

Stand Biomass Dynamics of Pine Plantations and Natural Forests on Dry Steppe in Kazakhstan

V.A. Usol'tsev¹ and J.K. Vanclay²

Abstract

Biomass dynamics were studied in isolated relict stands of scots pine (*Pinus sylvestris*) on the dry steppe of Kazakhstan (53-54°N) where potential evaporation is 500-600 mm yr⁻¹ and the rainfall is 250-260 mm yr⁻¹. Samples were taken from 7 plots in natural stands on sandy forest soils (age 13-110 years) and 10 plots in plantations on dark-chestnut-coloured soils (age 5-50 years). Nine or 10 sample trees were taken from each plot, giving a total of 68 and 96 sample trees in natural and plantation stands respectively. Root systems were excavated and fractionated in 11 plots.

Analyses indicated that the stability of these stands becomes critical at 10-20 years when foliage biomass reaches its maximum (7-13 t ha⁻¹ dry weight), both in plantations and natural stands. Self-regulating mechanisms in natural stands provide stability that may not develop not observed in some plantations. Natural stands may show an abrupt decrease in foliage biomass at the time of canopy closure, but it increases again by age 40-50 years. In plantations this critical period may cause dieback and may trigger stand collapse before maturity. Stem and root biomass increases monotonically and does not depend upon stand origin. The total biomass production is influenced by ground water level and the presence of and depth to the clay layer underlying the sandy sediments.

Key words: *Pinus sylvestris*, stability, resilience, critical growth period, stand structure.

Introduction

Scots pine (*Pinus sylvestris* L.) occurs naturally in scattered relict stands on the dry steppe of Kazakhstan (53-54°N, east of the Ural River). Plantations have been established in the region, and studies of development and stability in both natural and planted stands on these marginal sites near the limit of the forest ecotype may offer insights into the behaviour of stressed stands.

Natural pine stands on the Kazakhstan steppe occur on poor sandy forest soils, while the adjoining treeless steppe has dark chestnut-coloured soils with a well developed humus layer. A continental climate is experienced, with potential evaporation (500-600 mm yr⁻¹) exceeding precipitation (250-260 mm yr⁻¹). Site quality and drought resistance are determined mainly by the ground water level and the presence of and depth to clay underlying the sandy

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sediments. Lands available for afforestation may comprise five soil groups (Prokhorov et al. 1988). Three of these soil groups are suitable for afforestation, having ground water within 2-6 m, and offering an 80-100 % success rate for rotations of 35-40 years. The two remaining soil groups are unsuited to plantation establishment, having a 90 % probability of failure between the ages 7-25 years.

The Aman-Karagai pine forest (66°E, 53°N) comprises 80 000 ha in the Turgai deflection, the depression between the Urals and Kazakh hills. Since 1953, over 24 000 ha of pine plantation have been established, mainly on steppe lands that were previously devoid of forest. Seedlings were planted with 1.5-2.5 m between rows and 0.5-0.7 m within rows. These attempts at afforestation were not very successful. Only 25 % of these plantations survive, and only 2 % exhibit good growth. Most of these plantations have been abandoned, and the remnants are deteriorating. Death or dieback usually commences at 17-25 years, and may be acute if crown closure coincides with a period of drought. Unfortunately, no plantations over the age of 50 years are available for study.

In contrast to the plantations, natural pine stands on sandy forest soils show no evidence of degradation or decline. The present study contrasts the biological productivity and ecological stability of stands of natural and plantation origin. It reviews recent Russian research and presents some new results, but does not attempt a comprehensive review of the dynamics of stressed stands (for such a review, see e.g. Kozlowski 1982, Kozlowski et al. 1991, Nambiar 1990, Whitehead and Jarvis 1981).

Material and Methods

The investigation was carried out in the Aman-Karagai forest in stands of Scots pine (*Pinus sylvestris* L.). Samples were taken on 7 plots in natural stands on sandy forest soils (age 13-110 years, site index II-III, i.e. rather poor sites) and on 10 plots in plantations on chestnut soils (age 5-50 years, also site index II-III) of the three soil groups most suited to afforestation (Usol'tsev et al. 1985). Plot size was 65-630 m² (mean 215 m²) in plantations and 25-1230 m² (mean 236 m²) in natural stands. Sampling involved the harvesting of 68 trees in natural stands and 96 trees in plantations. Samples were stratified by diameter class, with 9 or 10 trees from each plot. Sample trees were felled, sectioned and weighed (Usol'tsev 1985, 1988). Boles were divided into 10 equal sections for volume and biomass determination. Basic density measurements on each of 10 sample disks enabled the stem biomass to be estimated. Crop biomass (t ha⁻¹) was estimated by linear regression.

