

AGE-RELATED CHANGES IN NUTRIENT RESORPTION PATTERNS AND TANNIN CONCENTRATION OF *CASUARINA EQUISETIFOLIA* PLANTATIONS

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YE GF, ZHANG SJ, ZHANG LH, LIN YM, WEI SD, LIAO MM & LIN GH. 2012. Age-related changes in nutrient resorption patterns and tannin concentration of *Casuarina equisetifolia* plantations. Tannin levels and nutrient resorption of *Casuarina equisetifolia* at different developmental phases (juvenile, mature and senescent phases) were examined to evaluate possible nutrient conservation strategies under nutrient limitation. Results showed that *C. equisetifolia* branchlets contained relatively higher contents of total phenolics, extractable condensed tannin, total condensed tannin contents and protein precipitation capacity in juvenile stands compared with those in mature and senescent stands. Nitrogen (N) concentrations in mature branchlets increased with stand development, while phosphorus (P) concentrations showed a decreasing trend. Nitrogen:phosphorus ratios in mature branchlets were above 20 and increased with stand development. Phosphorus resorption efficiencies were significantly higher than N resorption efficiencies, with the highest in mature stands. Tannin level, nutrient concentration and resorption were affected by stand age. Our results indicated that at intraspecific level, *C. equisetifolia* could adjust its nutrient conservation with stand development.

Keywords: Nutrient limitation, nutrient resorption efficiency, polyphenolics dynamics, stand development

YE GF, ZHANG SJ, ZHANG LH, LIN YM, WEI SD, LIAO MM & LIN GH. 2012. Perubahan corak erapan nutrien yang berkaitan dengan usia serta kepekatan tanin ladang *Casuarina equisetifolia*. Aras tanin serta erapan nutrien *Casuarina equisetifolia* pada fasa perkembangan yang berbeza (juvenil, matang dan senesen) dikaji untuk menilai strategi pemuliharaan nutrien di bawah keadaan nutrien yang terhad. Keputusan menunjukkan bahawa ranting *C. equisetifolia* mengandungi kandungan jumlah fenol, tanin terkondensasi boleh ekstrak dan kapasiti mendakan protein yang lebih tinggi dalam dirian juvenil berbanding dengan dirian matang dan senesen. Kepekatan nitrogen (N) dalam ranting meningkat apabila usia dirian bertambah. Sebaliknya kandungan fosforus (P) menurun. Nisbah N:P dalam ranting matang melebihi 20 dan meningkat apabila usia dirian meningkat. Kecekapan erapan P lebih tinggi dengan ketara daripada kecekapan erapan N, dengan nilai tertinggi dalam dirian matang. Aras tanin, kepekatan nutrien serta erapan dipengaruhi usia dirian. Keputusan kami menunjukkan bahawa pada pada tahap intraspecies, *C. equisetifolia* dapat menyesuaikan penyimpanan nutrien mengikut perkembangan dirian.

INTRODUCTION

Phenolic compounds, including tannins, are a significant component of plant secondary metabolites. Since high tannin concentrations in plants are often associated with infertile site conditions (Northup et al. 1995), it has been suggested that there is an evolutionary advantage to higher tannin production. By reducing decomposition rates of litter and decreasing

nitrogen (N) leaching potential, tannins may provide a nutrient conservation mechanism (Lin et al. 2010).

Plant chemistry, ranging from metabolic processes to morphology, often changes through the process of maturation (Donaldson et al. 2006). Plant developmental changes can occur rapidly, for example, as leaf matures and senesces

through a growing season, or slowly, as long-lived perennial plants reach reproductive maturity and senescence. These changes can have effects on ecological interactions and ecosystem processes (Kraus et al. 2003, Donaldson et al. 2006). At the ecosystem level, tannin contents variation can influence litter decomposition and nutrient cycling rates (Hattenschwiler & Vitousek 2000, Kraus et al. 2003). Whereas relatively little is known about the effects of stand age on tannin contents of plants, some studies have found that developmentally-based variation can significantly influence herbivore behaviour and performance (Swihart & Bryant 2001, Lawrence et al. 2003). Studies that have measured within-year and between-year developmentally-mediated changes in tannin contents indicate that such changes can be significant and suggest that these chemical shifts are likely to be ecologically important (Boege & Marquis 2005, Laitinen et al. 2005).

