

Avant-Propos

Le présent travail de recherche a été réalisé sur un essai génétique établi par le Centre Mondial pour l'Agroforesterie (ICRAF) dans l'Amazonie péruvienne dans le cadre d'un projet sur la domestication participative des arbres agroforestiers. Le but général du projet est d'augmenter la productivité agroforestière, de développer des stratégies durables d'utilisation des forêts dans les terrains agricoles, et de favoriser la conservation des ressources génétiques dans les communautés agricoles. Ainsi, des essais génétiques de certaines espèces d'arbre ont été établis sur des terrains agricoles dans le bassin du fleuve Aguaytía au Pérou, afin d'évaluer la variation génétique de la croissance des arbres et des propriétés du bois.

Une première partie des travaux a été effectuée à l'ICRAF, Pucallpa, et à la «Universidad Nacional Agraria La Molina», Lima, au Pérou soit celle relative à la récolte des données de croissance, à l'abattage des arbres et à la récolte des échantillons. L'autre partie, relative à la détermination des propriétés physiques et mécaniques du bois, ainsi qu'à l'analyse ultérieure a été effectuée à l'Université Laval.

Le présent document comprend cinq articles écrits en langue anglaise, qui sont présentés aux chapitres 2, 3, 4, 5 et 6. Ces articles ont été rédigés sous la supervision de mon directeur, Dr. Roger Hernández, professeur titulaire, et de mon co-directeur, Dr. Jean Beaulieu, chercheur à Ressources naturelles Canada, Service canadien des forêts, Québec, Canada, professeur associé à la Faculté de Foresterie et Géomatique, Université Laval. Les deux premiers articles ont été également écrits en collaboration avec Dr. John C. Weber, chercheur à l'ICRAF, Bamako, Mali, et professeur associé à la Faculté de Foresterie et Géomatique, Université Laval, Québec, Canada. Une description sommaire de ces articles est proposée ci-après :

Chapitre 2:

Sotelo Montes, C., R.E. Hernández, J. Beaulieu et J.C. Weber. 2006. Genetic variation and correlations between growth and wood density of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon. *Silvae Genetica*, 55(4-5): 217-228.

Chapitre 3:

Sotelo Montes, C., R.E. Hernández, J. Beaulieu et J.C. Weber. 2006. Genetic variation in wood color and its correlations with tree growth and wood density of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon. Il a été soumis pour publication dans la revue *New Forests*.

Chapitre 4:

Sotelo Montes, C., J. Beaulieu et R.E. Hernández. 2006. Genetic variation in wood shrinkage, and its correlations with tree growth and wood density of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon. Il a été soumis pour publication dans la revue *Canadian Journal of Forest Research*.

Chapitre 5:

Sotelo Montes, C., J. Beaulieu et R.E. Hernández. 2006. Genetic variation in wood mechanical properties, and their correlations with tree growth and wood density of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon. Il a été soumis pour publication dans la revue *Silvae Genetica*.

Chapitre 6:

Sotelo Montes, C., R.E. Hernández, J. Beaulieu. 2006. Radial variation in density and correlations with growth of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon. Il a été soumis pour publication dans la revue *Wood and Fiber Science*.

Quelques résultats de ce travail ont aussi été présentés sous forme d'affiches techniques aux congrès suivants: 48^{ème} Congrès annuel de la «Society of Wood Science and Technology» et 59^{ème} Congrès annuel de la «Forest Products Society», qui ont eu lieu à Québec, du 19 au 22 juin 2005: Sotelo Montes, C., R.E. Hernández, J. Beaulieu et J.C. Weber. Variation in growth, juvenile wood density and color of *Calycophyllum spruceanum* Benth.

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*A la memoria de mi abuelo Humberto Palacios,
devoto de la virgen de las Mercedes.*

A mis padres Nemesio y Alcira.

A tía Catalina Montes de Vergara.

A John, cubita, mi familia en Perú y Florida.

A todos mis amigos.

Question of feeling, voyons!!!

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Lexique

Retrait

| | |
|--|---|
| β_{LH}, β_L | retraits longitudinal partiel et total (%) |
| β_{RH}, β_R | retraits radial partiel et total (%) |
| β_{TH}, β_T | retraits tangentiel partiel et total (%) |
| β_{VH}, β_V | retraits volumique partiel et total (%) |
| $\beta_{TH}/\beta_{RH}; \beta_T/\beta_R$ | rappports d'anisotropie de retrait partiel et total |
| g_L | retrait différentiel longitudinal |
| g_R | retrait différentiel radial |
| g_T | retrait différentiel tangentiel |
| g_V | retrait différentiel volumique |

Propriétés mécaniques

| | |
|--------------------|---|
| σ | contrainte |
| σ_e | contrainte à la limite élastique en compression longitudinale |
| σ_r | contrainte de rupture en compression longitudinale |
| σ_L | module de rupture en compression longitudinale, résistance maximale |
| ε | déformation |
| ε_e | déformation à la limite élastique en compression longitudinale |
| ε_r | déformation à la rupture en compression longitudinale |
| E | module d'Young |
| E_d | module d'élasticité dynamique |
| E_s | module d'élasticité statique |
| s_{11} dynamique | coefficient de déformation dynamique en direction longitudinale |
| s_{11} statique | coefficient de déformation statique en direction longitudinale |

Propriétés physiques

| | |
|-------------|---|
| ρ | masse volumique à 12% de teneur en humidité |
| ρ_{20} | masse volumique de la lamelle à 12% de teneur en humidité |
| D | masse volumique de l'éprouvette à 12% de teneur en humidité |
| BD | masse volumique basale |
| EMC | teneur en humidité d'équilibre |
| MC | teneur en humidité |
| M_0 | masse anhydre |
| PSF | point de saturation des fibres |
| RH | humidité relative de l'air ambiant |
| V_s | volume saturé (volume vert) |

Introduction

Les forêts du bassin de l'Amazonie péruvienne sont exceptionnellement riches en biodiversité, et occupent la deuxième plus grande superficie d'Amérique du Sud (après le Brésil). Malheureusement, le taux de déforestation excède celui du reboisement. À cause de leur surexploitation, plusieurs communautés d'agriculteurs n'ont quasiment plus accès aujourd'hui aux espèces les plus utiles et possédant une bonne qualité génétique. De surcroît, il n'existe que très peu d'information concernant la variabilité génétique intraspécifique de celles-ci. Le maintien de la variabilité génétique intraspécifique est pourtant le pilier fondamental des activités de conservation des ressources génétiques forestières. Il s'agit donc là d'une information essentielle pour le développement de stratégies durables d'utilisation et de gestion des espèces forestières.

Calycophyllum spruceanum (Bentham) Hooker f. ex Shumann (famille Rubiaceae), connue sous le nom commun de Capirona, est une espèce feuillue très importante de l'Amazonie péruvienne. Le bois de capirona est utilisé pour la fabrication de meubles, de panneaux décoratifs et des planchers autant pour les marchés nationaux que pour ceux internationaux. Cette espèce est connue également sous les noms de Palo blanco en Argentine, Guayabochi en Bolivie, Pau mulato au Brésil, Guayabete et Alazano en Colombie, Corusicao en Équateur, Palo camarón en Espagne, Citronnier brésilien en France et Araguato au Venezuela.

Les agriculteurs de l'Amazonie péruvienne considèrent *C. spruceanum* comme une des espèces les plus importantes pour l'agroforesterie. Ils tirent de cette espèce, souvent gérée par de rejets de souche, des matériaux pour la fabrication de charpentes légères, de planches et de bois de feu, soit des produits qui contribuent de manière significative à leurs revenus. Étant donné que les rejets se développent rapidement après la coupe et que la régénération naturelle de cette espèce est abondante sur des terrains agricoles et dans les environnements alluviaux perturbés, l'aménagement durable de *C. spruceanum* présente de nombreux avantages pour les agriculteurs.

Peu de recherches ont été faites à ce jour sur la croissance et les propriétés du bois de *C. spruceanum*. Les connaissances sur la variation génétique et les effets de l'environnement sur ces caractéristiques sont encore plus limités. Il existe également peu d'information sur les corrélations entre les caractères de croissance et les propriétés du bois, ainsi que sur l'effet de

l'environnement sur ces corrélations. Cette information est toutefois essentielle pour améliorer l'aménagement de cette espèce dans l'Amazonie péruvienne afin de fabriquer des produits de qualité.

Les agriculteurs et l'industrie utilisent de façon courante le bois juvénile de *C. spruceanum*, ce qui sera probablement fait de plus en plus dans le futur avec la promotion de l'agroforesterie et de la foresterie de plantation à petite échelle. C'est pourquoi les chercheurs devraient entreprendre des recherches sur la variation génétique des propriétés du bois juvénile de cette espèce pour voir s'il est possible de les améliorer par la sélection et pour mesurer l'impact de cette dernière sur ces caractères et d'autres également.

Chapitre 1 Revue de littérature

1.1 Le rôle des essais de provenances/descendances dans la génétique forestière

L'amélioration génétique a comme but d'augmenter la performance de certains caractères de l'arbre tels la croissance et la masse volumique du bois (Falconer et Mackay 1996; Perron 2003). L'amélioration vise ainsi la réalisation du potentiel génétique afin d'augmenter les rendements. La sylviculture de son côté tente d'augmenter les rendements en modifiant l'environnement de l'arbre. Enfin, c'est la combinaison de l'amélioration génétique (facteur G) et de la sylviculture (facteur E) qui permet l'optimisation des rendements (phénotype) (facteur P).

Les essais de provenances/descendances sont utilisés pour étudier la variabilité entre provenances et descendances (Falconer et Mackay 1996). Une provenance est un groupe d'individus (généralement des semences) provenant de plusieurs arbres-mères ayant une origine géographique commune. Une descendance (famille) est un groupe d'individus apparentés (ayant un ou deux parents en commun) issus de reproduction sexuelle. L'essai de provenance/descendance est une plantation comparative qui permet d'évaluer la variation inter-population (c'est-à-dire entre les provenances) et intra-population (entre les familles dans chaque provenance) (Perron 2003).

Les essais de provenances/descendances permettent aussi d'estimer le contrôle génétique (h_i^2 – héritabilité au sens strict) d'un caractère et la corrélation génétique entre caractères (Falconer et Mackay 1996). L'héritabilité au sens strict est la proportion de la variation phénotypique totale due à la variance additive (i.e., la variance entre les valeurs en croisement des individus). Elle donne alors une mesure relative de l'efficacité d'une sélection génétique. Ainsi, si l'héritabilité du caractère est très faible, la plupart de la variation sera due à l'environnement et il sera difficile d'améliorer ce caractère par la sélection des arbres supérieurs; mais, si l'héritabilité est très forte, la plupart de la variation sera due au facteur génétique, ce qui permettra d'améliorer ce caractère par sélection. La corrélation génétique (r_g) exprime dans quelle mesure deux caractères distincts reflètent essentiellement le même caractère génétique. En d'autres termes, si deux caractères sont contrôlés par le même ensemble de gènes, la corrélation génétique entre ceux-ci devrait être égale à 1. Si les

caractères sont contrôlés par deux ensembles de gènes distincts, la corrélation génétique sera alors égale à zéro. Le signe de la corrélation génétique est très important dans la pratique. Par exemple, si deux caractères sont héréditaires et si la corrélation génétique entre ceux-ci est négative, la sélection pour augmenter la valeur d'un caractère aura pour conséquence de réduire celle de l'autre. D'un autre côté, si les deux caractères sont héréditaires et si leur corrélation génétique est positive, une sélection visant à accroître la valeur d'un d'entre eux aura pour effet indirect d'également hausser la valeur de l'autre.

L'héritabilité au sens strict (h_i^2) d'un caractère peut être estimée grâce à la ressemblance d'individus apparentés (Falconer et Mackay 1996). Cela peut être fait par l'analyse de la variation d'un caractère de manière à le décomposer en ses différentes sources de variation. Par exemple, si on inclut dans l'essai de provenance/descendance des semences fécondées par pollinisation libre d'arbres différents, les semences récoltées d'un arbre-mère donné ont le même parent maternel (l'arbre-mère) mais elles pourront avoir des parents paternels différents (ex: soit l'arbre-mère ou soit les arbres avoisinants peuvent fournir le pollen). Si on suppose que toute la descendance d'un arbre donné a des pères différents, la descendance est donc nommée demi-fratrie. En théorie, des demi-frères ont $\frac{1}{4}$ de leurs gènes en commun et la composante de la variance due aux familles dans l'analyse de variance d'un caractère donné (σ_{fx}^2) est estimée à $\frac{1}{4}$ de la variance génétique additive de ce caractère. Ainsi, on peut estimer la variance génétique additive (σ_A^2) comme étant égale à :

$$4\sigma_{fx}^2 \quad (1)$$

Cette variance est utilisée comme numérateur dans la formule qui sert à estimer l'héritabilité du caractère (h_i^2). Le dénominateur inclut toutes les composantes de variance qui contribuent à la variance phénotypique (σ_p^2) dans le caractère: par exemple, celles dues aux familles, à l'interaction entre familles et répétitions et la variance résiduelle. En pratique, les améliorateurs ne supposent pas nécessairement que la descendance est composée de demi-frères parce qu'il y a toujours un certain degré de consanguinité dans les populations naturelles ou aménagées. Si l'espèce est monoïque (ex: les structures reproductives mâles et femelles sont sur le même arbre), un certain pourcentage de la descendance peut être des pleins-frères, c'est-à-dire ils possèdent aussi le même père. Si toute la descendance est composée des pleins-frères, la composante de la variance due aux familles (σ_{fx}^2) est estimée à

½ de la variance génétique additive de ce caractère. Ainsi, la variance génétique additive devrait être estimée comme étant égale à :

$$2\sigma_{fx}^2 \quad (2)$$

Si on suppose que la descendance est composée de demi-frères tandis qu'elle est en réalité composée de pleins-frères, on surestime l'héritabilité.