Root biomass of a single tree may be determined reliably (s.e. 4-5 %) by nondestructive electrometric methods (Yakushev 1972), but root grafting with adjacent trees may cause bias. Therefore 22 root systems on 11 plots in our investigation were excavated layer-by-layer, washed and fractionated. Seven of these plots were in plantations (6 on chestnut soils and 1 on sandy forest soil) and 4 were in natural stands (1 and 3, respectively). Trees selected for excavation usually corresponded to the tree of mean basal area, but some smaller trees were also excavated. All above- and below-ground biomass fractions were oven dried.

The allometric equation provides a reasonable model for the relationship

between root biomass and stem diameter at breast height (Usol'tsev & Vanclay 1993). To investigate the effect on root biomass of other factors such as stand origin and soil type, the following equation was fitted to the data:

$$b_i = \exp(\beta_0 + \beta_1 \ln t + \beta_2 \ln d + \beta_3 \ln h + \beta_4 Z + \beta_5 S), \quad (1)$$

where b_i is root biomass (oven dry kg), t is tree age (years), d is diameter (cm dbh), h is tree height (m), Z is a binary variable indicating stand origin (plantation or natural) and S is a binary variable indicating soil type (chestnut or sandy forest). The parameters β_4 and β_5 were not significant at $P=0.05$, and were omitted in the final equations:

For total tree root biomass including stumps ($R^2=0.982$):

$$b_{tr} = 0.228 t^{-0.3622} d^{2.7226} h^{-0.4772} \quad (2)$$

and for fine (<1 mm diameter) root biomass ($R^2=0.980$):

$$b_{fr} = 0.227 t^{-0.4052} d^{2.8565} h^{-0.6942} \quad (3)$$

All parameters are significant at $P<0.05$ and the standard error of both equations is $\pm 20\%$.

As it may be impossible to find the theoretical tree of mean basal area for excavation, equations (2) and (3) were used to adjust estimates of root biomass for mean tree age, diameter and height. Estimates of stand total root biomass and fine root biomass were obtained by multiplying the corrected data by stand density (trees ha^{-1}).

Results and Discussion

Voronkov (1970) summarized results from studies in Scots pine plantations in several regions including the Aman-Karagai forest, and concluded that foliage biomass culminated at 10 years. Between years 10 and 20, foliage biomass decreased sharply, then increased a little again before stabilizing. Analogous results were obtained by Galitski & Krylov (1984) in their simulation studies of foliage dynamics in pure even-aged plant communities. They found that foliage dynamics exhibited a saddle-like curve: foliage biomass increased monotonically with age until canopy closure, when it decreased briefly before increasing and stabilizing. Evidently stand stability reaches a critical period at the time of canopy closure. The onset of this critical period has been attributed (Voronkov 1970) to the unfavourable balance between above- and below-ground biomass. If recurrent droughts coincide with canopy closure and maximum foliage, they may cause the death of up to 99 % of the fine roots in uppermost metre of soil (Voronkov & Nevzorov 1981).

This contention is confirmed by the Aman-Karagai data. In both plantations and natural stands, root biomass increases monotonically with age, whereas foliage biomass reaches a maximum just prior to canopy closure. At canopy closure, the root:foliage biomass ratio may become critical in any stand, irrespective of origin, but the recovery may differ because of different stand structures. Stand density in natural stands is usually higher than in plantations; it may be 50 times higher at age 5 and 10 times higher at age 10 years. The high stand densities in natural forests reduce the foliage biomass

of individual trees by hastening the onset of canopy closure to as early as age 3-4 years. Plantations maintain higher foliage biomass for many years (Fig. 1) because of the lower stand density and delayed canopy closure. Lower stand densities, ploughing and weed control in plantations, and the high humus and nutrient content of the chestnut soils, all provide favourable conditions for the development of surface roots which are more sensitive to water deficits than the deeper root systems which form in the sandy soils of natural stands. The high foliage biomass and shallow rooting cause dieback when water deficits first occur (Berezyuk 1959). This dieback is characterised by a marked decrease in foliage biomass, without a corresponding decline in branch biomass. This imbalance between assimilating and non-assimilating above-ground biomass may contribute to tree death. Increased plantation density may reduce yields marginally, but confers greater resilience (Rubtsov et al. 1976).