Growth of perennial plants is determined not only by the amount of nutrients they require but also by the amounts of stored nutrients that can be reused. Retranslocation from senescing leaves is the process by which plants withdraw nutrients from these leaves, making them available for later investment in new structure (Aerts 1996). This increases the use of absorbed nutrients and reduces plant dependence on soil supply (Pugnaire & Chapin 1993). The process of retranslocation is closely associated with leaf senescence and conservation of nutrients and, thus, is an important mechanism enabling plants to maintain growth at nutrient-poor sites (Lin et al. 2010). Nutrients may be used more efficiently at nutrient-poor sites and this efficient nutrient use can be important to the survival of individuals under such conditions (Aerts 1995). Although still in debate, nutrient resorption is often thought to change with soil nutrient availability (Yuan & Chen 2009). Soil nutrient availability changes with stand development and many ecophysiological plant traits have been linked to plant ageing (Groom et al. 1997); therefore, plant nutrient resorption may also change with stand age (Gholz et al. 1985, Yuan & Chen 2009).

Casuarina equisetifolia is a nitrogen-fixing tree of considerable social, economic and environmental importance in tropical/subtropical littoral zones of Asia, the Pacific and Africa. It is commonly used in agroforestry plantations for soil stabilisation, reclamation and coastal

protection (Pinyopusarerk & Williams 2000). It is one of the most extensively introduced tree species outside its natural range. There are more than 300,000 ha of *C. equisetifolia* plantations in the coastline of southern China (Zhong et al. 2005). Coastal sandy soils are generally low in nutrient contents, especially N. Low soil fertility will lead to slow growth. However, *C. equisetifolia* is characterised by high primary productivity. High tannin production and nutrient resorption may be important strategies for *C. equisetifolia* in coastal environments (i.e. arid, nutrient limitation) (Zhang et al. 2008, 2009). Despite the widespread planting and known ecological and physiological properties of *C. equisetifolia*, there is scant information about the nutrient resorption patterns and tannin concentrations of *C. equisetifolia* forest with stand development. Since plant ecophysiological traits are associated with ageing, we hypothesise that tannin contents and nutrient resorption efficiency change with stand development. To evaluate this hypothesis, a field investigation of *C. equisetifolia* stand covering juvenile, mature and senescent phases was conducted at Chihu Forestry Center of Huian County, Fujian Province, China.

MATERIALS AND METHODS

Materials

The study was carried out at Chihu Forestry Center of Huian County (23° 45' N, 118° 55' E), Fujian Province, China. The climate of the region belongs to southern subtropical maritime monsoon climate, with annual temperature ranging from 2.2 to 37 °C. Mean annual precipitation and evaporation are 1029 and 2000 mm respectively. The rainy season is from March till October and the dry season, November till February.

In October 2009, we selected *C. equisetifolia* forests which were planted in 2004 (juvenile phase, 5 years old), 1988 (mature phase, 21 years old) and 1971 (senescent phase, 38 years old) at Chihu Forestry Center of Huian County, Fujian Province, China. The stand characteristics and some soil properties are given in Table 1.

A total of 30 trees with similar height and growth condition at each stand-age class were chosen and two branches of each tree were randomly selected from the upper crown for branchlet sampling. The 30 trees were

Table 1 Some characteristics of the *Casuarina equisetifolia* stands at Chihu Forestry Center of Huian County Fujian Province, China

Stand age (years)	Community			Soil physiochemical properties (0–20 cm)				
	Density (trees ha ⁻¹)	Dbh (cm)	Height (m)	Soil bulk density (g cm ⁻³)	Total N in soil (mg kg ⁻¹)	Total P in soil (mg kg ⁻¹)	SOC (g kg ⁻¹)	Soil pH
5	2350	5.35 (1.52)	8.12 (2.31)	1.22 (0.05)	72.72 (3.81)	2.23 (0.13)	7.14 (1.14)	5.47 (0.08)
21	2202	17.32 (3.26)	15.43 (3.65)	1.24 (0.05)	76.90 (4.12)	2.98 (0.36)	12.00 (1.65)	5.24 (0.05)
38	1962	21.42 (4.12)	18.82 (4.35)	1.34 (0.09)	81.15 (4.26)	4.13 (0.39)	12.43 (1.69)	5.10 (0.05)

