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Selection of plants for sap feeding by the White-fronted Woodpecker *Melanerpes cactorum* in Chaco dry forest, Argentina

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Abstract. Woodpeckers feed primarily on insects, larvae and other arthropods; however, several members of this family include plant products in their diets, such as sap. Among them, the genera *Sphyrapicus* and *Melanerpes* include the most species that specialize in sap consumption. In semiarid forests of Argentina, sap is an important food item in the diet of the White-fronted Woodpecker, *Melanerpes cactorum*. The aim of this study is to investigate why White-fronted Woodpeckers only consume sap from certain plants while avoiding other available plants of the same species and explore seasonality of their plant selection. We expected that combinations of plant traits (i.e. sugars concentration of sap, sap flow intensity, plant size, plant health and plant microhabitat), rather than one particular trait, determine which tree they select for sap feeding in different seasons. We examined five plant species: *Sarcotoxicum salicifolium*, *Prosopis ruscifolia*, *Ziziphus mistol*, *Aspidosperma quebracho-blanco* and *Stetsonia coryne* that were used most frequently for sap consumption and were consumed in all seasons by ten groups of White-fronted Woodpecker in semiarid Chaco, Argentina. Plants selected by White-fronted Woodpeckers for sap consumption were mainly larger plants that yield high sugar concentration. Of the plant species we studied, individual plant selection in all seasons was more evident in those plant species that constitute an important part of their diet (i.e. *Prosopis ruscifolia* and *Stetsonia coryne*). The selection of plants offering a greater reward in sap quality strongly suggests that the White-fronted Woodpecker maximizes food energy intake as a response to the seasonality that characterizes semiarid climates of temperate regions and conditions of food resources availability. Our results show that large trees are selected as sap trees by White-fronted Woodpecker, therefore, we recommend activities that promote retention of large trees in Chaco region.

Key words: *Melanerpes cactorum*, sap-trees, sap traits, sap feeding, foraging, semiarid Chaco

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INTRODUCTION

Phloem sap is nutrient rich compared to many other plant products, with high concentrations of sugars that provide an abundant source of carbon, energy, and nitrogen, predominantly in the form of free amino acids (Taiz & Zeiger 2002). Although phloem sap is an excellent diet resource for animals, it is consumed as the dominant or sole diet by a restricted range of animals (Douglas 2006). Among vertebrates, certain species of birds (e.g. woodpeckers, parrots, honeycreepers) and mammals (e.g. marsupials, squirrels, primates) are able to overcome plant defences and exploit this resource by choosing specific plant species and individuals within species, which they use during certain seasons of the year (Snyder 1992, Eberhardt 2000, Pejchar & Jeffrey 2004, Thompson et al. 2013, Charles & Linklater 2014, Wallis & Goldingay 2014).

The literature suggests that animals do not choose a random sample of trees for sap feeding. Sap-tree selection by vertebrates probably reflects the need of a balance between nutrient acquisition and avoidance of deleterious compounds, and can be based on particular characteristics of plant species as well as of individual plants (Snyder 1992). Factors determining sap-tree selection remain poorly understood and there is little consensus between studies, although previous research on sap-feeding species suggests that multiple variables affect tree choice (Goldingay 1987). While most studies measured structural characteristics of plants (e.g. plant size) to infer sap attributes, few studies on sap-feeding species measured sap attributes (e.g. sap chemistry, sap flow) specifically to test sap-tree selection (Mancuso et al. 2014, Wallis & Goldingay 2014). Furthermore, the quality of the same food resource may change during different seasons of the year, or the consumer may change their requirements. Therefore, seasonality is another important factor to be considered in sap-tree selection, which have not been taken into account by previous studies.

Woodpeckers Picidae feed primarily on insects, larvae and other arthropods. However, several members of this family include plant products, such as sap, in their diets (Winkler & Christie 2002). Among them, the genera *Sphyrapicus* and *Melanerpes* include the most species that specialize in sap consumption, the Yellow-bellied Sapsucker *Sphyrapicus varius,* being the most well-known and studied sap-feeding woodpecker (Tate 1973, Eberhardt 2000). In semiarid forests of Argentina, the White-fronted Woodpecker *Melanerpes cactorum* drills holes in living branches and trunks of several species of plants (e.g. trees, shrubs, and cactus) to feed on sap flows, and sap is an important food in their diet mainly in autumn and winter when the availability of other food resources (e.g. arthropods, flowers and fruits) declines (Genise et al. 1993, Blendinger 1999). White-fronted Woodpeckers show a strong feeding preference for certain tree species from which to consume sap (Núñez Montellano et al. 2013). However, individuals of the same plant species are not used with the same intensity; certain individual plants contain sap holes in living branches and trunks, whereas other individuals of the same species do not. Nevertheless, the factors governing sap-tree selection by the White-fronted Woodpecker at the intraspecific tree level are unknown.

The aim of this study is to investigate why White-fronted Woodpeckers only consume sap from certain plants while avoiding other available plants of the same species. We predicted that combinations of the following plant traits, rather than a particular trait, would determine which tree they select for sap feeding in different seasons: 1) Sap trees should have higher sap quality, namely richer in non-structural carbohydrates and with lower concentration of tannins than sap of non-selected trees. Non-structural carbohydrates concentration is an indirect measure of the energy available within sap (Crawley 1983), whereas tannins may affect the nutritional availability of certain sap compounds (e.g. proteins, nucleic acids and polysaccharides), or may inhibit the digestion of protein (Swain 1979, Deshpande 2002). 2) Sap flow intensity should be greater in sap trees than in non-sap trees. Sap flow may affect the quantity of resource obtained from holes, thereby influencing the rate of energy gain. 3) Sap trees should be larger (e.g. greater diameter at breast height, tree height, and or crown spread) than non-sap trees. Tree size may impact sap quality or availability, and thus sap-tree selection, because larger trees may have increased surface area available for photosynthesis, which increases the hydrostatic gradient and rate of sap unloading at sinks (areas of metabolism or storage of plants) (Crafs & Crisp 1971, Mueller-Dombois & Ellenberg 1974, Pejchar & Jeffrey 2004). 4) Sap trees should have thinner bark than non-sap trees, allowing easier access to sap (Mackowski 1988). 5) Sap trees should be unhealthier than non-sap trees. Trees that are in poor health or in the beginning stage of senescence are likely to have higher levels of amino acids in their phloem sap (White 1984). Because nitrogen often is a limiting nutrient for phloem-feeding animals (Fitter & Hay 1987), woodpeckers may select dying trees over healthy trees. 6) Sap trees should be located in wetter sites than non-sap trees. Plant's microhabitat may influence light and water availability for sap and photosynthate transport (Hall & Milburn 1973, McNab 1989). Woodpeckers may select plants for sap extraction that grow in moist soils and high light intensity, because these may have higher quantity and quality of sap. To our knowledge, this is the first study that simultaneously tests intraspecific sap-tree selection in several plant species used for sap consumption, taking into account different seasons and the consequent changes in food resources availability.

METHODS

Study area

The study was conducted in Rivadavia Banda Sur (Rivadavia Banda Sur department 24°11'S, 62°53'W), province of Salta, Argentina. The area is located in the semiarid Chaco subregion of the Chaco phytogeographical province. The climate is subtropical, with warm summers and temperate winters. Mean annual temperature ranges between 22 °C and 23 °C, with mean values of 28 °C and 16 °C for the hottest (January) and coldest (July) months, respectively. Mean annual rainfall is 650 mm (1941–1990 period; http//www.inta.gov.ar), concentrated between November and March (Minetti 1999). Soils are saline and range from poorly drained to seasonally flooded. The vegetation is characterized by sparse secondary woodlands and shrublands subjected to anthropogenic disturbances such as fire, logging, and overgrazing.

Sampling sites were located along a 100-m wide strip surrounding ponds in woodland sectors characterized by a higher density of tall trees and with lower light levels and higher humidity in the understory than in the remaining vegetation matrix (Macchi et al. 2011). The water level in ponds varied significantly among seasons; by the end of the dry season (October), their surface area was reduced by > 75% with respect to the wet season (November to March). The upper tree stratum (8 to 11 m) is dominated by *Prosopis nigra* and *Aspidosperma quebracho-blanco*, and by the columnar cactus *Stetsonia coryne*. The intermediate stratum (4 to 8 m) harbours mainly *Bulnesia sarmientoi*, *Geoffroea decorticans*, *P. ruscifolia*, *Ziziphus mistol*, *Ruprechtia triflora*, and *Tabebuia nodosa*, whereas the shrub stratum is dominated by *Maytenus vitis-idaea*, *Sarcotoxicum salicifolium*, and *Anisocapparis speciosa*. We conducted sampling during: autumn (May–June 2009), winter (July–August 2008), spring (December 2008) and summer (February 2011).