The balance between foliage and root biomass is self-regulating in natural stands. It has been recognized that self-thinning in natural forest stands may be inhibited by climatic and ecological deterioration (Morozov 1930). High natural stand density may be a specific reaction to extreme conditions. For example, fire-regenerated stands of pure larch (*Larix dahurica* Turcz. ex Trautv.) may reach densities of 0.2-1.5 million trees (ha^{-1}) at 10-15 years over extensive areas near the northern limit of the forest ecosystem (Northern Yakutia, Verkhoyansk region). These dense stands exhibit strong ecological resistance to extreme growth conditions (Pozdnyakov 1980). Natural pine stands on sandy forest soils in the Aman-Karagai also may attain 300 000 trees (ha^{-1}) at age 20 (Usol'tsev 1985). This may exceed by a factor of 10 the "normal" stand density defined in regional yield tables, and may be 50-100 times higher than the usual plantation density. This intense intraspecific competition strongly differentiates trees according to vigour and tolerance (Sukachev 1953, Plotnikov 1979). High biological productivity may not be a basic function of plant cover, but may be secondary and subordinate to self-reproduction (Plotnikov 1979). This conforms to Allee's individual aggregation principle (Allee 1931, Odum 1971) that under unfavourable conditions, groups may exhibit lower mortality than individuals because the environmental contact surface relative to total biomass is less for a group than for individuals.

Natural pine stands continue to increase total foliage biomass for some ten years following canopy closure, but may compensate for any imbalance between above- and below-ground biomass by accelerating the recession of the crown base while retaining the upper crown. Self-thinning is inhibited except for some mortality amongst suppressed trees, and total biomass increases monotonically. There is considerable foliage loss in the inner crown, but the crown mantle is maintained. Natural forests do not remain in this limiting condition for long before self-regulating mechanisms trigger self-thinning. Both foliage and branch biomass decrease, but increase again after some self-thinning provides additional space in the canopy. In dense young pine forests, root grafting amongst as many as 5000 root systems (ha^{-1} , Makarenko 1984) may help recovery after the critical period.

Equations provide a convenient way to express these relationships concisely and concretely. Logarithmic polynomials provide a convenient summary of these and other dynamic processes (Usol'tsev 1985, 1988). Second order logarithmic polynomials can be used to model the monotonic responses exhibited by several biomass fractions (Table 1):

$$B_i = \exp (\beta_0 + \beta_1 \ln t + \beta_2 \ln^2 t + \beta_3 Z) \quad (4)$$

where B_i is stand biomass (total, stem, root or fine root, $t \text{ ha}^{-1}$), t is stand age (yr), Z is a binary variable indicating stand origin (natural or plantation).

TABLE 1 NEAR HERE

Parameter estimates for equation (4) suggested that there is no statistically significant ($P=0.05$) effect of stand origin on the dynamics of basal area (G , $m_2 \text{ ha}^{-1}$) and mean height (h_m , m), or on total stem biomass, total and fine (<1 mm) root biomass ($t \text{ ha}^{-1}$). The actual t -statistics for the parameter β_3 were 1.69, 0.75, 0.54, 0.71 and 0.80, respectively. However, a statistically significant influence of stand origin on stem bark biomass dynamics was observed ($t=2.34$, $P<.05$), and suggests higher bark biomass in natural stands with smaller mean stem diameters (Usol'tsev 1985).

A more comprehensive model was used to describe the non-monotonic relationships displayed by other variables:

$$Y = \exp(\beta_0 + \beta_1 \ln t + \beta_2 \ln^2 t + \beta_3 \ln^3 t + \beta_4 \ln^4 t + \beta_5 Z + \beta_6 Z \ln t) \quad (5)$$

Equation (5) was fitted to stand density data (N , 1000 ha^{-1}), as well as to total branch, branch bark, and foliage biomass ($t \text{ ha}^{-1}$). Parameter estimates suggest that stand origin may influence stand density dynamics significantly, but has little influence on foliage biomass (Student's t -statistics are 6.08, 3.37, 2.40, and 0.91 for the parameter β_5 and 5.41, 0.09, 2.17 and 0.94 for the parameter β_6 respectively). Seemingly, stand origin does not influence the dynamics of foliage biomass, and this allows a general equation (valid for ages 13-50 years) describing the relationship between foliage biomass and stand age for both plantations and natural stands ($R^2=0.766$, $SE=9.1\%$):

$$Y = \exp(-2.8965 + 3.0990 \ln^2 t - 1.2624 \ln^3 t + 0.1377 \ln^4 t) \quad (6)$$