Values in parentheses are SD of the mean, n = 3; Dbh = diameter at breast height; SOC = soil organic carbon

divided into five groups (six trees in a group) as five replications. The development stages of branchlets (leaves) were demarcated into two stages, i.e. mature branchlets (fully developed, usually 15–25 cm long and dark green in colour) and senescent branchlets (old branchlets, white or grey in colour). All samples were taken to the laboratory immediately after sampling and cleaned with distilled water.

Soil samples (0–20 cm depth) at each site were collected using an auger. Soil samples were air dried in the laboratory and then passed through a 2-mm mesh sieve to remove stones and large roots before oven-drying at 65 °C. The oven-dried samples were then crushed and passed either through a 0.25-mm sieve for determination of total N and phosphorus (P) or through a 2-mm mesh sieve for measurement of pH. Soil pH was measured with a pH meter in a 1:1 mixture of soil and CO₂-free water which had been agitated for 1 min.

Chemical analyses

All chemicals used for the analyses in this study were of analytical reagent purity grade. An additional standard denoted here as purified tannin was extracted from *C. equisetifolia* branchlets and purified on Sephadex LH-20 according to the procedure described by Hagerman (2002). The condensed tannins standard was freeze-dried and stored at -20 °C until required.

Procedures described by Lin et al. (2006) were used to determine total phenolics, extractable condensed tannins, protein-bound condensed tannins, and fibre-bound condensed tannins and protein precipitation capacity. Total phenolics

were measured with the Prussian blue method (Graham 1992) while extractable condensed tannin, protein-bound condensed tannins and fibre-bound condensed tannins were assayed by the butanol-HCl method (Terrill et al. 1992) using purified tannins from *C. equisetifolia* branchlets as the standard. Total condensed tannin content was calculated by adding the respective quantities of extractable condensed tannin, protein-bound condensed tannins and fibre-bound condensed tannins (Terrill et al. 1992). A radial diffusion assay was used to determine protein precipitation capacity (Hagerman 1987).

Plant samples were digested with sulphuric acid and hydrogen peroxide. The N concentrations of plant samples were determined by the microKjeldahl method (Yoshida et al. 1972), while the P concentrations were determined by ascorbic acid-antimony reducing phosphate colorimetric method (Nanjing Institute of Soil Science 1978).

Calculations

Resorption efficiency (RE) was calculated as the percentage of N or P recovered from the senescing leaves (Aerts 1996, Killingbeck 1996):

$$RE(\%) = (A_1 - A_2) / A_1 \times 100\%$$

where A₁ = N or P concentration in mature branchlets and A₂ = N or P concentrations in senescent branchlets.

Statistical analysis

All measurements were replicated five times. A one-way analysis of variance (ANOVA) was

performed with stand age as treatment factor. The Student–Newman–Keuls multiple comparison method was used to test significant differences between any two stand ages. All analyses were performed by SPSS13.0 for Windows.

RESULTS

Changes in total phenolic contents in mature and senescent branchlets during stand development

Total phenolic contents of mature branchlets decreased from 218.52 to 180.49 mg g⁻¹ during stand development. Total phenolic contents of senescent branchlets were in the order juvenile stand > senescent stand > mature stand (Figure 1). Total phenolics content decreased during branchlet senescence in all stands ($p < 0.05$).