Plant species and sap consumption: Identifying sap trees and controls

The White-fronted Woodpecker is the only species in the semiarid Chaco that drill holes in living branches and trunks to feed on sap flows (Núñez Montellano 2013). White-fronted Woodpeckers live in cooperative groups and maintain permanent group territories in which all individuals forage and cooperate in territorial defence and nestling care (Macchi et al. 2011). We followed 10 White-fronted Woodpeckers groups and delimited their territories to observe sap-consumption; all territories were occupied throughout the entire study period (July 2008–February 2011). Birds were mist-netted and colour-banded to ensure that the same territories were maintained by the same groups. Each group consisted of 3.0–4.4 birds. During each of the survey periods we conducted focal observations on individuals and groups in each territory for 2–3 days (~7 hours each day, in the early morning and late afternoon), and recorded each plant visited for sap-feeding as well as the time spent (in minutes) feeding on sap. This ensured that holes drilled in plants were for sap-consumption. Woodpeckers fed on the sap of 12 plant species, which varied by sampling period; however, one shrub — *Sarcotoxicum salicifolium* (Capparaceae), three trees — *Prosopis ruscifolia* (Fabaceae), *Ziziphus mistol* (Rhamnaceae), and *Aspidosperma quebracho-blanco* (Apocynaceae), and a columnar cactus *Stetsonia coryne* (Cactacea) were the most actively used for sap consumption and were consumed in all seasons (Núñez Montellano et al. 2013). *P. ruscifolia* was the most commonly used species during the dry season (autumn and winter, 50.6% and 84.8% of foraging observations respectively), while *S. coryne* was used the most in the wet season (spring and summer, 34.5% and 61.1% of the foraging observations respectively). *S. salicifolium*, *A. quebracho-blanco* and *Z. mistol* were less used in all seasons (between 2.2 to 19.6%; 0.7 to 15.5% and 1.8 to 11.8% of foraging observations respectively) (Núñez Montellano et al. 2013). Within these five species, we chose two individuals per species in each territory for further characterization of sap trees, making a total of 10 individuals per species, except for *S. salicifolium*, with only nine individuals. The chosen individuals (hereafter 'sap trees') were those more actively used for sap consumption (defined as the accumulated time spent feeding on sap per plant). 'Non-sap trees' were defined as those belonging to the same species as sap trees but without sap wells in them, and were identified as the closest unused neighbour to the used plant of the same species. Non-sap trees were used as control comparisons to sap trees. In most cases, measurements were taken at the same time for each sap/non-sap tree pair.

Sap and plant characteristics and microhabitat

Traits that may influence plant selection for sap feeding were identified from preliminary observations of White-fronted Woodpeckers and literature about other sap-feeding species. We measured the following variables for each individual plant: (1) Sap flow intensity, sugar concentration and tannin concentration, were used as food quantity and quality measures, respectively. We collected sap from sap and non-sap trees by making a hole to reach phloem tissue, at breast height using a punch on each plant, and collecting all the flowing sap with three square (2.5 cm side) filter papers placed on exposed tissue for 5 minutes. The punch had approximately the same diameter as the woodpecker's bill, to mimic their foraging techniques. Filter papers were previously dried in a 40 °C oven, weighed with a Mettler H54AR scale, and placed in Eppendorf tubes. After collecting the sap sample, filter papers were placed in Eppendorf tubes again and kept in a portable refrigerator at first and in a freezer at -18 °C later at the camp site. Plants were sampled between 12.00 and 17.00 h, under similar environmental conditions (we never sampled during rainfall and windy days) (Pejchar & Jeffrey 2004). In the laboratory, filter papers were thawed and weighed to record the fresh weight of each sample. The amount of sap in the sample was calculated as the difference between fresh and dry weight. Sap samples were then analysed for sugar and tannin composition. Filter papers of each sap sample were placed in assay tubes to which 3 ml of Methanol ACS (Sintorgan mark) at 100% were added. Sap samples were stored in a refrigerator at 4 °C for later analysis. Sugar concentration in each season was calculated by spectrophotometric analyses using the phenol-sulphuric acid method, with sucrose as a standard (Dubois et al. 1956), at wavelength settings of 490 nm. In order to minimize experimental errors, we prepared samples in duplicate, which were then averaged. This method determines total sugar concentration (sugar in mg per mg of sap sample [mg/mg]) expressed as an amount of sucrose equivalents. Tannins concentration was determined only for autumn and summer seasons and for 6 pairs of sap and non-sap trees per species through spectrophotometric analyses using the protein precipitable phenolics method (Hagerman & Butler 1978), with tannic acid as the standard at wavelength settings of 510 nm. In order to minimize experimental errors, we prepared samples in duplicate, which were then averaged. This method determines condensed and hydrolysable tannin concentration (mg of tannins per mg sap sample [mg/mg]) expressed as amount of tannic acid equivalents. (2) Crown area, main stem diameter and plant height were used as measures of plant size. For each plant, we calculated crown area as the area of the ellipse formed by the maximum diameter of the crown and its perpendicular. Main stem diameter was measured at 1.30 m height for trees and at 0.80 m for shrubs. These variables were measured only for tree and shrub species, and not for cactus. Height was estimated for all plant species, extrapolating from a known height reference to total plant height. (3) Bark thickness was measured using a punch to extract one to four bark samples from the main trunk of the plants at 1.30 m high in trees and at 0.80 m in small trees and shrubs. Bark thickness of each plant was measured with a calliper from the outer part of the bark to the phloem. (4) We determined plant health by recording the proportion of dead primary branches and trunks in the plant. (5) Plant microhabitat, defined as distance to centre of ponds, was determined by recording each plant position with a geographical positioning system (Garmin eTrex Legend). The shortest distance between the plant and the pond centre was then measured using the distance tool in Google Earth program version 2012 (www.earth.google.com). We assumed that structural, health and microhabitat variables did not change between sampling periods, thus they were measured only once, while the remaining variables were measured in each season.

Data analysis

We conducted generalized linear models (GLM) to determine sap tree traits chosen by White-fronted Woodpeckers. For each plant species, we performed a GLM with a binomial family distribution of errors and a logit link-function, where the response variable was sap consumption / non-consumption (sap tree = 1, non-sap tree = 0) in each season. We constructed simple correlation matrices to determine which predictor variables were correlated with one another, since high colinearity among predictor variables can lead to high standard errors and difficulties in interpreting parameter estimates in GLM (Graham 2003). We generated a set of competing models (with a maximum of three predictive variables per model) to be compared using an information theoretic approach (Burnham & Anderson 2002). The predictive variables used in the models of tree species were: sap flow intensity, sugar concentration, crown area, bark thickness, health and distance to ponds. Tree height, main stem diameter and crown area were highly intercorrelated for each plant species ($p < 0.01$); therefore, we only included crown area to represent tree size in each set of models. The predictive variables used in the models of *S. coryne* were: sap flow intensity, sugar concentration, height and distance to ponds. For each model, we calculated Akaike's information criterion corrected for small sample sizes (AICc) and Akaike weight (*w*; Burnham & Anderson 2002). To evaluate the strength of support in each model, we compared the models within a set based on ΔAICc (difference between the AICc of a given model and the lowest AICc model in the set) and Akaike weight (a measure of the support for a given model relative to the other models in the set; Burnham & Anderson 2002). We considered a model to be well supported by the data if it had a $\Delta AICc < 2$. To assess the relative importance of each predictor variable in the candidate set, we summed Akaike weights (w_i) for each model containing the variable (Burnham & Anderson 2002). Predictor variables with higher w_i provide the best plant selection inference.

We compared tannins concentration between used and unused trees of each plant species using t- tests for normally distributed continuous variables and Wilcoxon signed-rank tests for non-normally distributed continuous variables. We did not add tannin concentration to the models because we did not have this information for all sampled plants or for all seasons.

Statistical analyses were performed with InfoStat software version 2012 (Di Rienzo et al. 2008) and STATISTICA 7.0 (StatSoft 2004). We present descriptive statistics as percentages, ranges and means, with significance set at $p = 0.05$.

RESULTS

Plants selected by White-fronted Woodpeckers for sap consumption were mainly larger in size and yield high sugar concentration and sap flow intensity. Individual plant selection was more evident in those plant species that constitute an important part of their diet (e.g. *P. ruscifolia* and *S. coryne*).

Autumn plant selection

In autumn, sap plant selection by the White-fronted Woodpecker was best explained by sugar concentration and size in *S. coryne* and *P. ruscifolia* (Table 1, Appendix 1). Performance of these models received considerable weighting (*S. coryne*, w = 0.27, *P. ruscifolia*, w = 0.18). Sap-tree selection was explained by high sugar concentration (Fig. 1) and large size in both models. Summed weight showed that size provided the best inference for tree selection in both species (Table 2). Sap-plant selection in *S. salicifolium*, *A. quebracho-blanco*, and *Z. mistol* was explained by models containing sap flow intensity (w = 0.15), bark thickness (w = 0.13), and sap flow intensity and plant size (w = 0.12), respectively. Sap trees showed lower sap flow intensity in *S. salicifolium*, thinner bark in *A. quebracho-blanco* and higher sap flow intensity and larger size in *Z. mistol*, than non-sap trees when variables were included (Fig. 2). Bark thickness, crown area and sap flow intensity provided the best inference for tree selection in *A. quebracho-blanco*, *Z. mistol* and *S. salicifolium* respectively (Table 2).