A strict biological interpretation would restrict equation (6) to much narrower age range, spanning years 15-20. Prior to canopy closure, foliage biomass in plantations may be higher than in natural stands because of the better growing conditions. Conversely, after canopy closure, foliage biomass may be less if stand degradation has commenced. Thus it may be preferable to use specific parameter values for plantations and natural stands:

$$B_f = \exp (\beta_0 + \beta_1 \ln t + \beta_2 \ln^2 t + \beta_3 \ln^3 t + \beta_4 \ln^4 t) \quad (7)$$

TABLES 2 & 3 NEAR HERE

Parameter estimates for equations (4) and (7) are given in Tables 1 and 2. Table 3 provides estimates from these equations for years 10-50 in plantations and for years 10-70 in natural stands. It suggests that both plantations and natural stands may exhibit similar above-ground biomass dynamics between the ages 20 to 50 years. The ratio of the fine:total root biomass is very high, ranging from 80 % in young to 60 % in mature stands.

Biryukova & Biryukov (1984) observed that the ratio of foliage surface (or biomass) to total tree biomass is much higher in plantations than in natural

forests, and may be one factor contributing to the high failure rate of plantations. We compared the foliage:total biomass ratio for plantations and natural stands using the equation:

$$B_f/B_t = \exp(\beta_0 + \beta_1 \ln t + \beta_2 \ln^2 t + \beta_3 \ln^3 t + \beta_4 Z), \quad (8)$$

where B_f and B_t are foliage and total (above- plus below-ground) biomass (oven dry $t \text{ ha}^{-1}$), and found the parameter β_4 (stand origin) non-significant ($t=0.03$, $P>.05$). Thus the present data do not support their contention. However, we note that the argument by Biryukova & Biryukov (1984) was not based on biomass ratios. Significant parameter estimates for equation (8) were ($R^2=0.900$, $SE=11\%$):

$$B_f/B_t = \exp(-8.6210 + 9.1978 \ln t - 3.4930 \ln^2 t + 0.3711 \ln^3 t) \quad (9)$$

This describes a bell-shaped curve with a maximum at age 7.

Voronkov's (1970) proposition concerned the balance between above- and below-ground biomass, but the balance between foliage and fine roots may be more revealing. Foliage determines transpiration and fine roots control water uptake, so the foliage:fine root biomass ratio may be a better indicator of water balance. Fig. 1 illustrates that plantations attain much higher foliage:fine root ratios up until canopy closure, and this may predispose them to failure during drought.

It is informative to plot these ratios on a stand density diagram (Fig. 2). This reveals that ratios are highest (>0.5) when the stands are in the "free growth" stage prior to canopy closure, and that ratios fall below 0.25 as stands approach the self-thinning line. Raw data confirm the predictions derived from equations 4 and 7. Ratios exceeding 0.5 do not occur in natural forests, but occur in plantations up to age 14 years.

This suggests that on the dry steppe of Khazakstan, plantation survival may be enhanced by silvicultural practices which maintain low foliage:root ratios. High planting densities, pruning of the green crown, and delayed thinning (after canopy closure) may all help to confer greater stability. Site preparation practices which encourage a deeper root habit (e.g., ripping) may also enhance drought resistance.

Conclusions

Differences in growth and survival observed in plantations and natural forests on the dry steppe may be attributed in part, to the shoot-root ratio. The high foliage biomass attained in plantations prior to canopy closure predisposes these stands to drought losses when conditions are unfavourable.

Table 3 and Equations (4) and (7) give an indication of the dynamics of biomass fractions in pine stands of natural and plantation origin. These are synthesized in Fig. 1, which shows the extreme foliage:fine root biomass ratios attained in plantations. These findings are drawn from a limited series of temporary plots, and additional permanent plots in stands comprising a wider range of site and stand conditions are necessary to confirm these findings.

Afforestation in dry steppe involves a considerable risk regarding plantation

viability and stability. In dry steppe conditions, deep ripping, high planting densities, pruning of the green crown, and delayed thinnings may minimize the risks.