Les arbres tropicaux sont en majorité à fécondation croisée et ne tolèrent pas beaucoup de consanguinité (Bawa et Hadley 1990). L'inbreeding a lieu quand des parents apparentés génétiquement se croisent et produisent une descendance. Le degré d'inbreeding dépend du degré de parenté génétique allant de l'autofécondation au croisement entre pleins-frères, demi-frères, cousins au premier degré, au deuxième degré, etc. Une des conséquences de l'inbreeding est la dépression, qui peut résulter en une croissance moins rapide, etc. Si les parents ne sont pas apparentés génétiquement, il n'y a pas d'inbreeding. Dans les milieux naturels, il existe des modèles complexes de parenté génétique entre les arbres: quelques-uns sont des pleins-frères, d'autres des demi-frères, d'autres des cousins, etc. Ainsi, il peut arriver que les améliorateurs soupçonnent qu'il existe un certain niveau d'inbreeding dans les milieux naturels parce que des arbres apparentés génétiquement se croisent et produisent une descendance. Dans ce cas, ce ne sont pas toutes les semences d'un arbre-mère fécondé par pollinisation libre qui sont des demi-frères. Quelques-uns peuvent être des pleins-frères, d'autres des demi-frères et d'autres encore des produits du croisement de l'arbre-mère avec ses propres descendants, etc. Alors lorsque l'améliorateur soupçonne qu'une telle situation existe, il pourra considérer que la descendance ne partage pas ¼ de leurs gènes, mais une fraction plus élevée, comme 1/3. Dans ce cas, la variance génétique additive pourra être estimée comme étant égale à :

$$3\sigma_{fx}^2 \quad (3)$$

L'estimation de la corrélation génétique entre deux caractères (r_g) est aussi basée sur la ressemblance entre les membres d'une même famille (Falconer et Mackay 1996). Par contre, dans ce cas, on estime la composante de la covariance entre les caractères au niveau de la famille dans l'analyse de variance (σ_{fxy}^2) aussi bien que les composantes de variance de chaque caractère (σ_{fx}^2 et σ_{fy}^2). Tel que l'on a mentionné plus tôt, la composante de variance

due aux familles est estimée à $\frac{1}{4}$ de la variance génétique additive de ce caractère. D'une façon similaire, la composante de la covariance est estimée à $\frac{1}{4}$ de la covariance des valeurs en croisement des deux caractères. Par conséquent, la corrélation génétique entre les deux caractères peut être estimée comme étant égale à :

$$\frac{\sigma_{fxy}^2}{\sqrt{\sigma_{fx}^2 \sigma_{fy}^2}} \quad (4)$$

Un essai de provenance/descendance permet plus de flexibilité dans les choix de sélection. Par exemple, en se basant sur les informations obtenues par l'essai, on pourrait décider de sélectionner la meilleure provenance pour le diamètre à hauteur de poitrine et sélectionner ensuite les meilleures familles à l'intérieur des provenances pour la masse volumique du bois.

L'essai de provenance/descendance peut être conçu en fonction de plusieurs objectifs. Par exemple, l'essai peut servir à estimer les paramètres génétiques et choisir les meilleures familles parmi les familles étudiées. Les répétitions sont alors transformées en verger à graines pour la production des semences choisies. Le plan expérimental pourrait être optimal pour certains objectifs, mais moins pour d'autres. Par exemple, le bloc complet au hasard (BCH) est le plan expérimental le plus généralement utilisé pour les essais d'évaluation génétique. Cependant, si un grand nombre de familles sont incluses dans l'essai, la taille du bloc devient très grande. Dans ce cas, le plan de bloc incomplet est plus efficace que le BCH. Le programme d'amélioration doit ainsi assigner les priorités à chaque objectif et définir ensuite un plan expérimental en fonction de ces priorités (Vargas-Hernández et Lopez Upton 2004).

1.2 Variation génétique de la croissance

Les arbres croissent à partir de méristèmes en hauteur et en diamètre. La croissance en hauteur, appelée primaire, se fait grâce à l'action des méristèmes apicaux. La croissance en diamètre, ou secondaire, se fait pour sa part à partir de méristèmes latéraux, principalement le cambium. Contrairement à la croissance en hauteur, la division du cambium dépend essentiellement de la photosynthèse de la saison en cours. La nourriture mise en réserve pendant la saison antérieure peut cependant être utilisée pour la croissance du diamètre au début de la saison de croissance (Tsoumis 1991). Dans les zones tempérées, on peut distinguer un cerne par année en raison de l'arrêt de la croissance à l'automne, mais dans les

zones tropicales humides, on ne peut pas distinguer de cernes annuels car la croissance ne s'arrête pas (Cloutier 2004).

On s'attend en général à ce que les espèces qui dispersent leurs semences et/ou leur pollen sur de longues distances présentent des différences relativement petites entre les populations naturelles mais de fortes variations entre les arbres d'une même population (Hamrick et al. 1992). Les études sur la variation de la croissance dans des essais de provenances de *C. spruceanum* (Sotelo Montes et al. 2003; Boivin-Chabot et al. 2004; Weber et Sotelo Montes 2005) et de *Guazuma crinita* (Rochon 2004; Weber et Sotelo Montes 2006) dans le bassin amazonien du Pérou sont en accord avec cet énoncé général: les variations entre les provenances sont minimales lorsque comparées aux variations entre les arbres d'une même provenance.

Lors des essais de provenances, il a souvent été démontré que les différences de croissance entre les environnements de plantation sont plus grandes que les différences entre les provenances (Namkoong et al. 1988; Morgenstern 1996). Cela a aussi été observé chez *C. spruceanum* (Sotelo Montes et al. 2003; Weber et Sotelo Montes 2005) et *G. crinita* (Rochon 2004; Weber et Sotelo Montes 2006).

La sélection de provenances chez des espèces ligneuses à croissance rapide serait plus efficace lorsque les conditions environnementales des essais facilitent la croissance rapide (Campbell et Sorensen 1978). Ces environnements permettraient aux différences génétiques inhérentes aux taux de croissance de s'exprimer plus facilement. Les provenances ne pourraient pas exprimer ainsi leur plein potentiel génétique dans des environnements moins favorables. Par exemple, Roman et al. (1996) ont étudié la variation chez *Gliricidia sepium* lors d'une étude en pépinière: plus de variation en hauteur et en biomasse fut détectée entre les provenances dans les traitements qui recevaient des arrosages fréquents que dans les traitements avec un apport en eau limité. Des résultats similaires ont été observés chez *C. spruceanum* (Sotelo Montes et al. 2003; Weber et Sotelo Montes 2005).

Dans les zones tempérées, il est possible d'observer de grands écarts de croissance entre des provenances de latitudes différentes, puisque la latitude y détermine les importantes variations de température, de précipitation et de durée de la saison de croissance (Morgenstern 1996). Les provenances «locales» peuvent donc avoir des taux de croissance et de survie plus grands dans une plantation présentant des conditions environnementales

équivalentes aux conditions d'origine. Par exemple, une provenance du 50°N devrait mieux croître à cette même latitude que des provenances du 30 ou 40°N.

Près de l'équateur, les différences observées entre les taux de croissance et de survie selon la latitude d'origine de la provenance sont minimales puisqu'il y a relativement peu de variation en température, en précipitations et en durée de la saison de croissance entre les latitudes (Morgenstern 1996).

Il y a peu d'études portant sur la variation génétique de la croissance d'espèces feuillues tropicales comparé au grand nombre fait sur les feuillues de zones tempérées et sur les conifères. Les résultats de ces études suggèrent la présence d'une variation génétique dans la croissance à un jeune âge pour les espèces feuillues tropicales. Par exemple, on a détecté une variation significative de la croissance juvénile entre les provenances et/ou familles pour les espèces suivantes: *Alnus acuminata* (Cornelius et al. 1996), *Bombacopsis quinata* (Hodge et al. 2002), *Gmelina arborea* (Osorio 2004), *Grevillea robusta* (Shimizu et al. 2002), *G. crinita* (Rochon 2004) et *Vochysia guatemalensis* (Cornelius et Mesén 1997). La demande pour les semences sélectionnées des espèces feuillues tropicales est en nette progression; donc la recherche génétique est nécessaire pour répondre à certaines questions pratiques (Simons et al. 1994). Par exemple, quelle est la meilleure provenance, quelles sont les valeurs de l'héritabilité des propriétés du bois, et quelles sont les corrélations génétiques entre la croissance d'arbre et les propriétés du bois?

1.3 Variation génétique des propriétés du bois

1.3.1 Définition de la qualité du bois

La qualité du bois est l'ensemble de ses attributs qui font qu'il est valable pour un usage donné (Jozsa et Middleton 1994). Par exemple, le bois utilisé à des fins structurales doit être fort et résistant (Jozsa et Middleton 1994) tandis que le bois pour un instrument de musique doit avoir une structure anatomique régulière et de bonnes propriétés acoustiques (Bucur 2006). La masse volumique du bois est un attribut qui a une influence directe sur les propriétés du bois solide (la résistance, le retrait, l'usinage, l'acoustique, etc.). Les caractéristiques de qualité du bois peuvent être inhérentes à l'espèce, mais sont aussi influencées par les conditions de croissance de l'arbre. Beaucoup d'attributs de qualité du bois

sont héréditaires et les différences de qualité entre les arbres à l'intérieur de l'espèce peuvent être liées aux différences génétiques (Jozsa et Middleton 1994).

1.3.2 Le bois juvénile

On reconnaît généralement deux types de bois, soit le bois juvénile et le bois mature, lesquels possèdent des caractéristiques différentes (Zobel et Sprague 1998). Ainsi, les propriétés du bois juvénile varient de la moelle vers la partie mature de l'arbre. La frontière de ces zones, quoique dépendante des propriétés mesurées, se situe en moyenne entre le cinquième et le vingtième anneau de croissance, bien qu'il puisse exister une grande variation (Evans et al. 2000).

Comparé avec le bois mature, le bois juvénile des feuillus présente les caractéristiques suivantes: 1) la masse volumique est plus faible, 2) les fibres sont plus courtes, l'angle des micro-fibrilles est plus élevé, 3) les parois cellulaires sont plus minces, 4) le diamètre et la longueur des cellules sont plus petits, 5) la teneur en humidité est plus élevée, 6) le retrait longitudinal est plus grand, 7) la résistance mécanique est moindre pour une masse volumique de bois donnée, 8) il tend à y avoir plus de bois de tension, 9) la proportion de la cellulose est légèrement plus faible que pour le bois mature et celles d'extractibles et de lignine sont différentes (Zobel et Sprague 1998; Evans et al. 2000).

En général, les différences entre le bois juvénile et le bois mature sont relativement faibles pour le bois à pores diffus, comparé au bois à zones poreuses (et particulièrement comparé au bois des conifères) (Zobel et Sprague 1998). Chez le bois à pores diffus, les vaisseaux du xylème secondaire sont distribués uniformément dans l'anneau de croissance et sans différence sensible du diamètre entre le début et la fin de la saison de végétation. Alors que, pour le bois à zone poreuse, le diamètre des vaisseaux du bois initial est sensiblement plus grand que celui des vaisseaux du bois final, et les vaisseaux forment des zones bien définies ou cernes dans une section transversale de la tige (Esau 1977; Jodin 1994).

La foresterie de plantation est une option d'aménagement intéressante dans les tropiques parce que la période de rotation peut être significativement plus courte que dans les environnements naturels. Par contre, les propriétés du bois seront probablement affectées parce que les arbres qui y croissent ont, en général, une proportion plus grande de bois juvénile comparé à celle des arbres croissant dans un environnement naturel (Skaar 1988; Trockenbrodt et al. 1999; Ofori et Brentuo 2005). Puisque le bois juvénile sera probablement

de plus en plus utilisé dans le futur, il est essentiel que des recherches soient conduites sur la variation génétique de ses propriétés ainsi que leur corrélation avec la croissance de l'arbre et leur impact sur les produits du bois (Zobel et Sprague 1998).

1.3.3 La couleur du bois

La source principale de variation intra-arbre de la couleur du bois est due au processus de la duraminisation (Burtin et al. 1998), phénomène physiologique chez les végétaux ligneux conduisant à la dévitalisation complète de l'aubier en bois de cœur. On notera que, même pour les essences sans cœur coloré, de très légères différences de couleur sont notées entre le bois situé près de la moelle et celui situé près de l'écorce. Les variations de couleur du bois, notamment celles intervenant à l'intérieur de l'arbre, ont surtout été étudiées sur les bois feuillus destinés à l'ébénisterie et à la menuiserie car il s'agit de cas où les aspects esthétiques sont importants (Jodin 1994). La couleur naturelle du bois dépend des facteurs biologiques, dont l'âge du bois et de l'arbre (Klumpers et al. 1993), des propriétés anatomiques et structurelles du bois (Mosedale et al. 1996) et de la composition chimique des constituants de la paroi cellulaire (Janin 1987). La couleur dépend aussi d'autres facteurs tels que le plan de découpe, radial ou tangentiel, et l'orientation de la surface du bois en relation à la source de lumière (Janin 1987). En outre, la couleur du bois peut changer avec les traitements thermiques, le séchage et l'exposition à la radiation ultraviolette (Luostarinen et al. 2002; Kishino et Nakano 2004; Pastore et al. 2004).

La couleur est influencée par des facteurs génétiques et environnementaux (Phelps et al. 1983; Janin 1987; Rink et Phelps 1989; Wilkins et Stamp 1990; Mosedale et al. 1996; Zobel et Sprague 1998; Gierlinger et al. 2004; Hannrup et al. 2004). Par exemple, Klumpers et al. (1993) ont observé que la quantité d'humidité du sol disponible était le facteur principal qui influençait la couleur du bois de *Quercus robur*. Luostarinen et al. (2002) ont découvert que le bois de *Betula pendula* Roth était moins foncé et moins rouge/jaune sur un site plus fertile. Les différences entre les sites peuvent affecter la couleur du bois (Rink 1987; Wilkins et Stamp 1990; Klumpers et al. 1993), la masse volumique du bois et la croissance de l'arbre (Zobel et Jett 1995). Ainsi, on pourrait s'attendre à ce que la couleur du bois soit dans une certaine mesure reliée à la masse volumique du bois et la croissance de l'arbre, et ce au moins dans certains sites.

La couleur peut être évaluée en termes de clarté et nuance en utilisant le système CIELAB (BYK-Gardner 2004). La clarté du bois a tendance à être plus variable au niveau intraspécifique que ne l'est la nuance (Klumpers et al. 1993; Nishino et al. 1998). Cependant, la variation génétique de la couleur du bois d'espèces feuillues tropicales n'a pas encore fait l'objet d'études.

L'uniformité dans la couleur du bois est une préoccupation d'ordre pratique car elle affecte directement la valeur esthétique du bois. Janin et al. (2001) ont observé que la détermination précise de la couleur peut fournir un moyen utile pour classifier, regrouper et assembler des morceaux de bois identiques en couleur pour des fins diverses: planchers, menuiserie et manufacture de meubles.

