher sucrose concentration in the roots of the frequently harvested trees compared with the once harvested trees as the season progressed, suggests that sucrose was being mobilised to meet the demands of carbon in the refoliating shoots.

The preponderance of sucrose among the non-structural carbohydrates in the roots runs counter to general trends described by Loescher et al. (1990) and Kozłowski (1992). For example, in woody roots, the monosaccharides glucose and fructose often occur at higher concentrations than sucrose. However, in this study, concentration of sucrose was 20-fold and 44-fold higher than concentrations of fructose and glucose, respectively. Evaluation of a range of commercially available clones of *Salix*

species is recommended to determine the extent of this unusual carbohydrate distribution pattern.

The wetter and warmer spring weather during the trial, compared with long-term average conditions, likely encouraged relatively rapid initiation and expansion of leaves of both *Salix* species. This may partly account for the high concentration of sucrose in the roots, preparatory for transport through the phloem to the leaf sinks (Kozłowski 1992).

Morphological differences and management implications

The *Salix* species studied differed in the relative importance of the three yield components in contributing to edible DM yield. Stur et al. (1994) concluded that the optimum defoliation management was different for species with contrasting growth habits, and the use of a common management system may advantage some species while disadvantaging others. Length and basal diameter of the longest regrowth shoot were the most important determinants of edible DM for *S. matsudana* × *alba* and *S. kinuyanagi*, respectively. Similarly, Etienne (1989) reported that DM yield of woody plants is dependent on leader (main shoot) length and basal diameter.

The tree spacing and harvesting height used in this study are examples of those that might be used in special-purpose fodder blocks. Further research is required to determine the optimum plant spacing and harvesting height for trees in such systems. The harvesting frequencies examined have demonstrated that both *Salix* species can be harvested 2 or 3 times over the growing season.

CONCLUSIONS

The regrowth of *S. matsudana* × *alba* clone 'Tangoio' following a first harvest in mid spring exceeded that of *S. kinuyanagi*. However, over one growing season without harvesting, *S. kinuyanagi* had a higher edible DM yield than *S. matsudana* × *alba*, but the edible DM yield of *S. kinuyanagi* was more affected by frequent harvesting than that of *S. matsudana* × *alba*. Trees harvested initially in summer had relatively low regrowth DM yields. The experiment showed that spring harvesting provided relatively large quantities of edible browse in summer, and that, under this management, *S. matsudana* × *alba* clone 'Tangoio' had higher edible DM regrowth than *S. kinuyanagi*.

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