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References

- Allee, W.C., 1931. Animal Aggregations: A Study in General Sociology. University of Chicago Press, Chicago.
- Berezyuk I.E., 1959. O gustykh posadkakh lesokul'tur. Nauchnye trudy Kazniilkha 2:40-49. (In Russian.)
- Biryukova Z.P. & Biryukov V.N., 1984. Ekologo-fiziologicheskie aspekty ustoichivosti iskusstvennykh nasazhdenii v Severnom Kazakhstane. P. 8-16 in: Ekologiya lesnykh soobtshestv Severnogo Kazakhstana. Leningrad, Nauka, 198 p. (In Russian.)
- Galitski V.V. & Krylov A.A., 1984. Modelirovanie dinamiki rastitel'nykh soobtshestv: Dvumernaya model' odnovidovogo odnovozrastnogo soobtshestva. Putshino, Institut pochvovedeniya i fotosinteza, 47 p. (In Russian.)
- Kozlowski, T.T., 1982. Water supply and tree growth. 1. Water deficits. Forestry Abstracts 43(2):57-95.
- Kozlowski, T.T., Kramer, P.J. & Pallardy, S.G., 1991. The Physiological Ecology of Woody Plants. Academic, San Diego, USA, 657 p.
- Makarenko A.A., 1984. Zakonomernosti formirovaniya sosnovykh nasazhdenii Kazakhstana. P. 33-43 in: Ratsional'noe ispol'zovanie i vospoizvpdstvo lesnykh resursov Kazakhstana. Tshuchinsk, Kazniilkha. Deponir. v Kazniinti 02.07.84, no. 703 Ka-84 (In Russian.)
- Morozov G.F., 1930. Uchenie o lese. Moskva-Leningrad, Goslesbumizdat, 440 p. (In Russian.)
- Nambiar, E.K.S., 1990. Interplay between nutrients, water, root growth and productivity in young plantations. Forest Ecology and Management 30:213-232.
- Odum E.P., 1971. Fundamentals of Ecology. Third Edition. Philadelphia-London-Toronto, W.B. Saunders Company.
- Plotnikov V.V., 1979. Evolyutsiya struktury rastitel'nykh soobtshestv. Moskva, Nauka, 275 p. (In Russian.)
- Pozdnyakov L.K., 1980. Stroenie peregutshcennykh listvennichnykh molodnyakov v Yakutii. Lesovedenie 4:46-55. (In Russian.)
- Prokhorov A.I., Kreпки I.S., Oreshkin N.G., Verzunov A.I. & Usol'tsev V.A. et al., 1988. Vremennye rekomendatsii po novoi otsenke lesokul'turnogo fonda bora Aman-Karagai Kustanaiskoi oblasti i meropriyatiya po ego ratsional'nomu ispol'zovaniyu. Alma-Ata, Kazniilkha, 11 p. (In Russian.)
- Rubtsov, V.I., Novosel'tseva A.I., Popov V.K. & Rubtsov V.V., 1976. Biologicheskaya produktivnost' sosny v lesostepnoi zone. Moskva, Nauka,

- 223 p. (In Russian.)
- Sukachev V.N., 1953. O vnutrividovykh vzaimootnosheniyakh sredi rastenii. Soobtsheniya Instituta lesa AN SSSR 1:5-44. (In Russian.)
- Usol'tsev V.A., 1985. Modelirovanie struktury i dinamiki fitomassy drevostoev. Krasnoyarsk, Krasnoyarskii universitet, 191 p. (In Russian.)
- Usol'tsev V.A., Krepki I.S. & Prokhorov Y.A., 1985. Biologicheskaya produktivnost' estestvennykh i iskusstvennykh sosnyakov Aman-Karagaiskogo bora. Vestnik sel'skokhozyaistvennoi nauki Kazakhstana 8:74-79. (In Russian.)
- Usol'tsev V.A., 1988. Rost i struktura fitomassy drevostoev. Novosibirsk, Nauka, 253 p. (In Russian.)
- Usol'tsev, V.A. & Vanclay, J.K., 1993. Biomass growth and structure of pine plantations and natural forests on dry steppe in Kazakhstan. In J.K. Vanclay, J.P. Skovsgaard and G.Z. Gertner (eds) Growth and Yield Estimation from Successive Forest Inventories. Proceedings from the IUFRO conference held in Copenhagen, 14-17 June, 1993. Danish Forest and Landscape Research Institute, Forskningsserien 3:267-281.
- Voronkov N.A., 1970. Zapasy khvoi v kul'turakh sosny v svyazi s ikh vozrastom i vodnym rezhimom. Lesovedenie 5:37-45. (In Russian.)
- Voronkov V.A. & Nevzorov V.M., 1981. Kornevaya sistema sosny v svyazi s vodnym rezhimom peschanykh pochv. Lesovedenie 6:14-23. (In Russian.)
- Whitehead, D. & Jarvis, P.G., 1981. Coniferous forests and plantations. In T.T. Kozlowski (ed) Water Deficits and Plant Growth. VI. Woody Plant Communities. Academic, NY, p. 49-152.
- Yakushev B.I., 1972. Elektrometricheskiy sposob otsenki massy podzemnykh organov rastenii. Doklady AN BSSR 16(9):848-850. (In Russian.)