Winter plant selection

In winter, selection for *P. ruscifolia*, *S. coryne* and *Z. mistol* was explained by models containing sugar concentration, size and health; sugar concentration, sap flow intensity, and distance to ponds; and sap flow intensity, health and bark thickness, respectively (Table 1, Appendix 1). The performance of these models received considerable weighting (*P. ruscifolia*, w= 0.30; *S. coryne*, w= 0.26; and *Z. mistol*, w = 0.26). Sap-tree selection was explained by high sugar concentration, high sap flow intensity and low levels of health in all models (Fig. 1 and 2). Sap trees showed larger size, thinner bark and were closer to ponds than non-sap trees when variables were included. Summed weight showed that size, sugar concentration and sap flow intensity provided the best inference for tree selection in *P. ruscifolia*, *S. coryne* and *Z. mistol* respectively (Table 2). Sugar concentration also ranked highly in *P. ruscifolia* (Table 2). The best models for *A. quebracho-blanco* and *S. salicifolium* included sugar concentration, although model performance was weak (w = 0.09 in both models) (Table 1, Appendix 1). Sap trees showed lower sugar concentration than non-sap trees in both models (Fig. 2). Bark thickness and sugar concentration provided the best inference for tree selection in *A. quebracho-blanco* and *S. salicifolium*, respectively (Table 2).

Spring plant selection

In spring, the best model for *S. coryne* included sugar concentration and size, and received considerable weighting (w = 0.28). Sap plants showed lower sugar concentration and greater size than non-sap plants (Fig. 1). The most important trait explaining plant selection was size (Table 2).

Sap-tree selection in *P. ruscifolia*, *A. quebracho-blanco* and *Z. mistol* was explained by models containing health and size (w = 0.19); sugar concentration (w = 0.18); and sap flow intensity and bark thickness (w = 0.17), respectively. Sap trees showed lower levels of health, greater size, lower sugar concentration, higher sap flow intensity and lower bark thickness than non-sap trees in models when variables were included. Size, sugar concentration and bark thickness provided the best inference for tree selection in *P. ruscifolia*, *A. quebracho-blanco* and *Z. mistol*, respectively (Table 2).

The best model for *S. salicifolium* included health, although model performance was weak (w = 0.10) (Table 1, Supplementary Table 1). Sap trees showed higher levels of health than non-sap trees and sugar concentration provided the best inference for tree selection in this species (Table 2).

Table 1. Best supported models (ΔAICc < 2) of tree selection from species of plants used for sap consumption by the White-fronted Woodpecker during four seasons of the year. ΔAICc — difference in AICc (Akaike's information criterion corrected for small sample size) between this model and the minimum AICc model; w — Akaike weight. Sample size: 10 sap trees (cases) and 10 non-sap trees (controls). Models with the lowest ΔAIC and highest w values are in bold. Summary of all generalized linear models of tree choice are in Appendix 1.

Models	Autumn		Winter		Spring		Summer	
	ΔAICc	w	ΔAICc	w	Δ AICc	w	Δ AICc	w
Prosopis ruscifolia								
sugar concentration + size	0.00	**0.18**	0.46	0.23				
size	0.13	0.11			1.03	0.11	1.17	0.12
sugar concentration + size + health	1.69	0.05	0.00	**0.30**				
size + distance to ponds	1.06	0.07			1.99	0.07		
sugar concentration + size + distance to ponds			1.45	0.14				
distance to ponds	0.68	0.08			1.94	0.07		
size + health	1.45	0.06			0.00	**0.19**	0.00	**0.21**
sugar concentration + size + bark thickness			1.18	0.16				
size + bark thickness							1.96	0.08
size + health + bark thickness							0.00	0.21
Stetsonia coryne								
sugar concentration + size	0.00	**0.27**	1.99	0.10	0.00	**0.28**	1.82	0.11
size	0.54	0.21					0.00	**0.28**
sugar concentration	1.15	0.15						
sugar concentration + size + distance to ponds			0.37	0.22				
sap flow intensity + sugar concentration + size					0.71	0.20	1.97	0.10
sap flow intensity + size					0.21	0.25		
sugar concentration + distance to ponds			0.61	0.19				
sap flow intensity + sugar concentration + distance to ponds			0.00	**0.26**				
Ziziphus mistol								
sap flow intensity + size	0.00	**0.12**						
bark thickness	0.34	0.10			0.23	0.15	0.00	**0.18**
size	0.47	0.09					1.02	0.11
size + bark thickness	1.65	0.05						
sap flow intensity + bark thickness	1.72	0.05			0.00	**0.17**		
sugar concentration + bark thickness							1.75	0.08
sap flow intensity + health + bark thickness			0.00	**0.26**				
sap flow intensity + health			1.00	0.16				
sap flow intensity + health + distance to ponds			1.86	0.10				

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Models	Autumn		Winter		Spring		Summer	
	ΔAICc	w	ΔAICc	w	Δ AICc	w	Δ AICc	w
Aspidosperma quebracho-blanco								
size + bark thickness	0.60	0.09	1.16	0.05				
bark thickness	0.00	**0.13**	0.04	0.09			1.22	0.07
sugar concentration + bark thickness	1.85	0.05	1.55	0.04			1.67	0.06
sap flow intensity + bark thickness			1.36	0.05				
distance to ponds	1.82	0.05	1.01	0.06				
sap flow intensity			0.83	0.06				
sugar concentration			0.00	**0.09**	0.00	**0.18**	0.00	**0.14**
size			0.92	0.06				
health			1.30	0.05				
sap flow intensity + sugar concentration			1.82	0.04	1.24	0.10	1.45	0.07
sugar concentration + health					1.91	0.07		
sugar concentration + size							1.96	0.05
Sarcotoxicum salicifolium								
sap flow intensity + size	0.66	0.11					1.89	0.04
sap flow intensity + size + distance to ponds	1.81	0.06						
sap flow intensity	0.00	**0.15**	1.30	0.05	0.54	0.08	1.02	0.05
sugar concentration + size + health	1.93	0.06						
sap flow intensity + health	1.80	0.06	1.05	0.05				
sap flow intensity + sugar concentration			1.34	0.05			1.26	0.05
sap flow intensity + sugar concentration + health			0.68	0.06				
size			0.80	0.06	0.22	0.09	0.66	0.07
size + health			1.88	0.03	1.93	0.04	0.22	0.08
sugar concentration + health			0.76	0.06			1.15	0.05
health			0.42	0.07	0.00	**0.10**	0.35	0.08
sugar concentration + size			1.35	0.05				
bark thickness					0.77	0.07		
sugar concentration			0.00	**0.09**	0.65	0.07	0.00	**0.09**
distance to ponds			1.92	0.03	0.57	0.08		

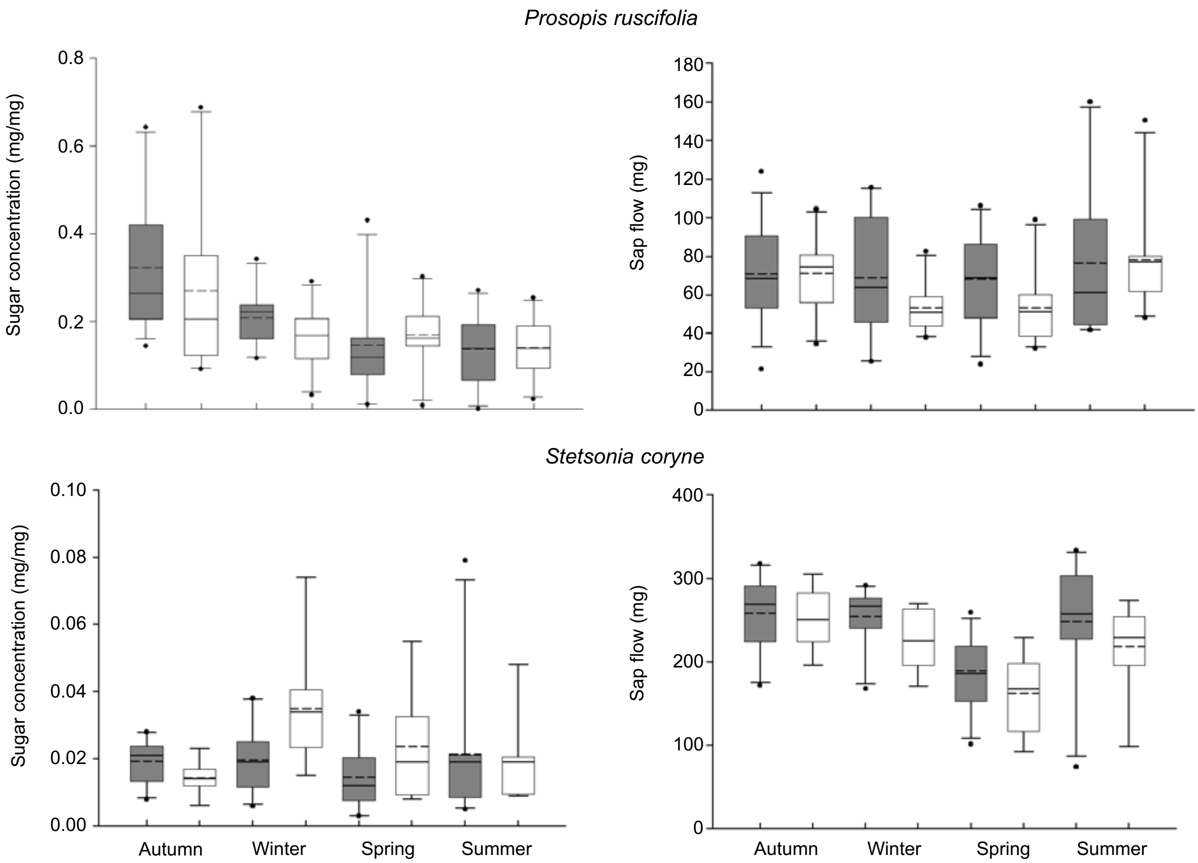

Fig. 1. Sap flow intensity and sugar concentration of *Prosopis ruscifolia* and *Stetsonia coryne* (the most used tree species) in sap and non-sap trees by the White-fronted Woodpecker in the semiarid Chaco during four seasons of the year. Sap trees are indicated with grey box plots and non-sap trees with white boxplots. Box plots represent 50% of the data; the horizontal line and dot in the boxes are the median and the mean, respectively. Whiskers represent 90% of the data and dots beyond whiskers are outliers. Y axis was not standardized due to the large differences in values among plant species.