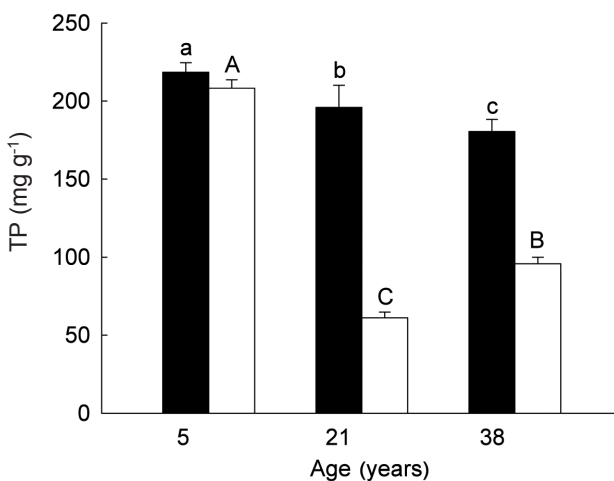


Figure 1 Content of total phenolics (TP) as a purified tannin standard in mature and senescent branchlets of *Casuarina equisetifolia*; black bars are for mature branchlets and white bars for senescent branchlets; for mature and senescent branchlets, means with different small and capital letters are significantly different at the $p < 0.05$ level respectively

Changes in condensed tannin contents in mature and senescent branchlets during stand development

The extractable condensed tannin contents in mature and senescent branchlets of *C. equisetifolia* were juvenile stand > senescent stand > mature stand. The extractable condensed tannin content of *C. equisetifolia* increased during branchlet

senescence both in the mature and senescent stands but decreased in the juvenile stand (Figure 2a).

The protein-bound condensed tannin content of branchlets increased during senescence in juvenile and mature stands ($p < 0.05$) and remained the same in senescent stands (Figure 2b). The fibre-bound condensed tannins of branchlets increased during senescence in mature stand and did not change in juvenile and senescent stands (Figure 2c).

Extractable condensed tannin was significantly higher than protein- or fibre-bound condensed tannin contents in mature and senescent branchlets of all stands. Total condensed tannin followed similar pattern as extractable condensed tannin during stand development (Figure 2d).

Changes in protein precipitation capacity in mature and senescent branchlets during stand development

Protein precipitation capacity in mature and senescent branchlets were significantly higher in juvenile stand than in mature and senescent stands (Figure 3). Protein precipitation capacity decreased during branchlet senescence in the three stands. Significant positive linear correlation was found between protein precipitation capacity and total phenolics or total condensed tannin (Figure 4).

Changes in N and P concentrations, N:P ratio and nutrient resorption during branchlet senescence with stand development

Nitrogen concentrations both in mature and senescent branchlets obviously increased during stand development. Phosphorus concentrations in mature branchlets were similar in juvenile and mature stands but lower in senescent stand. Phosphorus concentrations in senescent branchlets were significantly higher in juvenile stand than those in mature and senescent stands (Table 2).

Nitrogen:phosphorus ratios of mature branchlets also increased during stand development, and were all above 20 (Table 2). Nitrogen resorption efficiencies in three stands were basically below 50%, the lowest in senescent stand. Phosphorus resorption efficiencies were above 70% with the highest in mature stand (78.08%).

There were significant negative correlations between N and P concentrations in mature