Table 1. Parameter estimates and statistics for equation (4).

Y	b ₀	b ₁	b ₂	b ₃	R ²	SE %
Mean height (h_m)	-3.0741	2.1213	-0.1710	-	0.940	19
Basal area (G)	-3.6066	3.4804	-0.4015	-	0.779	9
Biomass:						
Total stem (B_{ts})	-7.3341	5.3893	-0.5776	-	0.926	19
Stem bark (B_{sb})	-8.7556	5.4760	-0.6799	0.0318	0.919	27
Total root (B_{tr})	-2.7409	3.2451	-0.3885	-	0.913	5
Fine root (B_{fr})	-2.6284	3.0956	-0.3844	-	0.891	6

All parameters are significant at $P < .05$

Table 2. Parameter estimates and statistics for equation (7).

Plantations	b_0	b_1	b_2	b_3	b_4	R^2	SE%
Stand density (N)	1.8607	1.0773	-0.3602	-	-	0.717	34
Foliage biomass (B_f)	-12.3072	13.9797	-4.2999	0.4094	-	0.865	17
Total branch biomass (B_{tb})	-10.2574	9.5327	-2.4695	0.2158	-	0.956	16
Branch bark biomass (B_{bb})	-6.5790	5.4801	-1.1194	0.0537	-	0.901	16
Natural stands							
Stand density (N)	9.0066	-1.8257	-	-	-	0.922	45
Foliage biomass (B_f)	-43.114	46.129	-16.688	2.499	-0.1287	0.766	19
Total branch biomass (B_{tb})	-219.869	249.571	-103.962	18.939	-1.2713	0.904	14
Branch bark biomass (B_{bb})	-260.501	293.617	-121.509	21.942	-1.4586	0.918	13

All parameters are significant at $P < .05$

Table 3. Tabulation of equations (4) and (7).

	Plantation age (yr)					Natural stand age (yr)					
	10	20	30	40	50	10	20	30	40	50	70
Mean diameter (d_m)	3	7	11	15	18	1	3	5	8	10	14
Mean height (h_m)	2	6	9	11	14	2	6	9	11	14	17
Basal area (G)	10	25	36	43	48	10	25	36	43	48	51
Stand density (N)	11	6	4	2	2	122	34	16	10	6	4
Biomass:											
Total stem (B_{ts})	8	38	75	108	136	8	38	75	108	136	170
Stem bark (B_{sb})	2	6	10	12	13	2	9	14	17	18	18
Total branch (B_{tb})	3	7	8	8	9	½	5	4	4	4	8
Branch bark (B_{bb})	2	3	3	3	3	¼	3	2	2	2	3
Foliage (B_f)	8	7	5	4	3	4	8	6	5	5	4
Above ground (B_{ag})	19	52	88	121	147	12	51	85	117	144	182
Total root (B_{tr})	14	33	45	52	55	14	33	45	52	55	56
Fine roots (B_{fr})	12	24	32	35	36	12	24	32	35	36	36
Total biomass	33	85	133	172	202	27	84	130	169	199	238