Summer plant selection

In summer, sap-plant selection in *S. coryne* and *P. ruscifolia* was explained by models containing size, and size and health, respectively (Table 1, Appendix 1). The performance of these models received considerable weighting (w = 0.28 in *S. coryne* and w = 0.21 in *P. ruscifolia*). Sap-plant selection was explained by larger size in both models and by low levels of health. Summed weight showed that size provided the best inference for tree selection in both species (Table 2). Sap-tree selection was explained by models containing bark thickness in *Z. mistol* (w = 0.18) and sugar concentration in *A. quebracho-blanco* (w = 0.14) and *S. salicifolium* (w = 0.09). Sap trees showed lower bark thickness and sugar concentration than non-sap trees in models where variables were included (Fig. 2). Bark thickness, sugar concentration and sap flow intensity provided the best inference for tree selection in *Z. mistol*, *A. quebracho-blanco* and *S. salicifolium* respectively (Table 2).

Tannin concentration

For tree and shrub species, tannin concentration did not differ between sap and non-sap trees. However, for the columnar cactus *S. coryne* tannin concentration was lower in sap plants than in non-sap plants, but only in summer (Table 3).

DISCUSSION

The White-fronted Woodpecker focuses its feeding activity on a few individual plant species among the many available in their territories (Núñez Montellano et al. 2013). We found that woodpeckers selected individual plants for sap consumption, mainly characterized by their large size, whose drilled holes provide higher sap flow

Table 2. Relative importance of each predictor variable for plant species used for White-fronted Woodpecker sap consumption during the four seasons of the year. Summed Akaike weights for each variable of all models are showed and highly ranked variables are highlighted in bold.

Plant species	Seasons	Summed Akaike weights ($\Sigma\omega_i$)					
		Sap flow intensity	Sugar concentration	Size (crown area, height)	Bark thickness	Health	Distance to ponds
Prosopis ruscifolia	Autumn	0.17	0.38	**0.75**	0.17	0.22	0.39
	Winter	0.09	**0.93**	**0.94**	0.19	0.32	0.22
	Spring	0.19	0.18	**0.75**	0.19	0.33	0.41
	Summer	0.13	0.14	**0.97**	0.36	0.60	0.13
Ziziphus mistol	Autumn	0.41	0.19	**0.54**	0.43	0.18	0.24
	Winter	**0.80**	0.12	0.16	0.39	0.67	0.16
	Spring	0.47	0.17	0.29	**0.72**	0.16	0.21
	Summer	0.19	0.24	0.37	**0.57**	0.18	0.24
Aspidosperma quebracho-blanco	Autumn	0.23	0.26	0.32	**0.57**	0.23	0.26
	Winter	0.29	0.36	0.28	**0.41**	0.21	0.23
	Spring	0.35	**0.66**	0.20	0.24	0.29	0.19
	Summer	0.24	**0.58**	0.28	0.38	0.21	0.19
Sarcotoxicum salicifolium	Autumn	**0.67**	0.24	0.47	0.16	0.32	0.21
	Winter	0.33	**0.80**	0.30	0.18	0.44	0.20
	Spring	0.26	**0.50**	0.32	0.24	0.33	0.27
	Summer	**0.58**	0.38	0.38	0.20	0.42	0.19
Stetsonia coryne	Autumn	0.21	0.58	**0.71**			0.20
	Winter	0.37	**0.92**	0.38			0.70
	Spring	0.53	0.61	**0.95**			0.19
	Summer	0.39	0.39	**0.68**			0.21

intensity and sugar concentration than in unselected plants. From the plant species we studied, individual plant selection was stronger in those that are more important in the woodpecker´s diet (e.g. *P. ruscifolia* and *S. coryne*).

P. ruscifolia sap trees in autumn and winter, and *S. coryne* sap trees in spring and summer showed a higher concentration of sugars and larger plant size in relation to non-sap trees. According to the optimal foraging theory, animals are expected to adjust their foraging strategies to the abundance and quality of available prey items (Stephens & Krebs 1986). Our results suggest that the White-fronted Woodpecker selects large plants with high concentration of sugars to maximize its net energy intake. Other sap-feeding birds and mammals also concentrate feeding on a few plant species and often focus their feeding on a few individuals within those species. Sap nutrient content appears to be an important trait involved in sap-tree selection by birds e.g. Yellow-bellied Sapsucker, Akiapolaau *Hemignathus munroi* (honeycreeper), Kaka *Nestor meridionalis* (parrot) and mammals e.g. Sugar Glider *Petaurus breviceps* and Yellow-bellied Glider *P. australis* (marsupials), Abert's Squirrel *Sciurus aberti* (squirrel) (Goldingay 1987, Howard 1989, Snyder 1992, Pejchar & Jeffrey 2004). Plant size is another trait frequently related to sap-tree selection (Eyre & Goldingay 2005, Varner et al. 2006, Kozma 2010, Charles & Linklater 2014, Mancuso 2014).

Tree selection patterns can change across seasons in relation to nutritional demands of specific woodpecker behaviours that occur during their annual cycle, such as breeding (Molokwu et al. 2011), increased metabolic costs during harsh conditions (Hulbert & MacMillen 1988, Whelan et al. 2000), and responses to food availability, which is typical of temperate dry forests (Dostine & Franklin 2002). White-fronted Woodpecker selection of individual trees with higher sugar concentration (e.g. in *P. ruscifolia*), higher sap flow intensity (e.g. in *Z. mistol*) and lower levels of health during autumn and winter could be a strategy to maximize energy and nutrient intake during a period of the year when food resources are less abundant in the semiarid Chaco (Codesido & Bilenca 2004). During summer, White-fronted Woodpeckers decrease their sap consumption and exploit a larger variety of resources, such as insects and fruits, to meet their nutritional requirements (Blendinger 2005, Núñez Montellano et al. 2013),