1.3.4 Masse volumique du bois

La masse volumique basale du bois, aussi connue sous le nom de densité basale, est le rapport entre la masse anhydre (M_0) et le volume saturé ou «volume vert» (V_S) de l'échantillon. C'est une caractéristique extrêmement importante car elle conditionne la plupart des propriétés mécaniques.

La masse volumique du bois varie selon les conditions de croissance, de la moelle vers l'écorce, en fonction de la hauteur dans l'arbre, et selon le type de bois (état de maturité du bois) (Panshin et de Zeeuw 1980; Zobel et van Buijtenen 1989; Zobel et Sprague 1998). La proportion de bois juvénile dépend des conditions de croissance de l'arbre et de l'âge de la plantation et est une variable importante lors de la transformation du bois.

Selon Woodcock et al. (2000), la masse volumique des espèces est faible dans les environnements humides tropicaux et plus élevée là où les conditions sont plus sèches. Dans une autre étude, Woodcock (2000) a trouvé que les espèces de l'Amazonie péruvienne avaient une masse volumique faible lorsqu'elles faisaient partie de la végétation de succession initiale où il existe une croissance plus rapide.

En plus des effets de l'environnement, la masse volumique du bois peut varier significativement en fonction de la provenance et/ou de la famille dans la provenance (Zobel et Jett 1995). La recherche sur les feuillus tropicaux a démontré des différences significatives de la masse volumique du bois entre les provenances et/ou descendances chez quelques espèces évaluées entre l'âge de 6 à 10 ans (par exemple: *Sterculia apetala* (Jacq.) Karst.

[Dvorak et al. 1998]; *Eucalyptus globulus* [Miranda et al. 2001a, 2001b]; *E. dunnii* [Arnold et al. 2004]; *E. grandis* [Santos et al. 2004] et *Gmelina arborea* [Lauridsen et Kjaer 2002]).

Peu de travaux ont porté sur la variation génétique de la masse volumique du bois à un très jeune âge dans les plantations de feuillus tropicaux. Khasa et al. (1995) ont rapporté des différences significatives de masse volumique à l'âge de 21 mois entre les provenances de *Racosperma auriculiformis* et *R. mangium* qui ont été échantillonnées à partir d'une vaste gamme d'environnements en Australie et testées au République démocratique du Congo.

Selon Wiemann et Williamson (2002), il y a en général plus de variation de la masse volumique du bois chez les essences feuillues tropicales que chez les essences feuillues des climats tempérés. Il y a peut-être aussi plus de variation intra spécifique de la masse volumique du bois dans les tropiques que dans les climats tempérés. Il est toutefois nécessaire de réaliser un plus grand nombre de recherches pour en avoir une meilleure idée.

1.3.5 Variation radiale de la masse volumique du bois

La variation radiale de la masse volumique du bois n'a pas été évaluée chez la capirona. Des différences de masse volumique selon la position radiale dans la tige ont été rapportées pour d'autres espèces (Williamson 1984; Wiemann et Williamson 1988, 1989a, 1989b; Corriveau et al. 1991; Rueda et Williamson 1992; de Castro et al. 1993; Hernández et al. 1998; Zobel et Sprague 1998; Wang et al. 2000; Quilhó et Pereira 2001, entre autres). Selon une recherche concernant d'autres bois à pores diffus, on pourrait prévoir que la masse volumique du bois de capirona augmente légèrement de la moelle vers l'écorce. Woodcock et Shier (2002) posent comme hypothèse qu'une augmentation de la masse volumique du bois de la moelle vers l'écorce est une caractéristique des espèces pionnières, alors que la tendance inverse (une diminution de la moelle à l'écorce) est une caractéristique des espèces du dernier stade de succession qui dominent le couvert forestier. Une étude de Parolin (2002) en Amazonie centrale a démontré que l'augmentation radiale de la masse volumique du bois de la moelle vers l'écorce était très commune dans les plaines alluviales, lesquelles reçoivent la sédimentation riche et nutritive des inondations annuelles: 35% des espèces pionnières étudiées et 16% des espèces non-pionnières étudiées avaient une augmentation radiale de la masse volumique de la moelle à l'écorce.

La compilation de nombreuses références bibliographiques permet de donner des ordres de grandeur quant aux écarts de masse volumique entre le bois situé près de la moelle (à cernes

larges) et le bois situé près de l'écorce (à cernes minces). Pour les feuillus à pores diffus, les écarts sont faibles et le signe des différences est moins clair, voire variable suivant les espèces (Zobel et Sprague 1998). Zobel et van Buijtenen (1989) ont suggéré quelques modèles généraux pour les bois de feuillus à pores diffus. En général, pour les bois des feuillus à pores diffus avec une masse volumique du bois moyenne à haute (par exemple, certaines espèces d'Eucalyptus), la masse volumique du bois semble être légèrement inférieure près la moelle et augmente légèrement vers l'écorce. En revanche, pour les feuillus à pores diffus dont la masse volumique du bois est faible (par exemple, certaines espèces de peuplier), la masse volumique du bois semble généralement être légèrement plus élevée près de la moelle que près de l'écorce, ou encore, il n'y a aucune différence entre la moelle et l'écorce. Ce sont cependant là des généralisations et il y a des exceptions.

Hernández et Restrepo (1995) ont également étudié la variation radiale de la masse volumique d'*Alnus acuminata* en Colombie. Ils ont rapporté que la masse volumique augmentait linéairement de la moelle vers l'écorce. Rochon (2004) a étudié la variation radiale de la masse volumique de *Guazuma crinita* jusqu'à l'âge de 12 mois. Les arbres ont été échantillonnés dans les plantations établies dans trois zones. Elle a montré des effets significatifs entre quelques zones de plantation pour la masse volumique moyenne de l'arbre et pour la masse volumique près de l'écorce. Mais il n'existait pas de différence significative entre les zones pour la masse volumique près de la moelle. De plus, il n'existait pas de différence significative entre la masse volumique près de l'écorce et près de la moelle, mais il existait une interaction entre les zones de plantation et la position radiale.

Woodcock (2000), a expliqué la variation radiale de la masse volumique en termes de principes biomécaniques selon lesquels l'arbre, au commencement de sa vie, met son énergie dans la croissance vers la lumière, en ne produisant que graduellement du bois d'une plus grande densité à la périphérie, où il est plus efficace pour le support.

Techniquement, la variation radiale des propriétés du bois est le résultat d'un effet d'âge (Zhang et Zhong 1991) parce qu'à la même hauteur sur la tige (par exemple à hauteur de poitrine) le bois près de la moelle est plus vieux que le bois près de l'écorce. Si les propriétés anatomiques du bois changent de manière significative avec l'âge, alors nous devrions nous attendre à une variation radiale de la masse volumique du bois. En général, la variation radiale de la masse volumique de la moelle vers l'écorce pour le bois à pores diffus peut être associée à un ou plusieurs des changements anatomiques suivants: 1) augmentation de la

longueur des fibres, 2) augmentation de l'épaisseur des parois de fibres; 3) augmentation de la proportion de fibres, 4) diminution de la proportion de parenchyme axial, 5) diminution du diamètre des cavités de fibres et/ou 6) du nombre de vaisseaux par unité de surface (Dadswell 1958; Butterfield et al. 1993; McDonald et al. 1995; Zobel et Sprague 1998). Par exemple, chez *Heliocarpus appendulatus*, une espèce pionnière des forêts humides néo tropicales, McDonald et al. (1995) ont signalé que la masse volumique du bois augmentait de la moelle vers l'écorce et que cette augmentation était liée principalement à une augmentation de la proportion de fibres de la moelle vers l'écorce et à une diminution correspondante de la proportion de parenchyme axial.

D'un point de vue pratique, les grandes différences de la masse volumique du bois dans l'arbre peuvent produire du gauchissement pendant le séchage et réduire la valeur du bois. Par exemple, si le bois de la partie supérieure de la tige a une masse volumique plus faible que le bois de la partie plus basse de la tige, alors le bois de la partie supérieure aura une résistance mécanique moindre. De même, si le bois de la moelle a une masse volumique plus faible que le bois près de l'écorce, alors le bois de la moelle aura une résistance mécanique moindre. Idéalement, nous voudrions produire des arbres où les propriétés physiques seront très uniformes.

La sélection précoce pour la masse volumique du bois peut être efficace chez la capirona et chez d'autres espèces, mais il est généralement difficile d'identifier des provenances supérieures à un jeune âge, comme cela a été démontré pour plusieurs espèces en Europe et en Amérique du Nord (Zobel et Jett 1995). Néanmoins, les avantages économiques potentiels de la sélection précoce peuvent justifier l'investissement dans ce type de recherche.

Dans le meilleur des cas, nous voudrions choisir le matériel génétique possédant des caractéristiques désirées à un jeune âge. L'attente de la maturité commerciale est évidemment longue et coûteuse. En règle générale, les spécialistes en amélioration des arbres suggèrent que pour évaluer de façon définitive le matériel génétique ce dernier doit au moins avoir atteint la moitié de l'âge de rotation (par exemple si les arbres sont commercialement récoltés à 20 ans, la période d'évaluation devrait être d'au moins 10 ans). De plus longues périodes d'évaluation sont particulièrement importantes si le choix est basé sur la masse volumique du bois parce que les corrélations juvénile-adulte pour la masse volumique du bois sont en général très faibles (Morgenstern 1996).

Il est néanmoins important de déterminer s'il y a une variation génétique significative de la masse volumique du bois et des autres caractéristiques du bois à un jeune âge. S'il y a une variation génétique significative, alors la sélection précoce pour la masse volumique du bois et autres caractéristiques peut être possible.

1.3.6 Le retrait du bois

Le retrait est la propriété physique du bois qui sert à évaluer la stabilité dimensionnelle et, par le fait même, le comportement du bois au séchage (Skaar 1988; Pliura et al. 2005). Le retrait est affecté par plusieurs facteurs, incluant la teneur en humidité, la masse volumique, la structure anatomique, les extractibles, les composants chimiques, l'effort mécanique et la proportion de bois juvénile (Tsoumis 1991; Jodin 1994).

Le retrait dépend totalement des changements de la teneur en humidité dans le bois. Dans la pratique, on considère que le retrait débute lorsque l'humidité diminue au-dessous du point de saturation des fibres (PSF). On considère également que la relation entre le retrait et la teneur en humidité est linéaire et négative au-dessous du PSF; c'est-à-dire que le retrait augmente lorsque la teneur en humidité diminue (Figure 1.1) (sauf pour le cas du retrait longitudinal, Goulet et Fortin 1975). Mais au-dessus de ce point, il n'existe pas de relation entre le retrait et la teneur en humidité (Tsoumis 1991; Simpson et TenWolde 1999).

La relation entre le retrait et la teneur en humidité est affectée par la taille de l'échantillon utilisé pour les mesures. Donc, de grands échantillons ne montrent pas de résultats consistants à cause du manque d'uniformité de la distribution de la teneur en humidité. Ainsi, ces échantillons développent des efforts internes qui affectent les changements de dimensions. C'est une raison pour laquelle, dans certains cas, un retrait peut débiter au-dessus du PSF (Tsoumis 1991).

La masse volumique affecte le rapport d'anisotropie du retrait, qui est le rapport du retrait tangentiel au retrait radial. Ce rapport diminue au fur et à mesure que la masse volumique augmente. Ceci signifie que chez un bois d'une masse volumique plus élevée, la différence entre les retraits tangentiel et radial est plus petite (c'est-à-dire que de tels bois ont un degré inférieur d'anisotropie) (Tsoumis 1991).

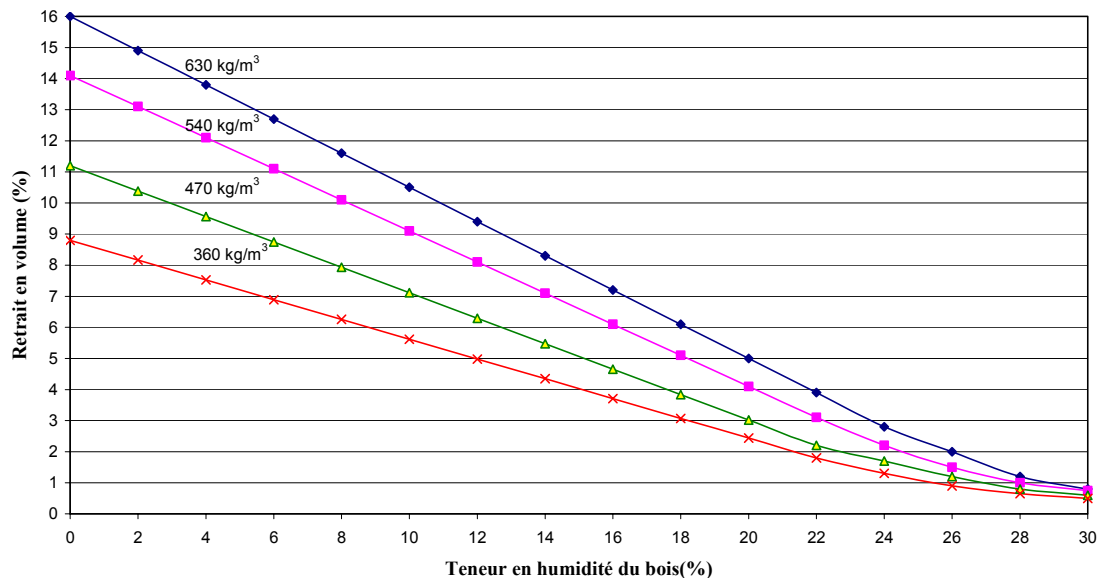


Figure 1.1. Relation entre le retrait volumétrique et la teneur en humidité pour quatre valeurs de masse volumique du bois (adapté de Tsoumis 1991).

Le retrait est souvent plus élevé à mesure que la masse volumique du bois augmente (Figure 1.1) mais cette relation varie selon l'espèce (Siau 1984; Skaar 1988; Shupe et al. 1995a; Koubaa et al. 1998; Ofori et Brentuo 2005). Ceci est dû à une plus grande quantité de matière ligneuse (une plus grande épaisseur des parois cellulaires) (Tsoumis 1991; Bowyer et al. 2003).

La teneur en extraits contribue à la réduction du retrait du bois. La réduction est proportionnelle à l'espace occupé par les extraits dans les parois cellulaires du bois (Hernández 2006a). Les substances secondaires pénètrent les espaces internes des parois cellulaires et occupent ainsi l'espace qui pourrait être consacré à l'adsorption de l'eau (Hernández 2006b). Le bois parfait contenant des extraits a un retrait plus faible que celui de l'aubier de la même espèce (Panshin et de Zeeuw 1980; Tsoumis 1991).