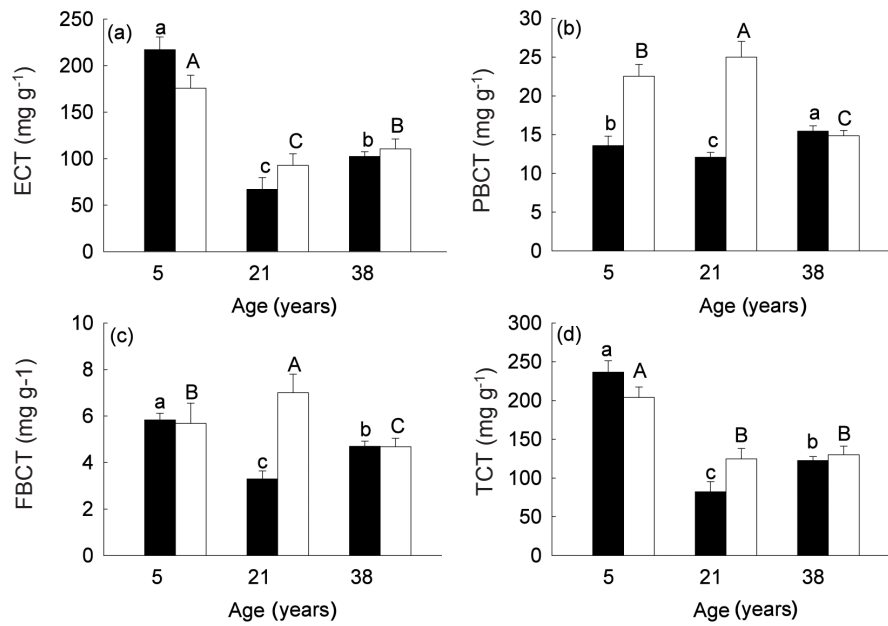


Figure 2 Changes in extractable condensed tannins (ECT), protein-bound condensed tannins (PBCT), fibre-bound condensed tannins (FBCT) and total condensed tannin (TCT) contents in mature and senescent branchlets of *C. equisetifolia*; black bars are for mature branchlets and white bars for senescent branchlets; for mature and senescent branchlets, means with different small and capital letters are significantly different at $p < 0.05$ level respectively

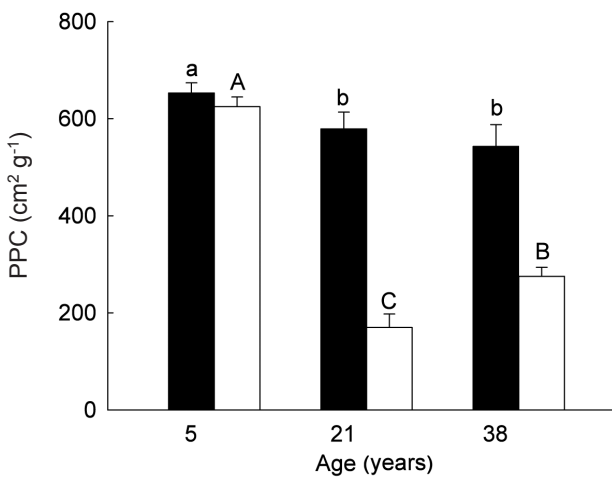


Figure 3 Changes in protein precipitation capacity (PPC) in mature and senescent branchlets of *C. equisetifolia*; black bars are for mature branchlets and white bars for senescent branchlets; for mature and senescent branchlets, means with different small and capital letters are significantly different at the $p < 0.05$ level respectively

and senescent branchlets (Table 3). Nitrogen resorption efficiency had a particular strong relationship with the N:P ratio of branchlets. On the other hand, P resorption efficiency was not related to N:P ratios of branchlets (Table 3).

There were significant correlations between total phenolics or total condensed tannin and N or P concentrations in branchlets except for the relationship between total condensed tannin and P concentrations in senescent branchlets (Table 4).

DISCUSSION

Total phenolic contents in mature branchlets decreased with stand development, indicating that stand age had an impact on total phenolic contents. *Casuarina equisetifolia* in juvenile stand possessed greater selective pressure for defense than mature and senescent trees. Phenolics provide protection against herbivores and this is a likely explanation for such patterns (Sasidharan et al. 2005). Total phenolic contents of mature branchlets were significantly higher than those of senescent branchlets in juvenile, mature and senescent stands. Several mechanisms may explain the decrease in phenolics during senescence of branchlets. First, much of the soluble carbon compounds (which also include polyphenols) are expected to be translocated from leaves during senescence (Mafongoya et al. 1998). Second, some low molecular weight phenols and external leaf phenolics are leached by rainfall from the leaves of trees (Hattenschwiler & Vitousek 2000).