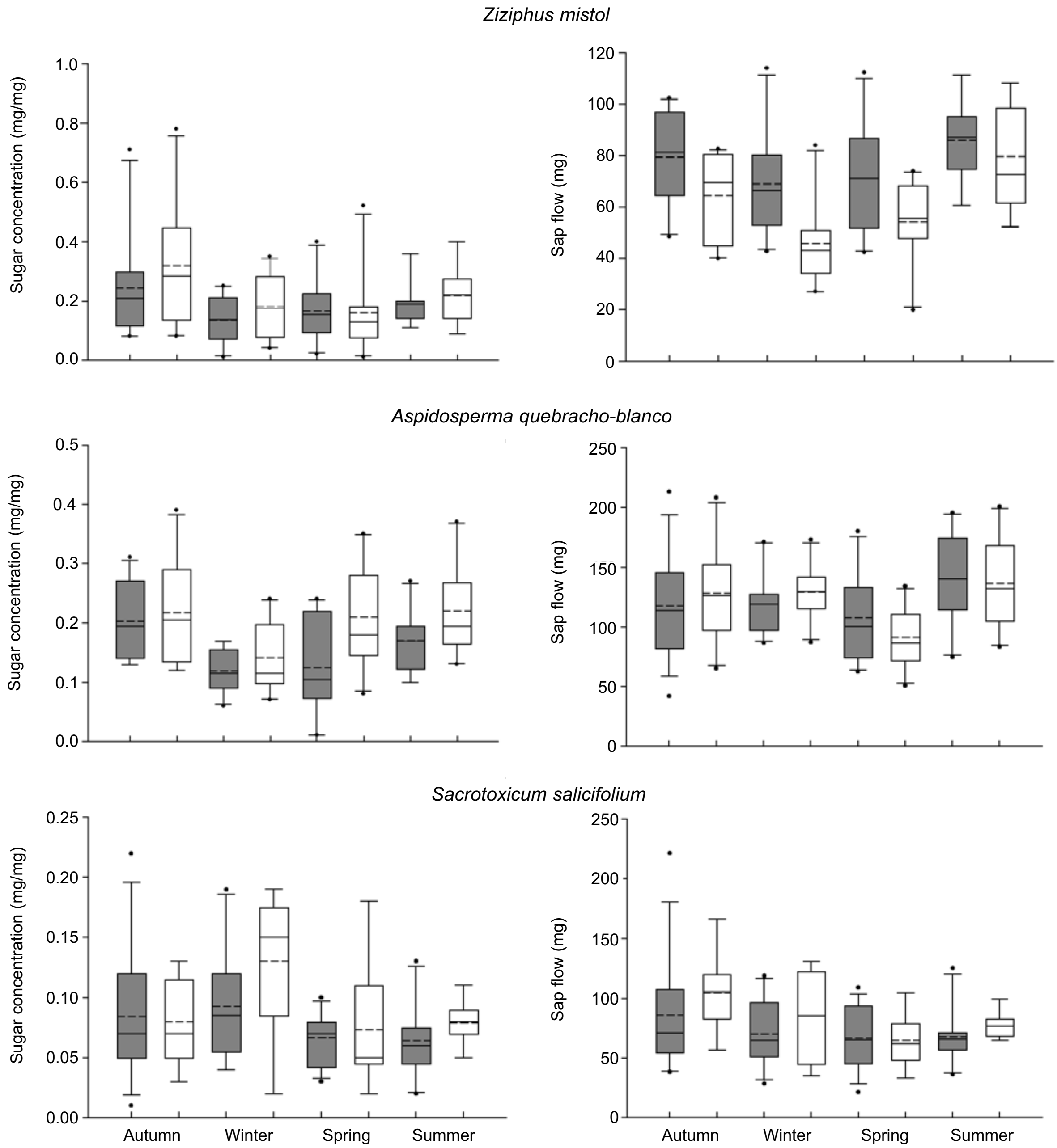

Fig. 2. Sap flow intensity and sugar concentration of *Ziziphus mistol*, *Aspidosperma quebrachoblanco* and *Sarcotoxicum salicifolium* for sap and non-sap trees by the White-fronted Woodpecker in the semiarid Chaco during the four periods of the year. Sap trees are indicated with grey box plots and non-sap trees with white boxplots. Box plots represent 50% of the data; the horizontal line and dot in the boxes are the median and the mean, respectively. Whiskers represent 90% of the data and dots beyond whiskers are outliers. Y axis was not standardized due to the large differences in values among plant species.

and they feed on sap from plants based on their size rather than on sap quality. Supporting this finding, woodpeckers selected *S. coryne* plants with greater size, which was the most consumed species during summer in this study.

Some plant traits, such as bark thickness and tannin concentration, could be not important in explaining White-fronted Woodpecker plant selection. Bark thickness may not be an access barrier to sap-carrying vessels for some sap feeding species e.g. Yellow-bellied Sapsucker, Kaka, and Yellow-bellied Glider (Eberhardt 2000, Charles & Linklater 2014, Wallis & Goldingay 2014). White-fronted Woodpeckers use different foraging

Table 3. Univariate analyses of tannin concentration between used and unused plant species trees consumed by the White-fronted Woodpecker during autumn and summer in the semiarid Chaco. For each plant species and season, the mean, SD, number of plants (n) and test t (t) or Wilcoxon test (W) are indicated.

Plant species	Seasons	Tannins concentration Mean ± SD sap-trees (n)	Tannins concentration Mean ± SD non-sap trees (n)	test	p
Prosopis ruscifolia	Autumn	3.05 ± 2.00 (6)	1.88 ± 0.97 (6)	t = -1.3	0.224
	Summer	3.76 ± 1.59 (6)	2.14 ± 1.26 (6)	t = -1.9	0.079
Stetsonia coryne	Autumn	0.15 ± 0.09 (6)	0.28 ± 0.12 (6)	W = 54	0.101
	Summer	0.12 ± 0.08 (6)	0.39 ± 0.07 (6)	t = 5.11	0.001
Sarcotoxicum salicifolium	Autumn	0.39± 0.38 (6)	0.30 ± 0.19 (6)	t = -0.57	0.582
	Summer	1.04 ± 0.53 (6)	0.88 ± 0.46 (6)	t = -0.58	0.577
Aspidosperma quebracho-blanco	Autumn	0.40 ± 0.21 (5)	0.35 ± 0.22 (5)	t = -0.37	0.718
	Summer	0.29 ± 0.14 (5)	0.48 ± 0.26 (5)	t = 1.44	0.187
Ziziphus mistol	Autumn	2.16 ± 1.22 (6)	1.31± 0.76 (6)	t = -1.46	0.176
	Summer	1.97 ± 0.55 (5)	1.48 ± 0.62 (5)	t = -1.31	0.225

strategies to exploit sap according to bark thickness, such as drilling sap holes on secondary branches or on main trunk bark fissures of thick-barked tree species (Núñez Montellano & Blendinger 2015). Therefore, analysis of the bark thickness in other plant structures, such as primary or secondary branches, and not only on the main trunk, would be interesting. Even though *Z. mistol* and *A. quebracho-blanco* present thick bark and White-fronted Woodpeckers drill sap holes on bark fissures, woodpeckers selected the thinner bark plants in those trees species. On the other hand, dietary tannins are often perceived as detrimental because of their potential to affect protein digestibility. White-fronted Woodpecker only selected plants of *S. coryne* with lower tannins concentration for sap consumption in summer, when was the most commonly used plant species (61.1% of the foraging observations of summer, Núñez Montellano et al. 2013). Some animals can neutralize tannins by producing salivary proteins which bind tannins in a highly specific manner (Hagerman 2002). Tannins also seem to be efficient in reducing gastrointestinal parasite infections in many animals, including birds (Niezen et al. 2002, Marzoni et al. 2005), and some tannins are potential biological antioxidants (Hagerman 2002). Food items high in tannin content such as acorns are important in the diet of other *Melanerpes* species (Acorn Woodpecker *M. formicivorus* and Red-bellied Woodpecker *M. carolinus*; Koenig & Faeth 1998, Richardson et al. 2013). Therefore, the lack of a relationship between tannin concentration and sap-tree selection by the White-fronted Woodpecker in autumn and summer (except for *S. coryne*) may highlight a trade-off between the costs and benefits of ingesting them. Elucidation of this trade-off requires deeper knowledge of this woodpecker´s physiological ability to digest and detoxify tannins.

In summary, the White-fronted Woodpecker selects plants for sap feeding, from those species it uses the most, based on a plant´s individual traits. The selection of plants which offer a greater reward in sap quality strongly suggests a response to maximize food energy intake according to seasonal changes in food availability, typical of semiarid climates of temperate regions. Birds are predicted to alter their diets to include food that allow maximizing energy intake when climatic conditions become harsher (Hayslette & Mirarchi 2001). These foraging strategies highlight the White-fronted Woodpecker´s ability to exploit a wide range of food resources using unusual and novel behaviours for the Picidae family (e.g. well drilling to gain access to sap, fly catching or the use of anvils to consume seeds; Núñez Montellano et al. 2013), and to use them efficiently by feeding on individuals of certain plant species with high values of sugar concentration, during harsh condition periods of the year. Future studies should involve the identification of factors that play a role in particular plant species selection for sap consumption by White-fronted Woodpeckers compared to other plant species that are avoided.

Sap wells drilled by the White-fronted Woodpecker enable several bird species access to an energy-rich food resource, mainly during months of low productivity (Núñez Montellano et al. 2013). The Chaco habitat type used by the White-fronted-Woodpecker has high deforestation rates (Gasparri et al. 2008) and vegetation is subjected to a variety of anthropogenic disturbances as livestock grazing, burning for pasture management and selective logging (Tálamo & Caziani 2003). Our results show that large trees are selected as sap trees by White-fronted Woodpecker, therefore, we recommend activities that promote retention of large trees in Chaco region.

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STRESZCZENIE

[Charakterystyka drzew wybieranych przez dzięciury białoczelne do żerowania na ich soku]
Dzięcioły żywią się głównie owadami i ich larwami oraz innymi stawonogami. Jednak w diecie kilku przedstawicieli tej rodziny znajdują się produkty roślinne, takie jak sok drzew. W suchych lasach Gran Chaco w Argentynie sok drzew jest ważnym składnikiem pożywienia dzięciura białoczelnego. Celem pracy było zbadanie powodów, dla których dzięcioły żerują na niektórych roślinach, unikając innych dostępnych roślin tego samego gatunku, jak również opisać wybiórczość sezonową.

Zakładano, że wybór roślin do żerowania w poszczególnych porach roku będzie lepiej tłumaczony przez kilka cech rozpatrywanych łącznie (np. stężenie cukrów w soku, natężenie wypływu soku, wielkość rośliny i jej kondycja oraz warunki mikrośrodowiskowe) niż jedną, konkretną cechę. Badaniami objęto pięć gatunków roślin, które są wykorzystywane przez te dzięcioły najczęściej i we wszystkich porach roku: krzew *Sarcotoxicum salicifolium* z rodziny kaparowatych, drzewa: *Prosopis ruscifolia* (rodzina bobowate), głożyna *Ziziphus mistol* (rodzina szakłakowate) oraz aspidosperma biała (quebracho białe, rodzina toinowate) oraz sukulent *Stetsonia coryne* (rodzina kaktusowate). Porównywano charakterystykę poszczególnych roślin, na których żerowały dzięcioły, z tymi znajdującymi się w najbliższej okolicy tej rośliny, jednak bez śladów żerowania. W analizach uwzględniono aspekt sezonowy.

Rośliny wybierane przez dzięcioły w poszczególnych sezonach były większe, z wyższą zawartością cukrów w ich soku, niż rośliny tych samych gatunków jednak nie wykorzystywane do żerowania. W pewnych sezonach na wybór poszczególnych roślin wpływają także grubość kory czy intensywność wypływu soku (Tab. 1, 2, Apendyks 1, Fig. 1, Fig. 2). Dla badanych drzew i krzewu nie stwierdzono wpływu ilości tanin w soku na wybór do żerowania (Tab. 3). Jednak w przypadku kaktusa *S. coryne*, rośliny na których żerowały dzięcioły miały znacznie mniej tanin niż te, na których ptaki nie żerowały, jednak różnica ta istotna była tylko w okresie letnim (Tab. 3).