L'influence de la composition chimique des parois cellulaires est généralement faible, parce qu'il n'y a pas de grandes différences entre les diverses espèces ligneuses, particulièrement

en ce qui concerne la teneur en cellulose. En général, la lignine exerce un effet restrictif sur le retrait. Elle peut ainsi diminuer le retrait d'un bois ayant une haute teneur en lignine. À masse volumique égale, les feuillus ont un retrait plus élevé que les conifères en raison de la faible teneur en lignine des feuillus (environ 20% de moins) (Tsoumis 1991).

Si les efforts mécaniques provenant des charges extérieures (ou se développant quand le bois perd ou adsorbe de l'humidité) sont suffisamment grands (au-dessus de la limite proportionnelle), ils peuvent causer une déformation permanente des cellules du bois. Cette déformation a comme conséquence des changements secondaires (réduction ou augmentation) du retrait. Quand une grande compression réduit de façon permanente la dimension des cellules, la conséquence est un retrait plus grand que la normale. Inversement, sous l'influence de grands efforts de tension, le retrait devient plus petit que la normale (Tsoumis 1991).

La variation du retrait dans différentes directions de croissance est attribuée principalement à la structure des parois cellulaires. Il est bon de se rappeler que les cellules possèdent une paroi primaire et une paroi secondaire. La paroi primaire est très mince et la paroi secondaire se compose de trois couches (S_1 , S_2 , S_3) ayant des orientations différentes des microfibrilles. Dans les couches externe (S_1) et interne (S_3), les microfibrilles sont arrangées presque transversalement à la longueur des cellules, tandis que dans la couche moyenne (et plus épaisse) (S_2), elles sont presque parallèles à la longueur des cellules (Tsoumis 1991).

Quand l'humidité est adsorbée, la couche moyenne (S_2) tend à gonfler proportionnellement au nombre de microfibrilles (c.-à-d., proportionnellement à son épaisseur), mais les deux autres couches (S_1 et S_3) exercent un effet de rétention en raison de l'orientation différente de leurs microfibrilles. Le faible retrait axial (longitudinal) est dû à l'orientation des microfibrilles dans la couche S_2 . Si ces microfibrilles étaient exactement parallèles, le retrait longitudinal serait de zéro. La faible amplitude de ce retrait est due à de petites déviations de parallélisme. De plus grandes déviations (par exemple dans le bois de compression ou juvénile) contribuent à un plus grand retrait (Tsoumis 1991).

On connaît mal les raisons expliquant la différence entre les retraits radial et tangentiel. Cet écart a été en partie attribué à la présence des rayons qui, à cause de leur orientation, exercent une influence de rétention du retrait radial. L'effet de rétention des rayons est attribué à la direction des microfibrilles dans les parois de leurs cellules de parenchyme. Les

microfibrilles y sont pour la plupart parallèles à la longueur des cellules, comme dans les autres types de cellules. Il est toutefois douteux que les rayons aient une influence majeure parce que si une telle influence existait, les bois ayant un contenu plus élevé en rayons devraient montrer une plus grande différence entre les retraits radial et tangentiel, mais ce n'est pas toujours le cas. Cependant, une relation significative a été observée entre le retrait et le nombre de rayons chez les feuillus (Tsoumis 1991).

La différence de masse volumique entre le bois initial et le bois final est également considérée comme une cause de l'anisotropie. Le bois final a un retrait plus élevé en raison de sa masse volumique plus élevée – jusqu'à 3,5 fois. Le bois final a un effet prédominant sur le bois initial qui suit la même tendance. Puisque les anneaux de croissance ont un arrangement tangentiel, le retrait tangentiel devient plus grand. Cette explication est particulièrement applicable aux bois présentant des différences prononcées de masse volumique entre le bois initial et le bois final. Cependant, beaucoup d'espèces à pores diffus montrent un retrait tangentiel plus élevé que le retrait radial, bien que de telles différences n'existent pas entre les bois initial et final (Tsoumis 1991).

Selon une autre théorie, le retrait serait influencé par la lamelle moyenne, qui est composée de lignine et de substances pectiques. Il a été observé que l'enlèvement partiel de la lignine causait une augmentation du retrait. Ce phénomène peut facilement être expliqué par le fait que les espaces occupés par la lignine sont alors vides et qu'ils peuvent être envahis par l'eau. L'effet est semblable à celui des extractibles, mais il faut noter que les substances pectiques restantes peuvent gonfler plus facilement. L'augmentation du retrait provoquée par l'enlèvement de la lignine s'avère plus grande dans la direction radiale. Ceci signifie que la lamelle moyenne contient plus de lignine dans les parois radiales. L'effet de la lignine est plus grand lorsque le bois a une masse volumique faible. Chez les bois de masse volumique plus élevée, le retrait est également influencé par l'épaisseur des parois cellulaires. On a observé que l'épaisseur des parois est plus grande tangentiellement, et la présence des rayons contribue également à une plus grande proportion des parois cellulaires dans cette direction (Tsoumis 1991).

Deux types de retrait sont généralement évalués, soient les retraits linéaires et le retrait volumique. Nous distinguons trois directions de retrait linéaire: la radiale, la tangentielle et l'axiale ou longitudinale. Comme le bois est un matériau anisotrope, les changements de dimensions varient selon la direction qui est considérée (Goulet et al. 2005) et sont appelés:

- Retrait volumique total (β_V). Retrait du bois lorsqu'il passe de l'état vert à l'état anhydre ($H = 0\%$), exprimé en pourcentage.
- Coefficient de retrait différentiel volumique (g_V). Retrait du bois lors d'une perte de 1% de teneur en humidité en dessous du PSF. Il est sans unités.
- Retrait tangentiel, radial ou longitudinal total ($\beta_T, \beta_R, \beta_L$). Retrait du bois dans la direction considérée lorsque le bois sèche d'au moins 1% au-delà du PSF et jusqu'à l'état anhydre ($H = 0\%$). Les retraits suivent une relation d'ordre: retrait tangentiel (β_T) > retrait radial (β_R) >> retrait longitudinal (β_L). Il existe même une relation, voulant que le coefficient de retrait volumique soit égal à la somme des coefficients de retrait dans les trois directions (Skaar 1988) :

$$(\beta_T + \beta_R + \beta_L - \beta_T \times \beta_R) \quad (5)$$

- Coefficient de retrait différentiel tangentiel (g_T), radial (g_R) ou longitudinal (g_L). Retraits directionnels du bois lorsque le bois perd 1% de teneur d'humidité et qu'il est sous le PSF.

Le bois juvénile de quelques espèces présente un retrait longitudinal plus élevé (peut dépasser 1%) que le bois mature (0,1 à 0,3%) (McAlister et Clark 1992; Jodin 1994; Ying et al. 1994; Simpson et TenWolde 1999). En outre, le bois juvénile a tendance à présenter un retrait transversal plus faible que le bois mature à cause de sa masse volumique moins élevée (Bowyer et al. 2003).

Le retrait longitudinal diminue rapidement de la moelle vers l'écorce dans le bois. Ce changement du retrait longitudinal est lié à l'augmentation de la longueur des cellules et de la teneur en cellulose et à la réduction rapide de l'angle des microfibrilles dans les parois cellulaires (Panshin et de Zeeuw 1980).

Le retrait, comme les autres propriétés du bois, peut varier selon les facteurs génétiques et environnementaux. Par exemple, des différences dans cette propriété ont été observées parmi des clones hybrides de peupliers (Nepveu et al. 1978; Koubaa et al. 1998; Pliura et al. 2005) et parmi les familles de *Betula pendula* (Nepveu et Velling 1983), *Eucalyptus dunnii* (Henson et al. 2004) et *E. urophylla* (Scanavaca et Garcia 2004); et provenances d'*E. camaldulensis* (Sesbou et Nepveu 1990). En outre, des différences dans le retrait selon le site de plantation ont été rapportées pour toutes ces espèces (Sesbou et Nepveu 1990; Yang et al. 2002; Pliura et al. 2005).

1.3.7 Le coefficient de déformation statique [s_{11} statique] et le module de rupture [σ_L] en compression longitudinale

Les propriétés mécaniques du bois sont une expression de son comportement sous les forces qui lui sont appliquées. La résistance mécanique et la rigidité sont deux des propriétés les plus importantes pour évaluer l'utilisation potentielle d'un bois pour des fins de charpente.

Lors d'une compression longitudinale, l'effort imposé est parallèle au fil du bois. L'effort, exprimé sur la base de l'unité de surface, est connu comme la contrainte (σ). La contrainte est définie comme l'effort total de compression divisé par la section du morceau de bois étant soumis à cet effort. Ainsi, le module de rupture ou résistance maximale (σ_L) est une mesure de la capacité d'un morceau à résister à des charges en compression parallèle au fil jusqu'au point de rupture. En outre, la déformation résultante de la contrainte appliquée est appelée déformation (ε). La déformation dans un morceau de bois est proportionnelle à l'application de la contrainte, quand la déformation est petite. Si le temps de l'application de la contrainte est court et si la déformation est faible, la pièce de bois reprendra son état initial. Ce comportement du bois a été décrit par Robert Hooke en 1678 et a été formulé sous la forme d'une équation, soit $\sigma = k\varepsilon$. La constante de proportionnalité (k) reliant ces deux termes est appelée le module d'élasticité (MOE). Le module d'élasticité est aussi connu sous le nom de module d'Young (E) (Panshin et de Zeeuw 1980). De plus, le coefficient de déformation statique [s_{11} statique] est l'inverse du module d'élasticité statique (E_s).

La courbe de contrainte-déformation (Figure 1.2) montre aussi une zone sensiblement linéaire, dite élastique, limitée par la contrainte à la limite d'élasticité en compression (σ_e), suivie d'une zone de déformation plastique, limitée par la contrainte de rupture en compression (σ_r). Lorsque l'élongation à la rupture en compression (ε_r) est grande par rapport à l'élongation à la limite d'élasticité (ε_e), on dit que l'on est en présence d'une rupture ductile (avec fort allongement à la rupture) (Panshin et de Zeeuw 1980; Jodin 1994).

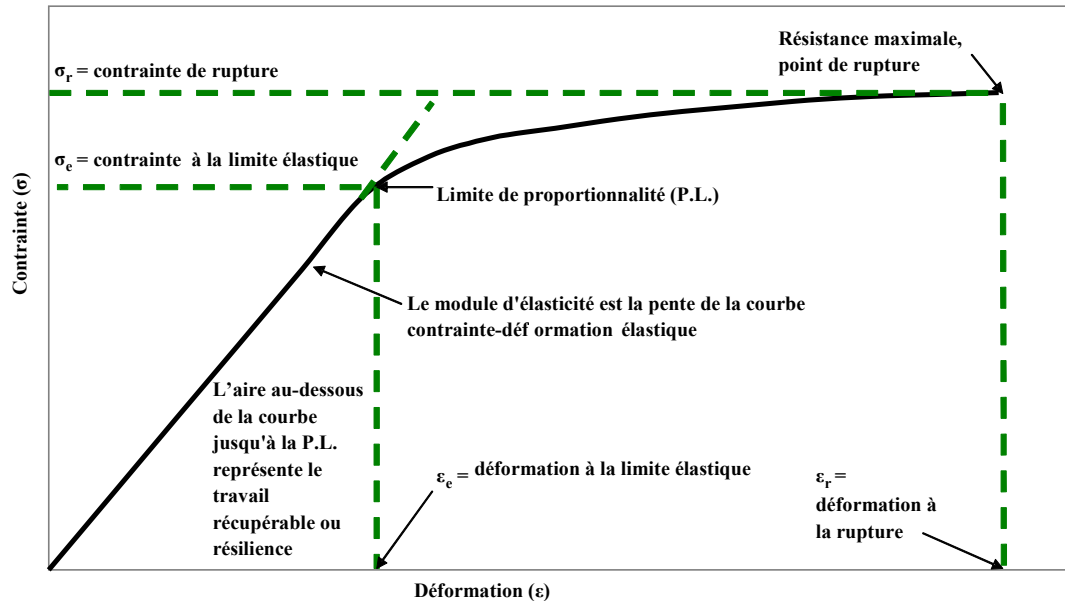


Figure 1.2. Relation entre la contrainte et la déformation lors d'un chargement statique jusqu'à la rupture (adapté de Panshin et de Zeeuw 1980, Jodin 1994).

Les facteurs qui influencent la résistance à la compression longitudinale sont: la taille de l'éprouvette, l'humidité, la température, la largeur des cernes de croissance et la masse volumique (Avalé 1984). La longueur de l'éprouvette doit être égale à 3 à 4 fois celle de la plus petite dimension de la section. En dessous de ce rapport les plateaux d'application de l'effort causent du gonflement transversal aux extrémités de l'éprouvette. Pour une longueur plus importante, l'essai n'est plus en compression pure : il y a présence de flambage (rupture par flexion d'une éprouvette du bois soumise à un effort de compression dans le sens de sa longueur). Finalement, la contrainte de rupture est liée à la teneur en humidité en dessous du PSF: plus la teneur en humidité est grande, plus le matériau est résistant.

Puisque le s_{11} statique est corrélé à la masse volumique chez des éprouvettes de bois clair, il devrait être possible de prévoir le s_{11} statique (et d'autres propriétés mécaniques) à partir de la masse volumique (Panshin et de Zeeuw 1980; Saranpää 2003). Cela serait utile car il est plus facile de mesurer la masse volumique que le s_{11} statique. Niklas (1997a) a évalué cette

question chez *Robinia pseudoacacia* et a conclu que les propriétés mécaniques du bois pourraient être bien estimées par une analyse de régression en utilisant la masse volumique du bois comme variable indépendante. Par contre, la variabilité des propriétés mécaniques peut être influencée par d'autres facteurs comme la variation existant à l'intérieur de l'arbre (Saranpää 2003) et les conditions environnementales qui affectent la croissance des arbres (Tsoumis 1991).

Des variations génétiques dans les propriétés mécaniques ont été observées chez des espèces feuillues. Par exemple, des variations significatives ont été rapportées pour le bois juvénile des clones de peuplier hybride (Hernández et al. 1998), entre familles d'*Eucalyptus grandis* (Santos et al. 2003), ainsi que pour le bois mature de clones de *Cryptomeria japonica* (Fujisawa et al. 1994) et de provenances de *Tectona grandis* (Bhat et Priya (2004).