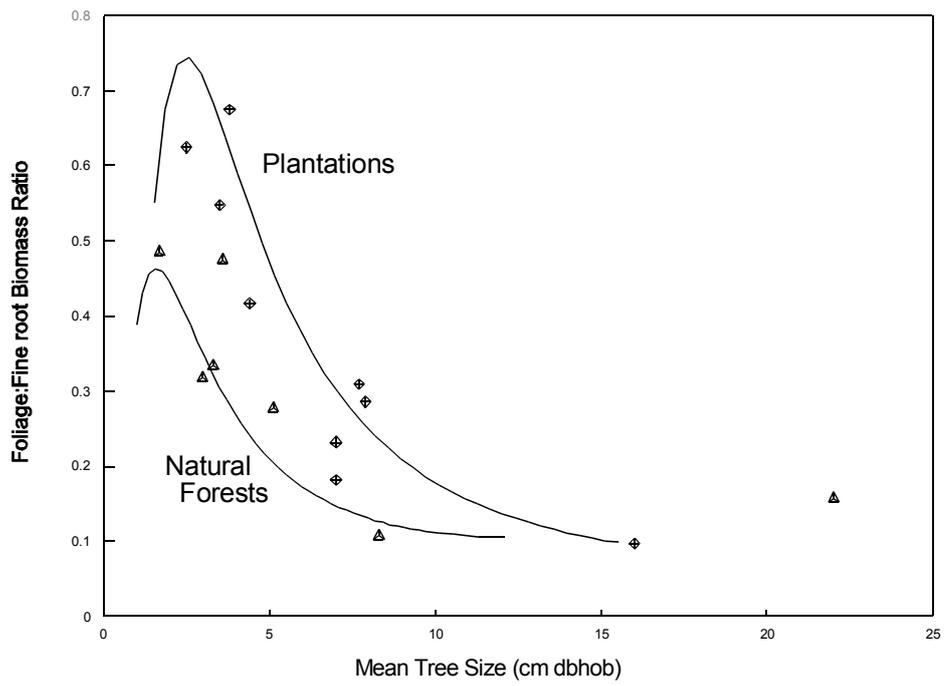


Figure 1. The development of the foliage: fine root biomass ratio with mean tree size in plantations (\diamond) and natural forests (Δ). The high ratio in plantations may help explain the high mortality when drought co-occurs with canopy closure.

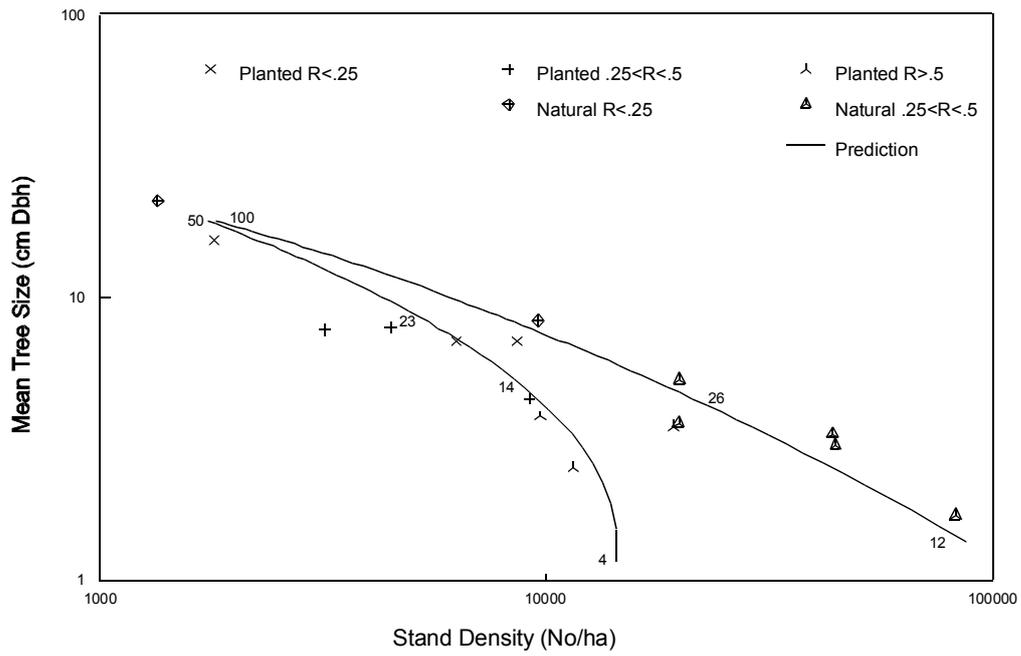


Figure 2. Foliage: fine root ratios and stand density. Ratios fall to 0.5 at 14 years, and to 0.25 at 23 in plantations, and to 0.25 at 26 in natural forest. Symbols show source and magnitude of ratios. Lines show predictions from equations 4 & 7.