Wybór roślin dostarczających bardziej wartościowego pożywienia wskazuje, że dzięciury maksymalizują ilość energii przyjmowanej w pokarmie w reakcji na sezonowość w dostępności pożywienia charakteryzującą suche lasy klimatu podzwrotnikowego.

Appendix 1. Summary of generalized linear models of tree choice from species of plants used for sap consumption by the White-fronted Woodpecker during four seasons of the year. AICc: Akaike's information criterion corrected for small sample size, ΔAICc: difference in AICc between this model and the minimum AICc model, w: Akaike weight. Sample size: 10 sap trees (cases) and 10 non-sap trees (controls). Models that best fit the data with the lowest delta AIC and highest weight are in bold.

Models/Variables included	Seasons											
	Autumn			Winter			Spring			Summer		
	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*
Prosopis ruscifolia												
sugar concentration + size	**31.12**	**0.00**	**0.18**	20.66	0.46	0.23	30.83	2.62	0.05	26.63	3.57	0.04
size	31.25	0.13	0.11	25.85	5.64	0.02	29.25	1.03	0.11	24.22	1.17	0.12
sugar concentration + size + health	32.81	1.69	0.05	**20.21**	**0.00**	**0.30**	33.12	4.90	0.02	25.69	2.63	0.06
size + distance to ponds	32.17	1.06	0.07	28.04	7.84	0.01	30.21	1.99	0.07	26.99	3.93	0.03
sugar concentration + size + distance to ponds	33.30	2.19	0.04	21.66	1.45	0.14	32.02	3.80	0.03	29.70	6.64	0.01
distance to ponds	31.80	0.68	0.08	28.28	8.07	0.01	30.16	1.94	0.07	29.72	6.66	0.01
size + health + distance to ponds	33.48	2.37	0.03	29.82	9.62	0.00	31.29	3.08	0.04	26.21	3.16	0.04
size + health	32.57	1.45	0.06	27.13	6.92	0.01	**28.22**	**0.00**	**0.19**	**23.06**	**0.00**	**0.21**
sugar concentration + size + bark thickness	33.80	2.68	0.03	21.39	1.18	0.16	33.52	5.31	0.01	27.91	4.85	0.02
sap flow + size + distance to ponds	33.85	2.74	0.03	30.94	10.74	0.00	32.20	3.99	0.03	29.79	6.73	0.01
sap flow + sugar concentration + size	33.87	2.75	0.03	23.83	3.62	0.05	33.79	5.57	0.01	29.69	6.63	0.01
size + distance to ponds + bark thickness	34.29	3.17	0.02	30.54	10.33	0.00	31.47	3.25	0.04	27.75	4.70	0.02
sap flow + size	33.35	2.23	0.04	28.06	7.85	0.01	30.88	2.66	0.05	26.70	3.64	0.03
size + bark thickness	33.70	2.58	0.03	28.28	8.07	0.01	30.59	2.37	0.06	25.02	1.96	0.08
sap flow + size + health	34.98	3.87	0.02	29.64	9.44	0.00	33.09	4.88	0.02	25.74	2.68	0.06
sap flow + distance to ponds	34.12	3.00	0.02	30.53	10.33	0.00	31.92	3.70	0.03	32.16	9.10	0.00
size + health + bark thickness	35.15	4.03	0.01	29.60	9.39	0.00	32.62	4.41	0.02	23.06	0.00	0.21
health + distance to ponds	34.20	3.08	0.02	30.96	10.76	0.00	32.71	4.49	0.02	31.75	8.70	0.00
sugar concentration + distance to ponds	34.31	3.19	0.02	24.79	4.59	0.03	32.23	4.01	0.03	32.20	9.15	0.00
distance to ponds + bark thickness	34.46	3.34	0.02	31.07	10.86	0.00	32.81	4.60	0.02	32.51	9.46	0.00
sap flow + size + bark thickness	36.30	5.18	0.01	29.63	9.42	0.00	33.53	5.32	0.01	28.13	5.07	0.02
bark thickness	35.25	4.14	0.01	31.72	11.51	0.00	35.28	7.07	0.01	31.88	8.83	0.00
sap flow + health + distance to ponds	36.93	5.81	0.00	33.57	13.37	0.00	34.79	6.58	0.01	34.58	11.52	0.00
sap flow + distance to ponds + bark thickness	36.98	5.87	0.00	26.59	6.39	0.01	34.80	6.59	0.01	35.29	12.23	0.00
sap flow + sugar concentration + distance to ponds	37.06	5.94	0.00	27.95	7.74	0.01	34.09	5.88	0.01	35.22	12.16	0.00
sugar concentration + health + distance to ponds	37.10	5.98	0.00	27.93	7.72	0.01	35.03	6.81	0.01	34.65	11.60	0.00
health + distance to ponds + bark thickness	37.15	6.04	0.00	34.13	13.92	0.00	35.66	7.45	0.00	34.92	11.86	0.00
sugar concentration	35.58	4.47	0.01	30.42	10.22	0.00	35.78	7.57	0.00	32.42	9.36	0.00
sugar concentration + distance to ponds + bark thickness	37.24	6.12	0.00	33.39	13.19	0.00	35.18	6.96	0.01	35.36	12.30	0.00
health	36.08	4.97	0.01	32.43	12.22	0.00	36.07	7.86	0.00	32.02	8.97	0.00
sap flow	36.09	4.98	0.01	30.13	9.92	0.00	34.09	5.88	0.01	32.42	9.36	0.00
sugar concentration + bark thickness	37.15	6.03	0.00	32.82	12.61	0.00	37.59	9.38	0.00	34.57	11.52	0.00

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Models/Variables included	Seasons											
	Autumn			Winter			Spring			Summer		
	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*
sap flow + bark thickness	37.70	6.58	0.00	32.84	12.63	0.00	36.64	8.42	0.00	34.51	11.45	0.00
health + bark thickness	37.90	6.79	0.00	34.51	14.30	0.00	37.89	9.67	0.00	34.21	11.16	0.00
sap flow + sugar concentration	38.18	7.06	0.00	31.59	11.38	0.00	36.07	7.86	0.00	35.21	12.15	0.00
sugar concentration + health	38.23	7.12	0.00	33.19	12.99	0.00	38.43	10.21	0.00	34.81	11.76	0.00
sap flow + health	38.75	7.63	0.00	32.90	12.69	0.00	36.73	8.51	0.00	34.81	11.75	0.00
sap flow + sugar concentration + bark thickness	40.08	8.96	0.00	34.65	14.44	0.00	38.94	10.73	0.00	37.65	14.60	0.00
sugar concentration + health + bark thickness	40.09	8.98	0.00	35.95	15.75	0.00	40.50	12.29	0.00	37.30	14.25	0.00
sap flow + health + bark thickness	40.66	9.54	0.00	35.97	15.76	0.00	39.55	11.34	0.00	37.22	14.17	0.00
sap flow + sugar concentration + health	41.13	10.02	0.00	34.76	14.55	0.00	39.01	10.79	0.00	37.98	14.92	0.00
Stetsonia coryne												
sugar concentration + size	**26.41**	**0.00**	**0.27**	24.95	1.99	0.10	**23.32**	**0.00**	**0.28**	29.56	1.82	0.11
size	26.95	0.54	0.21	28.37	5.41	0.02	26.96	3.64	0.05	**27.74**	**0.00**	**0.28**
sugar concentration	27.56	1.15	0.15	25.05	2.09	0.09	28.36	5.04	0.02	30.93	3.19	0.06
sugar concentration + size + distance to ponds	30.19	3.78	0.04	23.33	0.37	0.22	25.42	2.10	0.10	32.81	5.07	0.02
sap flow + sugar concentration + size	30.20	3.80	0.04	27.76	4.80	0.02	24.03	0.71	0.20	29.71	1.97	0.10
sap flow + size	29.04	2.64	0.07	28.83	5.87	0.01	23.53	0.21	0.25	30.29	2.55	0.08
size + distance to ponds	29.25	2.84	0.06	31.21	8.25	0.00	29.75	6.43	0.01	30.53	2.79	0.07
sugar concentration + distance to ponds	30.41	4.00	0.04	23.57	0.61	0.19	31.16	7.84	0.01	33.78	6.04	0.01
sap flow + sugar concentration	30.41	4.00	0.04	27.08	4.11	0.03	31.19	7.87	0.01	30.62	2.88	0.07
sap flow + size + distance to ponds	32.26	5.85	0.01	30.84	7.88	0.01	26.36	3.04	0.06	33.47	5.73	0.02
sap flow	30.83	4.43	0.03	27.90	4.94	0.02	29.99	6.67	0.01	29.94	2.20	0.09
distance to ponds	31.02	4.62	0.03	31.03	8.07	0.00	30.90	7.58	0.01	31.04	3.30	0.05
sap flow + sugar concentration + distance to ponds	33.67	7.26	0.01	**22.96**	**0.00**	**0.26**	34.39	11.07	0.00	33.87	6.13	0.01
sap flow + distance to ponds	33.64	7.23	0.01	29.61	6.64	0.01	32.83	9.50	0.00	32.77	5.03	0.02
Ziziphus mistol												
sap flow + size	**26.78**	**0.00**	**0.12**	26.96	4.29	0.03	29.25	4.05	0.02	28.97	3.94	0.03
bark thickness	27.12	0.34	0.10	27.06	4.40	0.03	25.43	0.23	0.15	**25.03**	**0.00**	**0.18**
size	27.26	0.47	0.09	29.19	6.52	0.01	27.40	2.21	0.06	26.06	1.02	0.11
sap flow + size + distance to ponds	29.42	2.64	0.03	29.91	7.25	0.01	31.12	5.93	0.01	31.34	6.30	0.01
size + bark thickness	28.43	1.65	0.05	29.52	6.85	0.01	27.30	2.11	0.06	27.21	2.17	0.06
sap flow + size + health	29.64	2.85	0.03	25.75	3.08	0.06	32.30	7.11	0.00	32.33	7.29	0.00
sap flow + bark thickness	28.51	1.72	0.05	29.24	6.57	0.01	**25.19**	**0.00**	**0.17**	27.88	2.85	0.04
sap flow + size + bark thickness	29.69	2.91	0.03	31.79	9.12	0.00	28.36	3.16	0.03	30.42	5.38	0.01
sap flow + sugar concentration + size	29.86	3.08	0.03	30.06	7.40	0.01	31.98	6.79	0.01	32.28	7.24	0.00
size + distance to ponds	28.81	2.02	0.04	31.91	9.25	0.00	29.99	4.79	0.02	28.11	3.07	0.04
sugar concentration + bark thickness	28.86	2.08	0.04	29.24	5.58	0.01	28.20	3.01	0.04	26.78	1.75	0.08
health + bark thickness	29.60	2.82	0.03	28.70	6.03	0.01	27.75	2.55	0.05	27.89	2.86	0.04