1.3.8 Le coefficient de déformation dynamique en direction longitudinale du bois [s_{11} dynamique]

Les propriétés acoustiques du bois se rapportent à l'utilisation du son pour la prédiction des modules d'élasticité du bois à partir des mesures non-destructives ou à l'utilisation du bois comme instruments de musique ou composantes d'instruments de musique (xylophones, violons, guitares, pianos, etc) (Goulet et al. 2005).

Le son se propage dans un milieu élastique sous forme d'ondes de compression (longitudinales). La vitesse de propagation d'une onde longitudinale dans une tige mince de longueur infinie est fonction de la masse volumique et de la constante d'élasticité. Elle peut être estimée comme étant égale à :

$$\sqrt{\frac{E}{\rho}} \quad (6)$$

La vitesse de transmission des ondes sonores dans le bois est fonction de l'espèce, de la dimension d'éprouvette et de la méthode utilisée pour sa détermination (Bucur 1983; Quintanar et al. 1998; Oliveira et al. 2002; Ilic 2003). Le tableau 1.1 donne les valeurs de transmission des ondes sonores dans le sens parallèle au fil dans différentes espèces feuillues.

Tableau 1.1. Masse volumique, module d'élasticité dynamique et vitesse du son de quelques espèces feuillues.

| Espèce | Origine | $\rho(\text{kg/m}^3)$ | $E_d(\text{GPa})$ | $v(\text{m/s})$ |
|--|------------------------|-----------------------|-------------------|-----------------|
| <i>Acacia mearnsii</i> ^{1,3,6,11} | Australie | 736 | 17,2 | 4840 |
| <i>Beilschmiedia tawa</i> ^{1,3,6,11} | Nouvelle Zélande | 725 | 21,0 | 4290 |
| <i>Castanospermum australe</i> ^{1,3,6,11} | Australie | 733 | 14,8 | 4490 |
| <i>Chlorophora excelsa</i> ^{1,3,6,11} | Afrique | 653 | 15,2 | 4830 |
| <i>Clethra mexicana</i> ^{1,5,7,9} | Mexique | 567 | 10,9 | 4384 |
| <i>Cleyera sp.</i> ^{1,5,7,9} | Mexique | 683 | 15,0 | 4680 |
| <i>Dysoxylum muelleri</i> ^{1,3,6,11} | Australie | 753 | 14,3 | 4360 |
| <i>Endiandra palmerstonii</i> ^{1,3,6,11} | Australie | 719 | 16,0 | 4710 |
| <i>Fagus sylvatica</i> ^{2,4,7,8} | France | 593 | 12,1 | 4150 |
| <i>Goupia glabra</i> ^{1,3,7,10} | Brésil | 827 | 16,9 | 4514 |
| <i>Grevillea robusta</i> ^{1,3,6,11} | Australie | 633 | 15,9 | 5010 |
| <i>Hyedua ogea</i> ^{1,3,6,11} | Afrique | 727 | 18,0 | 4980 |
| <i>Hymenaea sp.</i> ^{1,3,7,10} | Brésil | 1149 | 20,6 | 4279 |
| <i>Lovoa trichilioides</i> ^{1,3,6,11} | Afrique occidentale | 530 | 11,7 | 4700 |
| <i>Milletia sp.</i> ^{1,3,6,11} | Afrique australe | 790 | 18,8 | 4881 |
| <i>Paulownia tomentosa</i> ^{1,3,6,11} | Australie (plantation) | 303 | 6,9 | 4780 |
| <i>Populus sp.</i> ^{1,3,6,11} | Australie (plantation) | 448 | 13,3 | 5281 |
| <i>Prunus brachybotrya</i> ^{1,5,7,9} | Mexique | 692 | 16,0 | 4790 |
| <i>Swietenia macrophylla</i> ^{1,3,6,11} | Centrale/Sud Amérique | 600 | 13,2 | 4690 |

Notes: ¹masse volumique à 12% de teneur en humidité; ²masse volumique à 10% de teneur en humidité; ³petites éprouvettes; ⁴carottes de sondage; ⁵blocs; ⁶vibration; ⁷ultrasons ⁸Bucur 1983; ⁹Quintanar et al. 1998; ¹⁰Oliveira et al. 2002; ¹¹Ilic 2003.

L'atténuation du son suite au rayonnement dépend principalement du rapport entre la vitesse de propagation et la masse volumique. Le rayonnement acoustique peut être estimé comme étant égal à :

$$\frac{v}{\rho} = \sqrt{\frac{E}{\rho^3}} \quad (7)$$

Pour les instruments de musique, on privilégie l'amortissement dû au rayonnement acoustique ($r > 10$). Les luthiers préfèrent par exemple le bois d'épinette pour les tables de violon à cause du rayonnement acoustique élevé de ce bois. Cependant, pour certaines applications pour lesquelles on veut étouffer le son, on va préférer l'atténuation causée par la friction interne: c'est le cas par exemple du bois d'érable utilisé comme fond de violon ($r < 6$) (Tsoumis 1991, Goulet et al. 2005).

L'évaluation des propriétés mécaniques du bois faite à l'aide d'échantillons recueillis de façon non-destructive serait très utile aux améliorateurs si la corrélation entre celle-ci et l'évaluation obtenue à partir de méthodes destructives standards était suffisamment élevée (Hernández et al. 1998).

La précision des mesures du module d'élasticité dynamique des carottes de sondage a été vérifiée au moyen d'essais de compression statique sur éprouvettes normalisées (Herzig 1991). Chez l'épinette blanche (*Picea glauca*), le module dynamique est inférieur au module statique. Seul le module d'élasticité statique en compression longitudinale accuse des différences entre les éprouvettes découpées du côté nord du tronc et les éprouvettes découpées du côté sud; les premières montrant un module plus élevé.

Le coefficient de déformation dynamique et la masse volumique des carottes de sondage évalués chez des populations naturelles de *Alnus acuminata* ont montré de fortes variations entre les régions géographiques, entre les arbres et à l'intérieur de l'arbre (Hernández et Restrepo 1995). Par contre, pour *Guazuma crinita* à 12 mois en plantation, Rochon (2004) n'a pas trouvé de différence significative du coefficient de déformation dynamique en direction longitudinale (s_{11}) entre les zones de plantation.

Le coefficient de déformation dynamique est normalement plus faible que celui statique, tel qu'observé dans le bois mature de conifères (Bodig et Jayne 1982) et de feuillus (Bucur 1983; Oliveira et al. 2002), et la différence est plus grande quand les valeurs ne sont pas ajustées par le rapport de Poisson (Bucur 2006). La différence entre le coefficient s_{11} dynamique et statique dans l'essai de compression parallèle est moins élevée que celle retrouvée dans le test de flexion statique (Herzig 1991). C'est parce que la méthode d'ultrasons, employée pour déterminer le s_{11} dynamique, traite presque entièrement les effets élastiques (Bucur 1983), tandis que l'essai de flexion statique traite les effets élastiques et de cisaillement (Ilic 2001). D'ailleurs, la différence entre le s_{11} dynamique et statique dans les essais de flexion statiques est plus petite pour des carottes de sondage que pour les blocs (Bucur 1983).

Les conditions environnementales affectent la croissance de l'arbre et peuvent indirectement produire une variation dans les propriétés mécaniques du bois (Tsoumis 1991). Par exemple, des différences significatives selon les sites ont été observées pour le diamètre de l'arbre et le

module d'élasticité dynamique (E_d) du bois juvénile de clones sélectionnés de *Cryptomeria japonica* (Nakada et al. 2003).

1.4 Héritabilité de la croissance des arbres et des propriétés du bois

L'importance relative de l'hérédité dans les valeurs phénotypiques observées s'appelle l'héritabilité du caractère (Falconer et Mackay 1996). Il y a cependant deux définitions distinctes de l'hérédité et de l'héritabilité, selon qu'elles réfèrent à des valeurs génotypiques ou à des valeurs d'élevage. Un caractère peut être «héréditaire» dans le sens de la détermination par le génotype ou dans le sens d'être transmis par les parents à la descendance.

L'héritabilité au sens large, ou degré de détermination génétique exprime jusqu'à quel point les phénotypes des individus sont déterminés par les génotypes :

$$\frac{\sigma_G^2}{\sigma_P^2} \quad (8)$$

L'héritabilité au sens strict, ou simplement l'héritabilité exprime jusqu'à quel point les phénotypes sont déterminés par les gènes transmis à partir des parents.

$$\frac{\sigma_A^2}{\sigma_P^2} \quad (9)$$

Dans la section suivante, l'héritabilité se rapporte à l'héritabilité au sens strict.

Les estimations de l'héritabilité sont nécessaires pour évaluer le gain génétique potentiel qui peut découler de la sélection. Comme les estimations d'héritabilité dépendent des conditions environnementales, des dispositifs expérimentaux et de la population analysée (Falconer et Mackay 1996), elles devraient idéalement être évaluées en contrastant les différents environnements et les différentes populations.

En général, la masse volumique du bois a une héritabilité plus élevée que les caractères de croissance. Cela a été observé pour les bois de feuillus tropicaux (Wei et Borralho 1997; Raymond 2002; Arnold et al. 2004) ainsi que pour beaucoup d'espèces des zones tempérées (Zobel et Jett 1995). Par exemple, Corriveau et al. (1991) ont trouvé des héritabilités de 0,46 pour la masse volumique et 0,32 pour la largeur des cernes annuels chez le *Picea glauca* à

l'âge de 19 ans. Ignacio-Sánchez et al. (2005) ont évalué la variation entre clones d'*Eucalyptus urophylla* à un jeune âge: ils ont rapporté que l'héritabilité augmentait entre la première et la troisième année, et qu'elle était plus forte pour la masse volumique que pour le diamètre à hauteur de poitrine. Par contre, l'héritabilité de la masse volumique du bois et de la croissance n'a pas été estimée à ce jour pour les feuillus tropicaux à un jeune âge.

Campbell et Sorensen (1978) ont émis l'hypothèse voulant que l'expression de la variation génétique des caractères de croissance soit moins élevée dans des environnements où les arbres croissent lentement que dans ceux où les arbres croissent plus rapidement. Par conséquent, on pourrait s'attendre à ce que l'héritabilité des caractères de croissance soit moins élevée dans des zones où les arbres croissent lentement, tel qu'observé pour les eucalyptus (MacDonald et al. 1997; Ginwal et al. 2004).

L'héritabilité du retrait et de la couleur du bois n'a pas été étudiée chez les espèces d'arbres feuillus tropicaux à un jeune âge. Par contre des études ont été menées chez des feuillus des régions tempérées et boréales. Ainsi, Nepveu et Velling (1983) ont trouvé que le retrait volumique était fortement héritable chez *Betula pendula*. Chez les peupliers, Nepveu et al. (1978) ont rapporté que l'héritabilité au sens large du retrait tangentiel et longitudinal (partiel) était plus forte pour le *P. nigra* que pour le *P. x euramericana*. Koubaa et al. (1998) ont confirmé que l'héritabilité du retrait partiel chez *P. x euramericana* était relativement faible. En outre, Nepveu (1984) a observé que le niveau d'héritabilité était plus élevé pour la masse volumique du bois que pour le retrait.

En ce qui a trait aux propriétés mécaniques du bois juvénile des espèces tropicales, peu d'études ont été conduites pour estimer leur héritabilité. Santos et al. (2003) ont rapporté pour *Eucalyptus grandis* une héritabilité de l'ordre de 0,57 pour la contrainte maximale en compression longitudinale.

1.5 Corrélations génétiques et phénotypiques entre la croissance des arbres et les propriétés du bois

Les corrélations entre la croissance des arbres et les propriétés de leur bois peuvent varier en raison: a) de l'environnement, b) des provenances, c) de l'âge des arbres et d) de l'état physiologique du bois ou de la phase de la maturité du bois (Kozłowski et al. 1991; Zobel et Sprague 1998).

Il est important de noter que les corrélations phénotypiques sont le résultat des effets génétiques et environnementaux (Falconer et Mackay 1996). Les corrélations phénotypiques sont composées à la fois des corrélations génétiques et des corrélations environnementales entre deux caractères. Si les deux caractères ne sont pas sous fort contrôle génétique (i.e. qu'ils ont une faible héritabilité), alors les corrélations phénotypiques seront principalement déterminées par les corrélations environnementales. Si l'héritabilité est élevée, les corrélations phénotypiques seront alors déterminées principalement par les corrélations génétiques. Ceci signifie que la magnitude de la corrélation génétique ne peut pas être uniquement déterminée par la corrélation phénotypique.

Des études portant sur certaines espèces à pores diffus illustrent que la relation entre la croissance et la masse volumique du bois n'est pas uniforme entre les espèces. Zobel et van Buijtenen (1989) ont noté, lors d'une revue de littérature, que pour la plupart des espèces étudiées, il n'y avait pas de corrélation significative entre les taux de croissance et la masse volumique du bois. Il y avait par contre plusieurs exceptions qui reflétaient le fait que les études ont été faites dans différents environnements, en utilisant diverses provenances et des arbres d'âges et d'états physiologiques variables.

Par exemple, dans les tropiques, Bhat (2000) s'est penché sur la recherche portant sur *Tectona grandis* et il a conclu que les provenances à croissance rapide pouvaient être sélectionnées sans réduire la masse volumique du bois. La corrélation entre le taux de croissance et la masse volumique du bois était généralement non significative ou très faible en fonction des provenances.

Malan (1991) a rapporté que la corrélation phénotypique entre le taux de croissance et la masse volumique du bois juvénile n'était pas significative chez l'*Eucalyptus grandis*. Par contre, la corrélation génétique était négative et significative, ce qui suggère que la sélection de familles à croissance rapide pourrait mener à une diminution de la masse volumique du bois de cette espèce.

Hernández et Restrepo (1995) ont de leur côté démontré qu'il y avait une corrélation phénotypique négative entre la masse volumique et la hauteur des arbres d'*Alnus acuminata*. Mais il n'y avait pas de corrélation significative entre le diamètre à hauteur de poitrine et la masse volumique ou le module d'élasticité dynamique.

D'autre part, Rochon (2004) a signalé une corrélation phénotypique négative entre la masse volumique à hauteur de poitrine et la croissance (hauteur et diamètre) de *Guazuma crinita* pour les arbres âgés de 12 mois. Par contre, la force de cette corrélation différait selon la position radiale de l'échantillon dans la tige (corrélation négative plus forte pour le bois près de l'écorce que pour le bois près de la moelle).