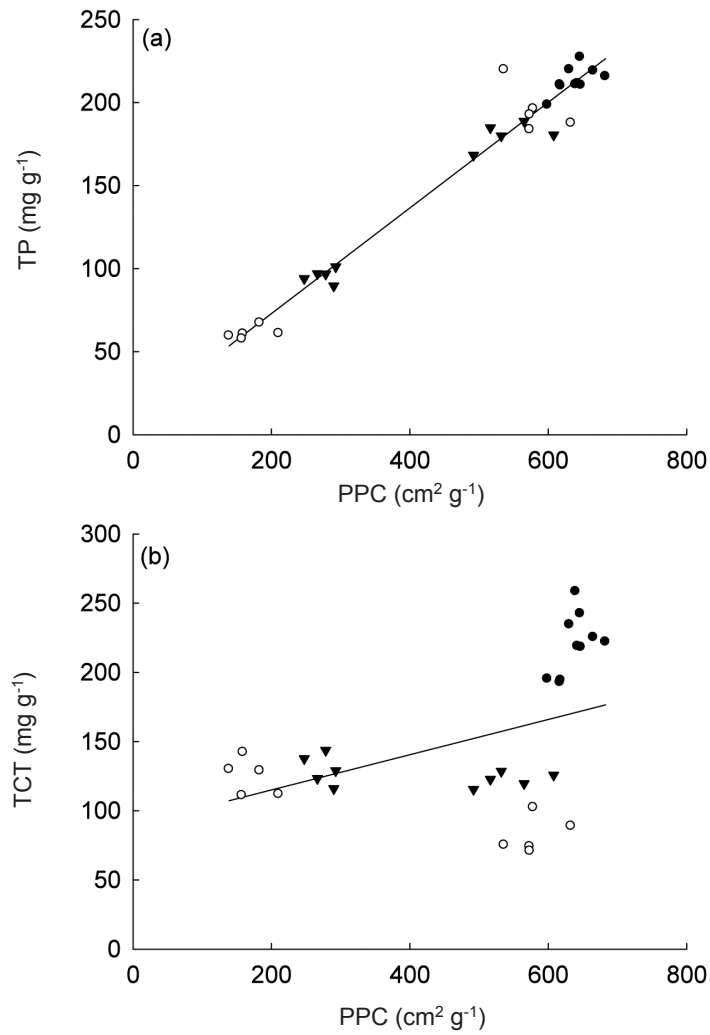


Figure 4 Relationships between (a) total phenolics (TP) and (b) total condensed tannin (TCT) with protein precipitation capacity (PPC) of the branchlets of *C. equisetifolia*; black circles are for *C. equisetifolia* in the 5-year-old stand, white circles for 21-year-old stand, black triangles for 38-year-old stand; TP–PPC: $y = 3.035x - 11.629$, $r = 0.983$, $p < 0.001$; TCT–PPC: $y = 1.505x + 248.403$, $r = 0.438$, $p < 0.05$

Table 2 Changes in nitrogen (N), phosphorus (P) concentrations, N:P ratios in mature and senescent branchlets, and resorption efficiencies of N and P (NRE and PRE respectively) with stand development

Variable	Branchlet	Age (years)		
		5	21	38
N (mg g ⁻¹)	MB	15.16 c	18.81 b	20.07 a
	SB	7.67 c	9.12 b	11.65 a
P (mg g ⁻¹)	MB	0.76 a	0.72 a	0.59 b
	SB	0.22 a	0.16 b	0.16 b
N:P ratio	MB	20.01 c	26.06 b	34.08 a
	SB	34.63 c	57.81 b	73.72 a
NRE (%)		49.19 a	51.47 a	41.88 b
PRE (%)		70.68 b	78.08 a	73.10 b

Data with different letters are significantly different ($p < 0.05$); MB = mature branchlets, SB = senescent branchlets

Table 3 Correlations between nutrient concentrations, nutrient resorption and N:P ratios of *C. equisetifolia* branchlets

Variable	r ²	F	p
N _m -P _m	0.370	7.650	0.016
N _s -P _s	0.518	13.983	0.002
NRE-N _m	0.052	0.713	0.414
NRE-N _s	0.516	13.839	0.003
PRE-P _m	0.047	0.634	0.440
PRE-P _s	0.484	12.194	0.004
NRE-N _m :P _m	0.310	5.829	0.031
NRE-N _s :P _s	0.279	5.023	0.043
PRE-N _m :P _m	0.009	0.124	0.730
PRE-N _s :P _s	0.153	2.339	0.150