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Models/Variables included	Seasons											
	Autumn			Winter			Spring			Summer		
	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*
distance to ponds + bark thickness	29.66	2.88	0.03	29.77	7.11	0.01	28.20	3.01	0.04	27.89	2.85	0.04
sap flow	28.88	2.09	0.04	25.49	2.82	0.06	28.53	3.34	0.03	29.12	4.09	0.02
sugar concentration + size	29.83	3.05	0.03	29.81	7.14	0.01	29.86	4.67	0.02	28.93	3.89	0.03
sugar concentration + size + bark thickness	31.05	4.26	0.01	31.79	8.12	0.00	30.32	5.13	0.01	29.89	4.85	0.02
size + health	29.99	3.20	0.02	31.27	8.61	0.00	29.98	4.79	0.02	28.97	3.93	0.03
size + distance to ponds + bark thickness	31.17	4.39	0.01	31.86	9.19	0.00	30.46	5.26	0.01	30.42	5.39	0.01
sap flow + sugar concentration + bark thickness	31.45	4.67	0.01	28.72	6.06	0.01	27.99	2.80	0.04	30.14	5.10	0.01
sap flow + distance to ponds + bark thickness	31.46	4.67	0.01	32.59	9.93	0.00	27.69	2.50	0.05	31.23	6.19	0.01
sap flow + distance to ponds	30.35	3.57	0.02	27.99	5.32	0.02	28.57	3.38	0.03	29.97	4.93	0.02
size + health + bark thickness	31.54	4.76	0.01	28.79	6.13	0.01	30.28	5.09	0.01	30.56	5.53	0.01
sugar concentration + size + distance to ponds	31.59	4.81	0.01	32.83	10.17	0.00	32.82	7.62	0.00	31.29	6.26	0.01
sugar concentration + distance to ponds + bark thickness	31.61	4.83	0.01	32.36	9.70	0.00	31.35	6.15	0.01	29.97	4.94	0.02
sap flow + health + bark thickness	31.64	4.86	0.01	**22.67**	**0.00**	**0.26**	28.36	3.17	0.03	31.15	6.12	0.01
size + health + distance to ponds	31.66	4.87	0.01	34.29	11.62	0.00	32.89	7.70	0.00	31.31	6.27	0.01
sugar concentration + health + bark thickness	31.95	5.17	0.01	30.52	7.86	0.01	30.88	5.69	0.01	30.13	5.10	0.01
health + distance to ponds + bark thickness	32.21	5.43	0.01	31.86	8.19	0.00	30.91	5.72	0.01	31.11	6.07	0.01
distance to ponds	30.29	3.50	0.02	31.79	9.12	0.00	31.26	6.07	0.01	28.36	3.33	0.03
sap flow + sugar concentration	31.67	4.88	0.01	28.28	5.62	0.02	31.15	5.96	0.01	31.11	6.07	0.01
sap flow + health	31.67	4.89	0.01	23.66	1.00	0.16	31.20	6.01	0.01	32.01	6.97	0.01
sugar concentration + size + health	32.98	6.19	0.01	31.57	8.90	0.00	32.83	7.64	0.00	32.29	7.26	0.00
health + distance to ponds	31.88	5.10	0.01	33.58	10.92	0.00	33.46	8.27	0.00	30.70	5.67	0.01
sap flow + health + distance to ponds	33.24	6.46	0.00	24.53	1.86	0.10	31.65	6.46	0.01	32.89	7.86	0.00
sugar concentration + distance to ponds	32.19	5.40	0.01	32.89	10.22	0.00	34.02	8.83	0.00	30.33	5.30	0.01
sap flow + sugar concentration + distance to ponds	33.49	6.70	0.00	31.14	8.48	0.00	31.26	6.07	0.01	31.26	6.22	0.01
sugar concentration	31.71	4.93	0.01	30.91	8.24	0.00	32.43	7.23	0.00	29.22	4.19	0.02
health	32.03	5.25	0.01	31.73	9.06	0.00	32.04	6.85	0.01	29.67	4.63	0.02
sugar concentration + health + distance to ponds	34.54	7.75	0.00	34.25	11.59	0.00	36.59	11.40	0.00	33.37	8.33	0.00
sap flow + sugar concentration + health	34.83	8.05	0.00	26.60	3.93	0.04	34.19	9.00	0.00	34.46	9.42	0.00
sugar concentration + health	34.32	7.54	0.00	32.46	9.79	0.00	34.83	9.64	0.00	32.13	7.09	0.01
Aspidosperma quebracho-blanco												
size + bark thickness	35.34	0.60	0.09	32.23	1.16	0.05	33.20	5.49	0.01	32.09	2.51	0.04
bark thickness	**34.73**	**0.00**	**0.13**	**31.11**	**0.04**	**0.09**	30.75	3.04	0.04	30.80	1.22	0.07
sugar concentration + bark thickness	36.58	1.85	0.05	32.62	1.55	0.04	30.29	2.58	0.05	31.25	1.67	0.06
size + health + bark thickness	37.74	3.01	0.03	35.00	3.93	0.01	33.78	6.07	0.01	34.82	5.24	0.01
sap flow + bark thickness	36.84	2.11	0.04	32.43	1.36	0.05	32.40	4.69	0.02	33.43	3.85	0.02
size + distance to ponds + bark thickness	37.96	3.22	0.03	35.14	4.07	0.01	36.15	8.44	0.00	35.19	5.61	0.01