S'il y a une corrélation génétique significative entre la masse volumique du bois et la croissance de l'arbre, on pourrait s'attendre à une corrélation du même type entre la croissance du bois et d'autres propriétés du bois parce que la masse volumique du bois est considérée comme l'élément le plus important pour la prédiction des propriétés du bois (Panshin et de Zeeuw 1980).

La couleur du bois pourrait être reliée à la croissance de l'arbre mais cette relation dépend probablement de plusieurs autres facteurs pour une espèce donnée comme la population, l'âge, la position de l'échantillon dans l'arbre, l'environnement et les fertilisants qui ont été utilisés. Par exemple, Wilkins et Stamp (1990) ont observé que les arbres d'*Eucalyptus grandis* qui croissaient plus vite produisaient un duramen plus rouge à l'âge de 9,5 ans. Cependant, Rink (1987) a rapporté que les arbres de *Juglans nigra* à croissance plus rapide produisaient un duramen plus clair à l'âge de 10 ans. Dans la même plantation de *J. nigra*, Rink et Phelps (1989) ont observé que les arbres plus hauts avaient un duramen plus dense et de couleur plus foncée. Klumpers et al. (1993) ont découvert que les arbres de *Quercus robur* provenant de sites où l'eau au niveau du sol était abondante durant le printemps produisaient du bois plus foncé et plus rouge. La couleur devenait ainsi plus foncée et plus rouge de la moelle vers l'écorce de même que le duramen en vieillissant devenait de plus en plus rouge.

Les relations entre la croissance de l'arbre et le retrait du bois ont été étudiées pour certaines espèces et elles dépendent probablement de la relation sous-jacente entre croissance et masse volumique pour chaque espèce. Par exemple, la corrélation entre la croissance de l'arbre et le retrait du bois était négative pour *Betula pendula* (Nepveu et Velling 1983) et *Terminalia superba* (Hock et Mariaux 1984), positive pour *Gilbertiodendron dewevrei* (Hock et Mariaux 1984) et absente pour *Tectona grandis* (Hock et Mariaux 1984) et pour les clones de *Populus x euramericana* (Koubaa et al. 1998). En outre, Pliura et al. (2005) ont rapporté que la corrélation variait considérablement selon les sites pour *P. deltoides* x *P. nigra*, *P. trichocarpa* x *P. deltoides* et pour les clones de *P. maximowiczii* x *P. balsamifera*.

Il semble y avoir une relation générale entre la masse volumique et la couleur chez les feuillus tropicaux à pores diffus. En effet, la majorité des espèces ayant une masse volumique plutôt faible (400 – 550 kg/m³) tendent à avoir un bois plus clair avec un ton jaunâtre tandis que ceux qui ont une masse plus élevée (750 – 950 kg/m³) tendent à avoir un bois plus foncé avec un ton rougeâtre (Rodríguez et Sibille 1996; Nishino et al. 1998; Janin et al. 2001; Kishino et Nakano 2004). Par conséquent, on pourrait s'attendre à ce qu'il y ait une corrélation positive entre la masse volumique du bois et la couleur parmi des arbres d'une espèce donnée. Aucune corrélation génétique entre la couleur et la masse volumique du bois n'a pas été rapportée à ce jour pour les espèces de feuillus tropicales à un jeune âge. Par contre, Hannrup et al. (2004) ont observé des corrélations génétiques significatives entre la couleur du bois et la masse volumique du bois chez *Picea abies* à l'âge de 40 ans.

On pourrait s'attendre à une relation positive entre la masse volumique du bois et le retrait tangentiel, radial et volumétrique parce qu'un bois plus dense a un plus grand volume de parois cellulaires (Tsoumis 1991). Des corrélations positives entre la masse volumique et le retrait tangentiel, radial et/ou volumétrique ont été observées chez plusieurs espèces de feuillus comme *Betula pendula* (Nepveu et Velling 1983), *Quercus petraea* et *Q. rubra*, (Nepveu 1984), *Populus x euramericana* (Hernández et al. 1998), *Petersianthus macrocarpus* (Poku et al. 2001), *Swietenia macrophylla* (Arévalo 2002), ainsi que pour neuf espèces péruviennes d'origine tropicale (Hernández 2006a). Par contre, aucune relation significative entre la masse volumique et le retrait n'a été trouvée pour *Liriodendron tulipifera*, *Populus deltoides* et *Liquidambar styraciflua* (Shupe et al. 1995a, 1995b, 1995c). Cependant, ces derniers travaux doivent être considérés comme préliminaires car ils ont été conduits avec un ou deux arbres seulement.

On pourrait aussi s'attendre à ce que le rapport entre le retrait tangentiel et radial diminue avec une plus grande masse volumique du bois (Tsoumis 1991). Cette relation pourrait toutefois dépendre de l'espèce. En effet, Hock et Mariaux (1984) ont observé une corrélation phénotypique positive entre la masse volumique et le rapport tangentiel/radial pour *Terminalia superba*, mais ils n'ont pas trouvé de corrélation significative pour *Tectona grandis*. De son côté, Nepveu (1984) a observé que des corrélations positives (phénotypique et génétique) étaient présentes chez *Quercus petraea*, mais absentes pour *Q. robur* et *Q. rubra*.

Une corrélation positive devrait aussi exister entre la masse volumique du bois et la résistance et rigidité du bois (Evans et al. 2000). Par exemple, la masse volumique du bois a été corrélée positivement avec la valeur de E_s chez *Petersianthus macrocarpus* (Poku et al. 2001) et corrélée négativement avec le s_{11} dynamique dans *Populus x euramericana* (Hernández et al. 1998).

1.6 Information générale de *Calycophyllum spruceanum*

1.6.1 Distribution, écologie et sylviculture

Le Pérou possède 41,1 millions d'hectares de forêt, dont 250000 correspondent à des forêts plantées. Le taux actuel de déforestation est estimé être de l'ordre de 269000 hectares par année (ITTO 2006).

C. spruceanum est une espèce pionnière des plaines alluviales de l'Amazonie. Elle colonise également les forêts secondaires, les sites perturbés et les forêts matures (Linares et al. 1992; Toledo 1999). Au Pérou, l'aire de distribution de *C. spruceanum* s'étend des terres basses de l'Amazonie jusqu'à une altitude de 650 m au-dessus du niveau de la mer. Elle est abondante dans les zones de forêts inondables ainsi que dans celles non inondées. Par exemple, dans la zone du fleuve Abujao à Pucallpa, on retrouve 1,30 arbres par hectare avec un volume moyen de 5,58 m³ en forêts inondables et 1,19 arbres par hectare avec un volume moyen de 6,71 m³ en forêt non inondée (Toledo et Rincón 1996).

C. spruceanum est une espèce intolérante à l'ombre qui présente une croissance régulière. Selon le Ministère de l'Agriculture du Pérou, cette espèce présente un statut de conservation assuré puisqu'elle se retrouve à la fois dans les unités de conservation et hors de celles-ci. Elle forme des populations abondantes et n'est pas considérée comme vulnérable (Toledo 1999).

Les arbres atteignent la maturité sexuelle à un jeune âge (2 ou 3 ans) en conditions de croissance à découvert. Le système de reproduction de *C. spruceanum* n'a pas été étudié, mais il est probable qu'il soit principalement à pollinisation croisée, comme c'est le cas pour la plupart des arbres tropicaux (Bawa et Hadley 1990). Des études faites au Costa Rica ont démontré que les plantes de la famille des Rubiaceae étaient systématiquement intolérantes à l'endogamie (Kress et Beach 1994). Les plantes sont monoïques et les fleurs sont petites, blanches, parfumées et hermaphrodites, présentant deux étamines et le pistil. Une fois la

maturité sexuelle atteinte, les arbres produisent annuellement des millions de très petites semences ailées qui sont dispersées par le vent et l'eau, permettant à l'espèce de coloniser des vastes secteurs. Il semble que la dispersion du pollen soit assurée par les abeilles et les chauves-souris, entre autres. Vu ces caractéristiques reproductrices, il est probable qu'il y ait un flux génétique élevé entre les populations naturelles de *C. spruceanum* (Russell et al. 1999).

On reconnaît d'excellentes qualités à *C. spruceanum* pour la plantation à découvert, soit en plantation pure ou dans un système agroforestier (Toledo 1999). Sa croissance est rapide et deux ou trois ans après la plantation, son bois peut être utilisé pour la fabrication de perches de construction légère ou comme bois de chauffage. Entre quinze et vingt ans, les tiges atteignent des dimensions permettant la fabrication de matériaux pour la construction. Lorsque les arbres sont abattus, les souches dont le diamètre est de moins de 15 cm ont la capacité de produire des rejets (Torres 1993). *C. spruceanum* peut être utilisée dans plusieurs systèmes de production agroforestière, comme les multi-strates et les systèmes sylvopastoraux, dans lesquels il n'y a pas d'attaques d'insectes pendant les premiers mois suivant l'établissement (Couturier et Gonzales 1994).

1.6.2 Utilisations et valeur économique

Le bois de *C. spruceanum* est commercialisé sur le marché intérieur du Pérou (ITTO 2006) pour la fabrication de divers produits d'usage domestique et industriel, tels que la construction de murs et de planchers pour des maisons rurales, la fabrication de poutres et de traverses de chemin de fer et la production de bois de chauffe et de charbon à haute valeur calorifique (Toledo 1999). La commercialisation du bois de cette espèce est importante pour les communautés rurales (Labarta et Weber 1998).

Selon les résultats d'études industrielles (Toledo 1999; Toledo et Rincón 1996), *C. spruceanum* est une des espèces péruviennes qui possèdent le plus fort potentiel économique sur les marchés internationaux en raison de sa productivité, de l'uniformité de la coloration du bois et de la facilité à le scier, et ce malgré sa forte masse volumique. Divers produits à valeur ajoutée peuvent en être tirés dont des goujons pour l'assemblage de meubles, des planches et bois de plancher, des portes et fenêtres, et des poutres et poutrelles décoratives.

Les marchés nationaux et internationaux préfèrent actuellement le bois de *C. spruceanum* avec une couleur jaune uniforme pour les meubles, les boiseries et les planchers (Toledo et

Rincón 1996), mais les préférences peuvent changer dans le futur. Par conséquent, il est important pour les programmes d'amélioration du bois de répondre aux besoins du marché actuel, tout en prévoyant les possibilités de changements futurs. Les agriculteurs et l'industrie utilisent normalement le bois de jeunes arbres de cette espèce et ils l'utiliseront de plus en plus dans le futur avec la promotion de l'agroforesterie et de la foresterie de plantation à petite échelle.

1.6.3 Propriétés du bois

Le bois de *C. spruceanum* est du type à pores diffus. La largeur des cernes de croissance dans le bois mature a une moyenne de 3 mm, ils sont réguliers et se distinguent légèrement par des cercles foncés. Les éléments de vaisseaux ont une perforation simple, un diamètre plutôt constant (diamètre moyen tangentiel de 58 à 74 μm) et sont répartis uniformément dans le cerne annuel (15 à 24 pores par mm^2). Les fibres possèdent des parois cellulaires épaisses étant ainsi du type fibre-trachéides. Le parenchyme apotrachéal est dispersé et typiquement isolé des vaisseaux. Les rayons sont hétérogènes et composés de cellules couchées et de cellules dressées et sont petits (grosseur de 1 à 5 cellules, hauteur de 320 μm ou 7 à 106 cellules). Des inclusions de gomme et silice dans les rayons ont aussi été notés (JUNAC 1981; Chavesta 1995).

Le bois mature de *C. spruceanum* d'environ 20 ans est très dense: une masse volumique basale de 760 kg/m^3 selon Acevedo et Kikata (1994) et de 645 kg/m^3 selon Woodcock (2000). Il est très stable au séchage (retrait volumique total de 15%, et un rapport d'anisotropie de 1,8 entre le retrait tangentiel et le retrait radial). Il possède aussi de bonnes propriétés mécaniques, et ce en lien avec sa masse volumique élevée (Chavesta 1995). Le bois est relativement facile à usiner (Meléndez 1999). La longévité du bois non traité est modérément élevée (Toledo 1999).

La composition chimique du bois de *C. spruceanum* a été peu étudiée. En revanche, des études de sa valeur calorifique à un jeune âge ont été réalisées (Sotelo Montes et al. 2003; Weber and Sotelo Montes 2005). La valeur calorifique était du même ordre de grandeur que celle des autres espèces de l'Amazonie péruvienne (branches à 18 mois = 472,7 kcal/100g, bois de la tige = 425.6 kcal/100g à 32 mois, 0% de teneur en humidité). Il y avait peu de variation de la valeur calorifique entre les arbres, et il n'y avait pas d'effet significatif de

l'environnement (sites de plantation) ou de la source géographique de la semence (provenance) sur cette propriété.

1.6.4 Variation génétique et environnementale

En 1995, le Centre International pour la Recherche en Agroforesterie (ICRAF, actuellement connu comme le Centre Mondial pour l'Agroforesterie) et ses partenaires ont mis en place un programme de domestication participative dans le bassin de l'*Aguaytia* et dans la région de l'*Alto Amazonas*, de l'Amazonie péruvienne. Ce programme, ayant pour but principal la promotion de la conservation des ressources génétiques (O'Neill et al. 2001; Weber et al. 2001), a commencé par l'identification des espèces qui devraient être utilisées en priorité dans des programmes d'agroforesterie (Sotelo Montes et Weber 1997). Quatre espèces ont été sélectionnées: *C. spruceanum* (Rubiaceae), *Guazuma crinita* (Sterculiaceae), *Inga edulis* (Mimosoideae) et *Bactris gasipaes* (Palmae). Des semences fécondées par pollinisation libre ont été récoltées sur les arbres-mères sélectionnés sur le terrain des agriculteurs, et utilisées pour établir des essais de descendance en blocs aléatoires complets, les blocs étant dispersés chez plusieurs agriculteurs collaborateurs. Actuellement, ces essais produisent des semences et les agriculteurs ont créé des coopératives pour la production de bois et de semences (Cornelius et al. 2006).