N_m, N_s = nitrogen concentrations in mature and senescent branchlets respectively; P_m, P_s = phosphorus concentrations in mature and senescent branchlets respectively

Table 4 Correlative coefficient of selected branchlets data of *C. equisetifolia*

Variable	r ²	F	p
TP _m -N _m	0.577	17.759	0.001
TP _s -N _s	0.370	7.637	0.016
TCT _m -N _m	0.680	27.603	< 0.001
TCT _s -N _s	0.501	13.062	0.003
TP _m -P _m	0.485	12.243	0.004
TP _s -P _s	0.859	79.144	< 0.001
TCT _m -P _m	0.162	2.518	0.137
TCT _s -P _s	0.799	51.575	< 0.001

TP_m, TP_s = total phenolic concentrations in mature and senescent branchlets respectively; TCT_m, TCT_s = total condensed tannin concentrations in mature and senescent branchlets respectively

Both extractable and total condensed tannin contents were highest in juvenile stand, unlike extractable and total condensed tannins of mature branchlets which were lowest in mature stand. *Casuarina equisetifolia* trees grow rapidly in mature stand (Ye et al. 2000). According to the protein competition model hypothesis, protein demand should be highest when plant is growing rapidly, and phenylalanine allocation to phenolics should simultaneously decrease (Jones & Hartley 1999) because it is the common precursor of either protein or condensed tannins synthesis (Hattenschwiler & Vitousek 2000). There was no consistent pattern of enrichment or depletion for the condensed tannins during

senescence. Both increase and decrease in contents of polyphenols have been reported during senescence (Constantinides & Fownes 1994). In another study, it was observed that leaf age had no significant effects on condensed tannins and total phenolics (Kumar et al. 2006). It has been suggested that plasticity in tannin production may be adaptive and provide benefits such as compensatory defense, UV protection, oxidative prevention and nutrient uptake (Close & McArthur 2002). However, the changes in content do not necessarily reflect the quantitative allocation of tannins to the leaves because of rapid turnover of labile compounds (Kleiner et al. 1999) and because the content is

affected by concomitant changes in proportions of other components of leaves, e.g. structural leaf components (Koricheva 1999).

Protein precipitation capacity is related to the tannin biological activity (Martin & Martin 1982). Protein precipitation capacity in mature branchlets were higher than those in senescent branchlets in all stands. It had positive linear correlation with total phenolics and total condensed tannin. This result is consistent with that reported in a previous study by Zhang et al. (2008). These observations suggested that both hydrolysable and condensed tannins contributed to the protein precipitation capacity of the branchlets. The capacity of tannins to bind proteins is related to the molecular size of the tannins (Makkar et al. 1987). The decrease in protein precipitation capacity with senescence and the possible increase in degree of polymerisation suggested that, as branchlet senescence, tannin active sites specific for the interaction with proteins became fewer by the condensation of the tannin molecules, causing them to become too large to fit the protein orientation for cross-linking (Lin et al. 2006).

Total phenolics and total condensed tannin contents were inversely related to N contents in mature branchlets. It is common to find negative correlation between N and secondary compound contents such as phenolics and tannins (Mansfield et al. 1999). This pattern leads to support source-sink hypotheses such as the carbon–nutrient balance hypothesis (Bryant et al. 1983) and the growth-differentiation hypothesis (Herms & Mattson 1992) that predict increased carbon allocation to secondary carbon compounds under low nutrient conditions.

There were significant shifts in nutrient concentrations of *C. equisetifolia* branchlets along the stand age chronosequence. Some studies indicated that the nutrient concentrations in *Populus tremuloides* (Yuan & Chen 2009) and slash pine (Gholz et al. 1985) varied with stand development. Nitrogen concentrations in branchlets increased with stand development which was in accordance with the observation of Yuan and Chen (2009). Increasing N concentration with stand age can be a direct consequence of increasing soil N supply because green-leaf N concentration, in some instances, reflects site fertility (Lambers et al. 2008). However, it had been reported that soil N availability did not change with stand age (Yuan

& Chen 2009). The changes in green-leaf N with stand development might be related to the dilution effects because the greater leaf biomass production rates in younger stands could result in reduced N concentrations even if absolute uptake rates were high (Yuan & Chen 2009).