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Models/Variables included	Seasons											
	Autumn			Winter			Spring			Summer		
	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*
health + bark thickness	37.14	2.41	0.04	33.82	2.75	0.02	32.29	4.58	0.02	33.23	3.65	0.02
sap flow + size + bark thickness	38.08	3.35	0.02	34.59	3.52	0.02	34.48	6.77	0.01	35.26	5.68	0.01
distance to ponds	36.56	1.82	0.05	32.08	1.01	0.06	32.07	4.36	0.02	32.41	2.83	0.03
sugar concentration + size + bark thickness	38.11	3.37	0.02	34.18	3.11	0.02	33.42	5.71	0.01	31.81	2.23	0.04
distance to ponds + bark thickness	37.20	2.47	0.04	33.66	2.59	0.03	33.34	5.63	0.01	33.59	4.01	0.02
sap flow	36.80	2.07	0.05	31.90	0.83	0.06	30.98	3.27	0.04	32.38	2.80	0.03
sugar concentration	36.86	2.12	0.04	31.07	0.00	0.09	**27.71**	**0.00**	**0.18**	**29.58**	**0.00**	**0.14**
size	36.88	2.15	0.04	31.99	0.92	0.06	32.42	4.71	0.02	32.20	2.62	0.04
health	36.91	2.17	0.04	32.37	1.30	0.05	30.65	2.94	0.04	32.07	2.49	0.04
sugar concentration + distance to ponds + bark thickness	38.54	3.81	0.02	35.57	4.50	0.01	33.36	5.65	0.01	33.92	4.34	0.02
sugar concentration + distance to ponds	37.95	3.22	0.03	33.59	2.52	0.03	30.40	2.69	0.05	32.13	2.55	0.04
sap flow + sugar concentration + bark thickness	38.95	4.22	0.02	33.53	2.46	0.03	31.89	4.19	0.02	32.90	3.33	0.03
sugar concentration + health + bark thickness	39.25	4.51	0.01	35.50	4.43	0.01	32.65	4.95	0.02	34.08	4.50	0.01
sap flow + health + bark thickness	39.46	4.73	0.01	35.51	4.43	0.01	34.43	6.72	0.01	36.30	6.72	0.00
size + distance to ponds	38.68	3.95	0.02	34.41	3.34	0.02	34.85	7.14	0.01	34.90	5.32	0.01
sap flow + distance to ponds + bark thickness	39.69	4.96	0.01	35.44	4.37	0.01	34.88	7.17	0.01	36.60	7.02	0.00
sap flow + distance to ponds	38.99	4.26	0.02	34.40	3.33	0.02	32.76	5.05	0.01	35.14	5.56	0.01
health + distance to ponds	39.03	4.29	0.01	34.82	3.75	0.01	33.25	5.54	0.01	34.86	5.28	0.01
health + distance to ponds + bark thickness	39.94	5.20	0.01	36.73	5.66	0.01	35.34	7.63	0.00	36.31	6.73	0.00
sap flow + sugar concentration	39.08	4.34	0.01	32.89	1.82	0.04	28.95	1.24	0.10	31.03	1.45	0.07
sap flow + health	39.14	4.41	0.01	34.63	3.56	0.02	32.10	4.39	0.02	34.85	5.27	0.01
size + health	39.16	4.43	0.01	34.64	3.57	0.02	32.85	5.14	0.01	34.63	5.05	0.01
sugar concentration + health	39.21	4.48	0.01	33.61	2.53	0.03	29.62	1.91	0.07	32.05	2.47	0.04
sap flow + size	39.26	4.53	0.01	34.50	3.43	0.02	33.44	5.73	0.01	34.99	5.41	0.01
sugar concentration + size	39.36	4.63	0.01	33.49	2.42	0.03	30.50	2.79	0.04	31.54	1.96	0.05
sugar concentration + size + distance to ponds	40.69	5.96	0.01	36.33	5.26	0.01	33.57	5.86	0.01	34.65	5.08	0.01
sap flow + sugar concentration + distance to ponds	40.70	5.97	0.01	35.86	4.79	0.01	32.11	4.40	0.02	34.10	4.53	0.01
sugar concentration + health + distance to ponds	40.81	6.07	0.01	36.53	5.46	0.01	32.69	4.99	0.01	34.66	5.08	0.01
size + health + distance to ponds	41.38	6.65	0.00	37.45	6.38	0.00	35.83	8.12	0.00	37.79	8.21	0.00
sap flow + size + distance to ponds	41.53	6.79	0.00	37.32	6.25	0.00	35.32	7.61	0.00	38.05	8.47	0.00
sap flow + sugar concentration + health	41.69	6.96	0.00	35.79	4.72	0.01	31.45	3.75	0.03	34.12	4.54	0.01
sap flow + health + distance to ponds	41.71	6.98	0.00	37.48	6.41	0.00	34.59	6.88	0.01	38.02	8.44	0.00
sap flow + size + health	41.82	7.08	0.00	37.54	6.47	0.00	33.53	5.82	0.01	37.80	8.22	0.00
sugar concentration + size + health	41.94	7.21	0.00	36.22	5.15	0.01	32.56	4.85	0.02	34.34	4.76	0.01
sap flow + sugar concentration + size	41.95	7.21	0.00	35.95	4.87	0.01	31.91	4.21	0.02	33.65	4.07	0.02
Sarcotoxicum salicifolium												
sap flow + size	28.50	0.66	0.11	32.10	3.30	0.02	35.18	2.62	0.03	30.53	1.89	0.04

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Models/Variables included	Seasons											
	Autumn			Winter			Spring			Summer		
	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*
sap flow + size + distance to ponds	29.65	1.81	0.06	34.99	6.19	0.00	37.39	4.82	0.01	33.79	5.14	0.01
sap flow	**27.84**	**0.00**	**0.15**	30.09	1.30	0.05	33.10	0.54	0.08	29.66	1.02	0.05
sugar concentration + size + health	29.76	1.93	0.06	31.26	2.46	0.03	37.55	4.99	0.01	31.66	3.01	0.02
sap flow + health	29.64	1.80	0.06	29.84	1.05	0.05	34.99	2.43	0.03	30.91	2.27	0.03
sap flow + size + health	30.74	2.90	0.04	32.72	3.92	0.01	37.12	4.55	0.01	31.11	2.47	0.03
sap flow + sugar concentration + size	31.17	3.33	0.03	32.69	3.89	0.01	38.23	5.67	0.01	32.58	3.94	0.01
sap flow + size + bark thickness	31.38	3.54	0.03	34.86	6.06	0.00	38.10	5.53	0.01	32.61	3.97	0.01
sap flow + bark thickness	30.47	2.63	0.04	32.84	4.04	0.01	35.84	3.28	0.02	32.35	3.71	0.01
sap flow + distance to ponds	30.51	2.67	0.04	32.68	3.88	0.01	35.65	3.08	0.02	32.07	3.43	0.02
sap flow + sugar concentration	30.56	2.73	0.04	30.13	1.34	0.05	35.70	3.13	0.02	29.90	1.26	0.05
sap flow + sugar concentration + health	31.98	4.15	0.02	29.48	0.68	0.06	37.93	5.36	0.01	31.97	3.33	0.02
size	30.49	2.65	0.04	29.60	0.80	0.06	32.79	0.22	0.09	29.30	0.66	0.07
size + distance to ponds	31.52	3.68	0.02	31.79	2.99	0.02	34.68	2.12	0.03	31.93	3.29	0.02
size + health	31.56	3.72	0.02	30.68	1.88	0.03	34.49	1.93	0.04	28.86	0.22	0.08
sap flow + health + bark thickness	32.69	4.86	0.01	32.39	3.59	0.01	38.08	5.52	0.01	34.13	5.49	0.01
sap flow + health + distance to ponds	32.70	4.86	0.01	32.84	4.05	0.01	37.90	5.33	0.01	33.71	5.07	0.01
sugar concentration + health	31.89	4.06	0.02	29.55	0.76	0.06	35.17	2.61	0.03	29.80	1.15	0.05
health	31.20	3.36	0.03	29.21	0.42	0.07	**32.56**	**0.00**	**0.10**	28.99	0.35	0.08
size + health + distance to ponds	33.08	5.25	0.01	33.40	4.60	0.01	36.54	3.98	0.01	31.59	2.95	0.02
sugar concentration + size	32.22	4.39	0.02	30.14	1.35	0.05	35.50	2.93	0.02	31.04	2.39	0.03
sap flow + distance to ponds + bark thickness	33.49	5.65	0.01	35.78	6.99	0.00	38.73	6.17	0.00	35.21	6.57	0.00
sap flow + sugar concentration + bark thickness	33.50	5.66	0.01	33.39	4.59	0.01	38.78	6.22	0.00	32.40	3.76	0.01
sugar concentration + size + distance to ponds	33.57	5.73	0.01	32.90	4.10	0.01	37.77	5.21	0.01	34.05	5.41	0.01
sap flow + sugar concentration + distance to ponds	33.59	5.75	0.01	33.08	4.28	0.01	38.62	6.05	0.00	33.02	4.38	0.01
size + distance to ponds + bark thickness	33.94	6.10	0.01	33.89	5.10	0.01	37.02	4.46	0.01	34.35	5.71	0.01
sugar concentration + health + bark thickness	34.23	6.39	0.01	32.79	4.00	0.01	38.25	5.69	0.01	32.95	4.31	0.01
size + bark thickness	33.24	5.40	0.01	32.10	3.31	0.02	35.42	2.86	0.02	31.83	3.18	0.02
size + health + bark thickness	34.58	6.74	0.01	33.20	4.41	0.01	37.26	4.70	0.01	31.61	2.97	0.02
bark thickness	32.82	4.99	0.01	31.04	2.24	0.03	33.33	0.77	0.07	31.04	2.39	0.03
health + bark thickness	33.69	5.85	0.01	32.03	3.24	0.02	35.31	2.74	0.03	31.82	3.18	0.02
sugar concentration + health + distance to ponds	34.88	7.05	0.00	32.31	3.52	0.02	38.09	5.53	0.01	33.05	4.41	0.01
health + distance to ponds	33.94	6.10	0.01	31.68	2.89	0.02	35.11	2.54	0.03	31.75	3.11	0.02
sugar concentration	33.29	5.45	0.01	**28.79**	**0.00**	**0.09**	33.22	0.65	0.07	**28.64**	**0.00**	**0.09**
distance to ponds	33.35	5.51	0.01	30.72	1.92	0.03	33.13	0.57	0.08	30.99	2.35	0.03
sugar concentration + size + bark thickness	35.29	7.46	0.00	33.31	4.51	0.01	38.44	5.88	0.01	33.87	5.23	0.01
sugar concentration + bark thickness	35.37	7.53	0.00	31.57	2.77	0.02	35.96	3.40	0.02	31.35	2.70	0.02
distance to ponds + bark thickness	35.56	7.73	0.00	33.56	4.76	0.01	35.87	3.31	0.02	33.84	5.20	0.01
health + distance to ponds + bark thickness	36.78	8.94	0.00	34.85	6.06	0.00	38.19	5.63	0.01	34.97	6.33	0.00
sugar concentration + distance to ponds	36.03	8.19	0.00	31.26	2.47	0.03	35.77	3.21	0.02	31.48	2.84	0.02
sugar concentration + distance to ponds + bark thickness	38.43	10.59	0.00	34.48	5.69	0.01	38.86	6.30	0.00	34.57	5.93	0.00