La croissance et les propriétés du bois des essences forestières sont influencées par des facteurs environnementaux, des facteurs génétiques et leur interaction. Les différences entre les provenances peuvent être d'autant plus réduites si l'espèce étudiée a un flux génétique élevé (comme c'est le cas pour *C. spruceanum* [Russell et al. 1999]) mais de fortes variations entre les arbres d'une même population (Hamrick et al. 1992). Les résultats des études sur la variation de la croissance dans des essais de provenances de *C. spruceanum* dans le bassin amazonien du Pérou concordent avec cette théorie: les variations entre les provenances sont minimales lorsque comparées aux variations entre les arbres d'une même provenance (Sotelo Montes et al. 2003; Boivin-Chabot et al. 2004; Weber et Sotelo Montes 2005). Par exemple, Sotelo Montes et al. (2003) et Weber et Sotelo Montes (2005) ont montré que ces trois sources de variation (zone de plantation, provenance, interaction entre zone et provenance) étaient significatives pour la croissance de l'arbre à un jeune âge. D'autre part, Boivin-Chabot et al. (2004) ont étudié la variation des rejets de souche après la coupe dans le même essai de provenances. Les résultats ont montré des différences significatives pour le nombre

de rejets et leur hauteur entre les provenances testées, mais il n'y avait pas de différence significative entre les zones de plantation.

Lors des essais de provenances, il a souvent été démontré que les différences de croissance entre les zones de plantation sont plus grandes que celles entre les provenances (Namkoong et al. 1988; Morgenstern 1996). Ce comportement a été observé également pour *C. spruceanum* par Sotelo Montes et al. (2003) et Weber et Sotelo Montes (2005). Il est illustré à la figure 1.3 pour l'effet des zones de plantation et à la figure 1.4 pour l'effet des provenances.

La sélection de provenances d'espèces ligneuses à croissance rapide serait plus efficace lorsque les conditions environnementales des essais facilitent cette croissance (Campbell et Sorensen 1978). Ces environnements permettraient aux différences génétiques inhérentes aux taux de croissance des provenances de mieux s'exprimer. Les provenances pourraient ainsi ne pas exprimer leur plein potentiel génétique dans des environnements moins favorables. Des résultats similaires ont été observés pour *C. spruceanum* par Sotelo Montes et al. (2003). À 18 mois, quatre caractéristiques de croissance variaient significativement entre les provenances dans la zone de plantation où les précipitations étaient élevées et les sols fertiles, alors que dans les zones où les précipitations étaient faibles et les sols infertiles, seule une caractéristique de croissance variait significativement entre les provenances.

Il y a eu relativement peu de recherches sur la variation des propriétés du bois de *C. spruceanum*. La masse volumique du bois d'arbres de 32 mois est légèrement plus grande vers la base de la tige que dans la partie supérieure: 564 kg/m^3 et 525 kg/m^3 , respectivement (Weber et Sotelo Montes 2005). Le bois de la partie supérieure de la tige est significativement plus dense dans la zone de plantation où les arbres croissent lentement en comparaison avec la zone de croissance rapide (moyenne = 545 kg/m^3 et 509 kg/m^3 , respectivement). Par contre, la masse volumique vers la base de la tige ne varie pas significativement entre les zones de plantation. De plus, la différence de masse volumique entre la base et la partie supérieure de la tige est plus faible dans la zone où les arbres croissent lentement que dans la zone à croissance rapide (différence moyenne = 36 kg/m^3 versus 66 kg/m^3). Malgré les différences entre les zones de plantation, aucune différence significative de masse volumique du bois n'a été notée entre les provenances.

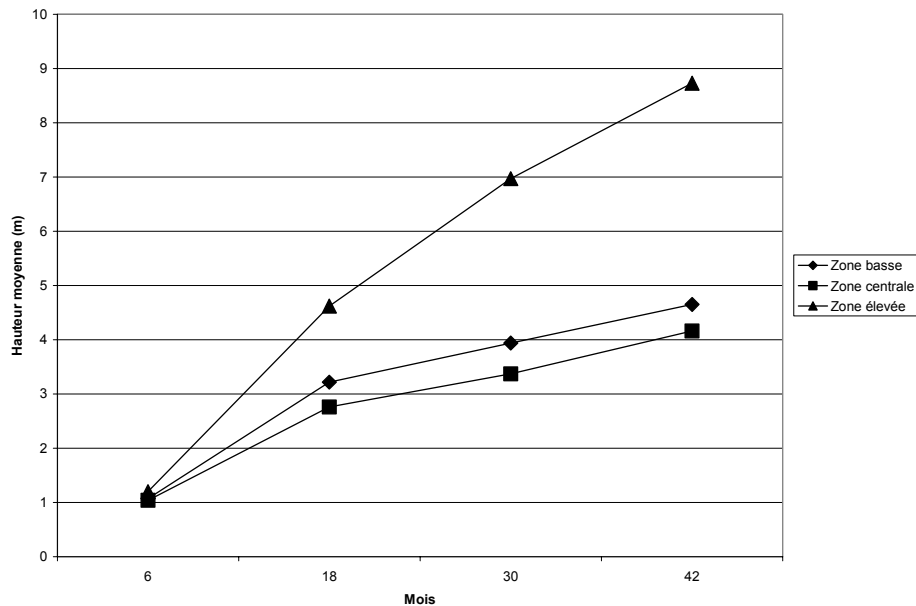


Figure 1.3. Hauteur moyenne des arbres de *Calycophyllum spruceanum* de 6 à 42 mois pour trois zones de plantation situées au bassin du fleuve Aguaytía au Pérou (adapté de Weber et Sotelo Montes 2005).

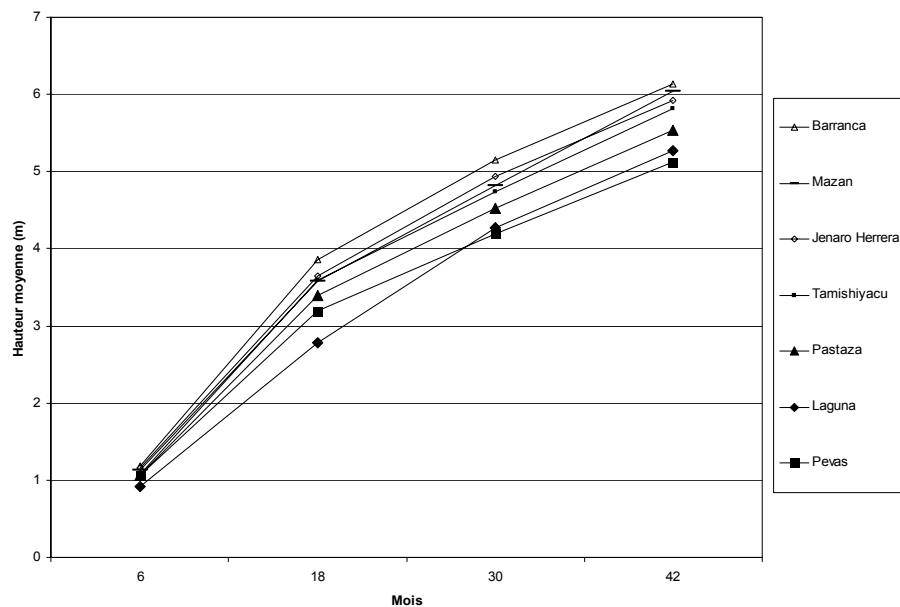


Figure 1.4. Hauteur moyenne des arbres de sept provenances de *Calycophyllum spruceanum* de 6 à 42 mois croissant au bassin du fleuve Aguaytía au Pérou (adapté de Weber et Sotelo Montes 2005).

De plus, la masse volumique des branches à 18 mois a été étudiée (Sotelo Montes et al. 2003): la valeur moyenne est plutôt faible (masse volumique basale de 494 kg/m^3). Cette valeur est du même ordre de grandeur que celles des autres espèces étudiées en Amazonie. La masse volumique des branches ne varie pas significativement entre les zones de plantation ou les provenances.

1.6.5 Corrélations phénotypiques entre la croissance des arbres et la masse volumique du bois

Chez *C. spruceanum*, la corrélation phénotypique entre la masse volumique du bois et la croissance varie selon la position verticale de l'échantillon dans la tige et selon la zone de plantation (Weber et Sotelo Montes 2005). Lors des analyses statistiques pour l'ensemble des zones de plantation, la masse volumique moyenne de la tige n'était pas corrélée significativement à la hauteur ou au diamètre à 32 mois. La hauteur et le diamètre étaient cependant corrélés positivement à la masse volumique du bois mesurée en bas de la tige, mais corrélés négativement à la masse volumique du bois mesurée en haut de la tige. Lors des analyses à l'intérieur des zones, la corrélation entre le diamètre et la masse volumique du bois dans le bas de la tige était négative dans la zone présentant des précipitations faibles et des sols infertiles, mais positive dans la zone présentant des précipitations élevées et des sols fertiles.

Chez *C. spruceanum*, la corrélation phénotypique entre la croissance et la masse volumique du bois semble donc être négative dans des environnements où les arbres croissent lentement et positive dans des environnements où la croissance est rapide (Weber et Sotelo Montes 2005). En d'autres mots, la relation entre la croissance et la masse volumique du bois pourrait être en forme de «U» plutôt que linéaire. Cela suggère que la sélection d'arbres à croissance rapide pourrait conduire à une diminution ou augmentation de la masse volumique du bois dépendant des environnements, et n'aurait aucun effet dans d'autres. Il est malgré tout nécessaire de déterminer les corrélations génétiques dans différents environnements pour pouvoir évaluer si la sélection d'arbres à croissance rapide va affecter la masse volumique du bois et si les effets varieront selon les environnements. La figure 1.5 présente un sommaire des corrélations attendues entre le diamètre de la tige et la masse volumique du bois dans une zone de croissance rapide (Weber et Sotelo Montes 2005) ainsi que les corrélations attendues selon la théorie entre la masse volumique, le retrait, la résistance et la rigidité du bois (Panshin et de Zeeuw 1980).

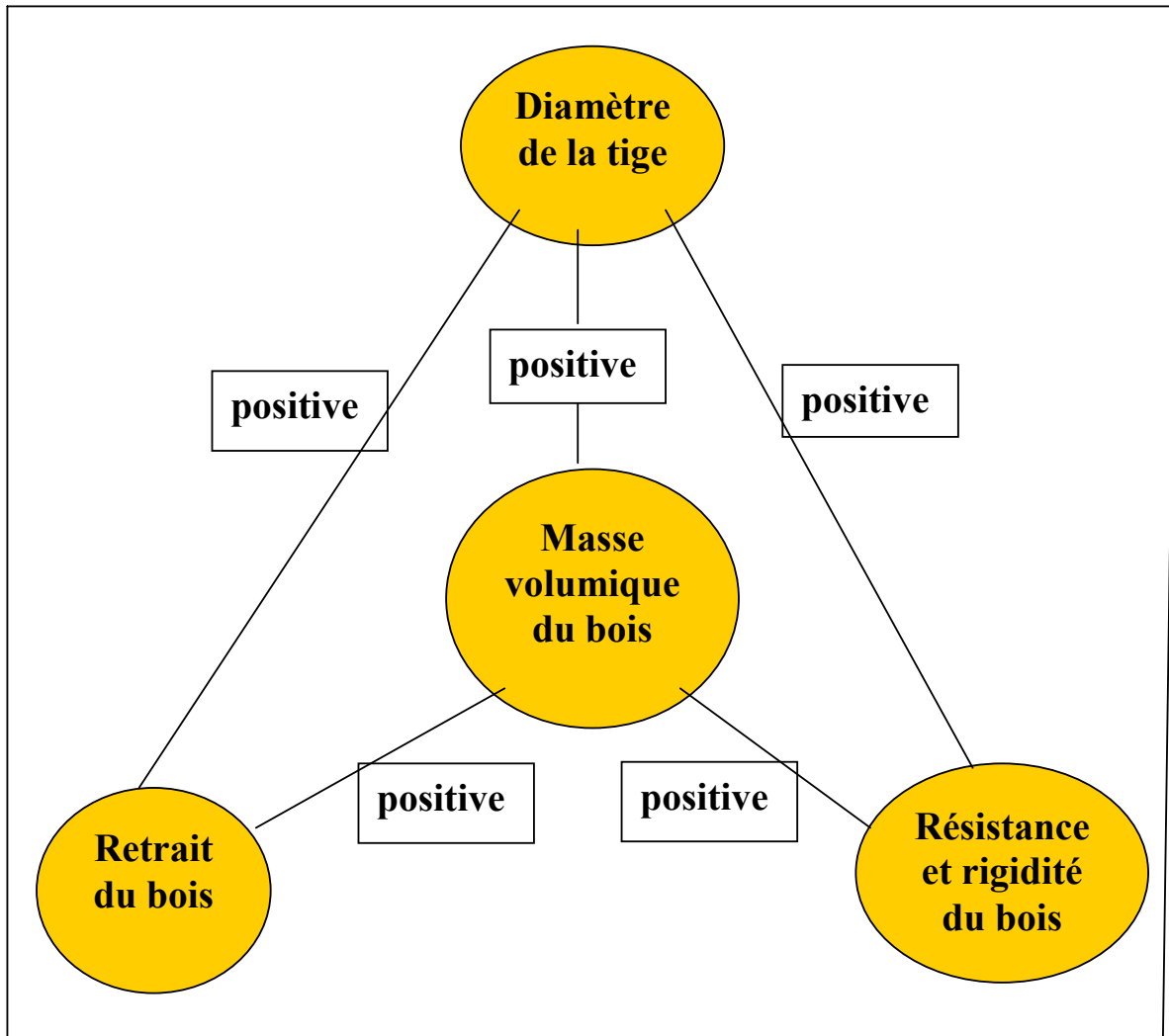


Figure 1.5. Les corrélations attendues entre le diamètre de la tige de *C. spruceanum* et les propriétés du bois. L'exemple est pour une zone de plantation où les arbres croissent rapidement. Le signe des corrélations demeure dans tous les cas positifs (d'après Panshin et de Zeeuw 1980; Weber et Sotelo Montes 2005).

La corrélation entre la croissance et le retrait, la résistance et la rigidité dépend de la corrélation entre la croissance et la masse volumique. C'est-à-dire, si la corrélation entre la croissance et la masse volumique est positive, on s'attend à ce que les corrélations entre la croissance et ces propriétés du bois soient aussi positives.

Objectifs et hypothèses

Un essai de provenance/descendance de *C. spruceanum* a été établi dans le bassin du fleuve Aguaytía en Amazonie péruvienne et répliqué dans trois zones qui diffèrent en termes de précipitations et fertilité du sol.

En raison de sa composition, l'analyse des données de cet essai nous permet d'estimer à la fois la variation génétique des caractères de croissance et du bois et la variation génétique au niveau géographique (entre les populations), l'héritabilité et les corrélations phénotypiques et génétiques entre les caractères. Les données proviennent de jeunes arbres qui contiennent du bois juvénile, mais les résultats fourniront un aperçu du potentiel futur à partir de la sélection précoce de *C. spruceanum* basée sur ces caractères.