Nitrogen resorption efficiency in this study was below 50% and P resorption efficiency, above 70%. Mature stand had higher P resorption efficiency than juvenile and senescent stands, while senescent stand had lower N resorption efficiency than juvenile and mature stands. Compared with old stands, young stands have rapid biomass production and thus higher N demands (Miller 1995), which can be a possible driver of higher N resorption efficiency in young stands. Higher nutrient resorption is often explained by stronger nutrient sinks—faster growing plants have stronger requirement for nutrients (Lambers et al. 2008). In the present study, no significant difference in N resorption efficiency was observed between juvenile and mature stands, reflecting a possible N-fixing effect of *C. equisetifolia*. Nitrogen:phosphorus ratio has been applied to identify thresholds of nutrient limitation (Güsewell & Koerselman 2002, Rejmánková 2005). Thresholds of foliar N:P ratios were found to be < 14 for N limitation and > 16 for P limitation (Güsewell & Koerselman 2002). In present study, the N:P ratios of mature branchlets were all above 20, indicating that three stands were P-limited. Accordingly, P-limited stands had significantly higher P than N resorption efficiencies. The type of limitation indicated by N:P in mature leaves could be important in the response of resorption efficiency to nutrient availability. High nutrient resorption efficiency would favour retention of P relative to N (Aerts & Chapin 2000, Güsewell 2005). Plants growing in P-limiting conditions would thus be more favoured by high resorption efficiency than plants growing in N-limiting conditions.

Resorption is considered to be biochemically complete when nutrient concentrations are reduced below 0.7% N and 0.04% P in senescing leaves (Killingbeck 1996). In our study, N concentration in senescent leaves was > 0.7% but P concentration was below 0.04%. Obviously, N resorption was mostly incomplete and P resorption, complete.

Some researchers reported close relationship between resorption and plant nutrient status (Lal et al. 2001, Cote et al. 2002). The significant

positive correlation between N resorption efficiency and N concentration in senescent branchlets in our study is consistent with that reported in previous studies (Yuan et al. 2005, Zhang et al. 2008). However, the values were not correlated in mature branchlets. This could result from partial control of leaf N resorption over leaf N concentration by providing a large source of osmotically active substances in the senescent leaves (Aerts 1996). Nitrogen resorption efficiency had significant linear correlation with N:P ratios in mature and senescent branchlets. Phosphorus resorption efficiencies exhibited significant linear correlation with P concentration in senescent branchlets, but no correlation was found with either P concentration in mature branchlets or N:P in branchlets, which was similar to previous studies (Huang et al. 2007, Zhang et al. 2008).

Growth of perennial plants is determined not only by the amount of nutrients they require but also the amount of stored nutrients that can be reused. The degree of nutrient resorption affects litter quality, which consequently affects decomposition rates and nutrient availability. Knowledge of resorption patterns and their determinants is thus critical for understanding plant roles in ecosystem nutrient cycling (Rejmankova 2005). The tannin level, nutrient concentration and resorption were affected by stand age. Our results indicated that at the intraspecific level, *C. equisetifolia* could adjust its nutrient conservation with stand development. Thus, high tannin production and nutrient resorption may be important strategies for *C. equisetifolia* in arid and infertile environments, making it more adaptable to environmental stress.

CONCLUSIONS

Casuarina equisetifolia branchlets contained relatively higher total phenolics, extractable condensed tannin, total condensed tannin contents and protein precipitation capacity in juvenile stands compared with those in mature and senescent stands. Nitrogen concentrations in mature branchlets increased with stand development while P concentrations showed a decreasing trend. Nitrogen:phosphorus ratios in mature branchlets were above 20 and increased with stand development. Phosphorus resorption efficiency was significantly higher than N resorption efficiency, with the highest in mature

stands. Tannin level, nutrient concentration and resorption were affected by stand age. Our results indicated that at the intraspecific level, *C. equisetifolia* could adjust its nutrient conservation with stand development.

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