Les principaux objectifs de la présente recherche sont les suivants:

1. Étudier les patrons de variation des caractères de croissance dans le temps et des propriétés du bois à un jeune âge pour déterminer (a) si la variation observée est due principalement aux effets géographiques/génétiques, de l'environnement, ou de l'interaction entre l'environnement et les autres effets, et (b) si l'expression de la variation géographique/génétique diffère entre les environnements;
2. Estimer les corrélations génétiques et phénotypiques entre les caractères de croissance et les propriétés du bois et déterminer si elles diffèrent selon l'environnement.

Ces caractéristiques sont le diamètre et la hauteur des arbres, la masse volumique du bois, la couleur du bois, le retrait du bois, le coefficient de déformation statique [S_{11} statique], le module de rupture [σ_L] en compression longitudinale et le coefficient de déformation dynamique en direction longitudinale du bois [S_{11} dynamique].

Les hypothèses générales de la présente recherche sont les suivantes :

Hypothèse 1: Il existe des différences significatives au niveau de la croissance et des propriétés du bois entre les provenances et les familles à l'intérieur des provenances mais ces différences sont aussi affectées par l'environnement.

Nous nous attendons à ce que les différences génétiques observées au niveau de la croissance soient plus grandes dans les environnements (zones de plantation) qui favorisent une croissance plus rapide des arbres et soient plus faibles dans les environnements où les arbres

se développent lentement. Nous nous attendons également à ce que le contrôle génétique des caractères de croissance soit plus faible que celui de certaines propriétés du bois comme la masse volumique.

Hypothèse 2: La force des corrélations entre la croissance et les propriétés physiques et mécaniques du bois dépendent de l'environnement.

La force et le signe de la corrélation peuvent varier selon l'environnement où les arbres se développent. Par exemple, selon les résultats des autres études de cette espèce, la corrélation entre la croissance d'arbre et la masse volumique du bois peut être fortement positive dans un environnement qui favorise la croissance mais négative dans un environnement où les arbres croissent lentement.

Chapitre 2 Genetic variation and correlations between growth and wood density of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon

2.1 Résumé

Calycophyllum spruceanum (Benth.) Hook. f. ex K. Shum. est une espèce importante dans le bassin amazonien péruvien. Du fait que les agriculteurs et l'industrie utilisent du bois provenant de jeunes arbres, il est important d'étudier la variation génétique des caractéristiques du bois juvénile de cette espèce. Un essai de provenance/descendance a été effectué afin d'évaluer la variation génétique de la croissance et des propriétés du bois de jeunes arbres, la force de leur contrôle génétique, ainsi que leurs relations au niveau génétique et phénotypique, dans différentes zones de plantation. Dans cet article, nous présentons les résultats obtenus pour la hauteur de l'arbre et pour le diamètre de la tige (près du niveau du sol) à l'âge de 16, 28 et 39 mois ainsi que le diamètre de la tige et la masse volumique basale du bois à hauteur de poitrine à l'âge de 39 mois. Nous avons trouvé des variations significatives dues aux provenances et particulièrement dues aux familles à l'intérieur des provenances pour la croissance et la masse volumique du bois. Les corrélations phénotypiques et génétiques ont indiqué que de plus gros arbres ont tendance à avoir un bois plus dense. La masse volumique a présenté une héritabilité plus élevée que la hauteur et le diamètre. Le contrôle génétique sur la hauteur, le diamètre et la masse volumique étaient généralement plus grands dans les zones de plantation où les arbres croissaient plus rapidement.

2.2 Abstract

Calycophyllum spruceanum (Benth.) Hook. f. ex K. Shum. is an important timber-tree species in the Peruvian Amazon Basin. As farmers and industry often use wood from young trees, it is important to investigate variation in juvenile wood properties in this species. A provenance/progeny test was established to evaluate genetic variation in growth and wood properties of young trees, the strength of their genetic control as well as their interrelationships both at the genetic and the phenotypic level in different planting zones. In this paper, results are presented for tree height and stem diameter (near ground level) at 16, 28 and 39 months; and stem diameter and basic density of the wood at breast height at 39 months. Significant variation due to provenances and especially due to families within

provenances was found in growth and wood density. Phenotypic and genetic correlations indicated that larger trees tended to have denser wood. Wood density had higher heritability than height and diameter; and genetic control over height, diameter and density was generally highest in the planting zone where trees grew most rapidly.

2.3 Introduction

The Peruvian Amazon has many valuable timber-tree species, but there has been little research on genetic variation in these species. Farmers and industry commonly use juvenile wood, and they will probably use it even more in the future with the promotion of agroforestry and small-scale plantation forestry. Tree breeders, therefore, should initiate research on genetic variation in properties of juvenile wood to see whether it is possible to improve them through breeding work and to measure the impact of selection for juvenile wood traits on other traits (Zobel and Sprague 1998).

Calycophyllum spruceanum (Bentham) Hooker f. ex Shumann (Rubiaceae family) is a pioneer species that colonizes the floodplain and disturbed forests in the Amazon Basin (Linares et al. 1992). The breeding system has not been studied, but is assumed to be primarily out-crossing like the majority of tropical trees (Bawa et al. 1990). Trees have hermaphroditic flowers, and mature in 2 to 3 years in open-grown conditions. There is probably extensive gene flow, producing high levels of genetic variation within populations and relatively low genetic differentiation among populations (Russell et al. 1999).

Farmers rank *C. spruceanum* as a priority for lumber, poles, firewood and charcoal in agroforestry systems in the Peruvian Amazon (Sotelo Montes and Weber 1997). Adult trees (age unknown) in natural stands can attain heights of 35 m with stem diameters of 1.8 m at breast height (Sears 2003). The wood is diffuse-porous, with a basic density of 740 kg/m³ for mature wood (age unknown) in natural stands (measured at 1.3 m above ground; Keenan and Tejada 1984) and 563 kg/m³ at 32 months of age in plantations (measured from 35 to 65 cm above ground, Weber and Sotelo Montes 2005). It is generally assumed that mature wood is formed after 15-20 years in natural stands, but this has not been confirmed by studies. Stems can be harvested for construction poles after 2 to 3 years, or sawn timber after 15 to 20 years, and then coppiced for successive harvests. The wood has demand in national and international markets for furniture, wall paneling and parquet (Toledo and Rincón 1999).

Tree growth and wood density are known to be influenced by both genetic and environmental factors (Zobel and Jett 1995; Zobel and Sprague 1998). The first provenance test of *C. spruceanum* established in Peru demonstrated that plantation yield could be increased by selecting fast-growing provenances (Sotelo Montes et al. 2003; Weber and Sotelo Montes 2005). However, phenotypic correlations between growth and wood density differed in sign among planting zones, suggesting that selection of fast-growing provenances may produce wood with lower density in some zones and higher density in other zones.

Heritability estimates are needed to assess the potential genetic gain that can be realized by selection, and estimates of genetic correlations are necessary to assess if selection based on growth significantly affects wood density. Since heritabilities and genetic correlations depend on the specific test environment and population of trees (Falconer and Mackay 1996), they should be evaluated in contrasting environments and in different populations. In general, wood density has a higher heritability than growth traits, and the genetic correlation between growth and density is low for diffuse-porous hardwoods (Zobel and Jett 1995).

This paper presents results from a provenance/progeny test of *C. spruceanum* in the Peruvian Amazon Basin. The objectives of this study were to (a) determine the relative magnitude of variation in tree growth and wood basic density at an early age that is due to provenances and families, (b) evaluate the heritability of these traits, and phenotypic and genetic correlations between these traits in different planting zones. Tree growth was measured at 16, 28 and 39 months, while wood density was measured at 39 months. The major results are compared with other tropical hardwoods, and some practical implications are discussed.

2.4 Materials and methods

2.4.1 Sample region and study area

The sample region is located in the Aguaytía watershed of the Peruvian Amazon (Figure 2.1). Large natural stands of *C. spruceanum* occur along the rivers in the lower, middle and upper parts of the watershed, and on upland soils in the upper part of the watershed; whereas smaller stands occur on upland soils in the lower and middle parts of the watershed. Trees are also scattered throughout most of the watershed, so it is assumed that the stands are not genetically isolated and are subpopulations of the same genetic population. Moreover, it is assumed that some inbreeding has occurred and continues to occur in these subpopulations.

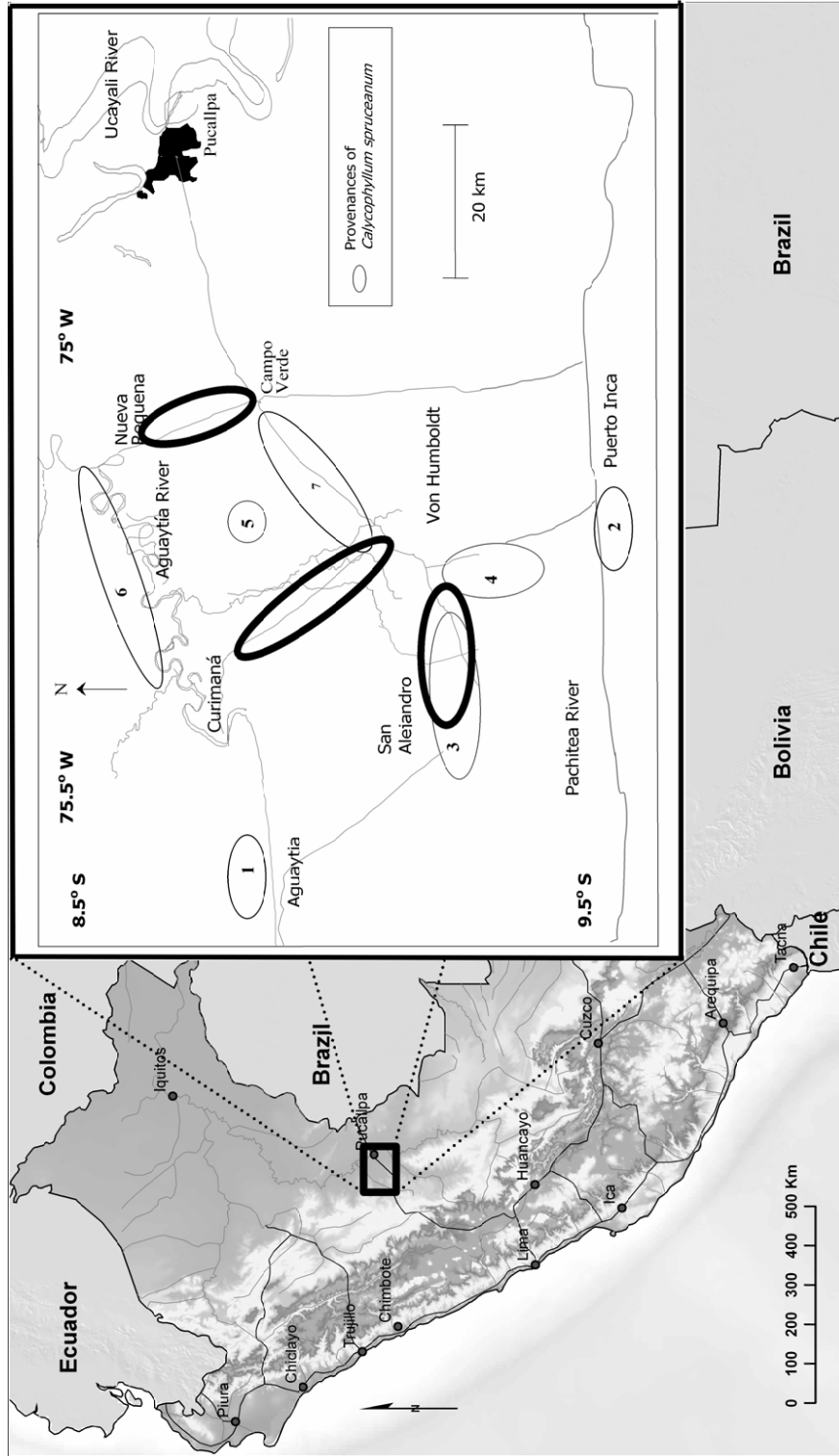


Figure 2.1. Geographic location of the sample region and study area in the Aguaytía watershed of the Peruvian Amazon: inset shows the location of the seven proveniences of *Calycophyllum spruceanum* and the three planting zones (bold circles).

Open-pollinated seeds were collected in September-October 1998 from 200 mother trees of *C. spruceanum* growing in seven natural stands located in the lower, middle and upper parts of the Aguaytía watershed (Figure 2.1). The stands are referred to hereafter as provenances, using this term in the broad sense as the source of seed (Morgenstern 1996). Farmers selected the trees that had good bole form and no external diseases. To reduce the chance of sampling siblings, at least 100 m was maintained between any two selected trees. Selection intensity was only about 20%, so there is probably little difference between the selected trees and the entire population in each provenance. The number of selected trees (13, 20, 47, 47, 10, 47 and 16 for provenance codes 1 to 7, respectively) was roughly proportional to the total number in each provenance.

The provenance/progeny test was established in the lower, middle and upper parts of the Aguaytía watershed (hereafter called planting zones), but restricted to upland, non-alluvial soils (Figure 2.1). In this region, June through September is a dry season, which is most severe in the lower zone and least severe in the upper zone. General information about rainfall and soils of the study area is given in Table 2.1.

2.4.2 Experimental design and management of the provenance/progeny test

Seedlings of the 200 families were grown in a nursery for 15 months and then transplanted into the experimental sites in February 2000. The experimental design was a randomized complete block (RCB): five replications were established on different farms in each of the lower, middle and upper zones of the watershed. In each replication, the 200 families were randomly assigned to 200 experimental plots. Experimental plots consisted of two trees of the same family. Spacing was 2.5 by 2.5 meters within and between rows. Two rows of border trees surrounded the experimental design on each site. Dead trees were replaced during the first dry season, but data collected on replants were not included in the analyses.

Table 2.1. Site details for the provenance/progeny test of *Calycophyllum spruceanum* established in the lower, middle and upper zones of the Aguaytia watershed in the Peruvian Amazon.^{a, b}

| Location in watershed | Altitude (masl) | Rainfall (mm / yr) | Soil texture, acidity and available cations (Ultisols) |
|-----------------------|-----------------|--------------------|---|
| Lower zone | 150 | 1400 | <ul style="list-style-type: none"> • Sandy • Very acidic (pH 4 to 4.5, 20 to 50% aluminum saturation) • Low levels of available phosphorous, and intermediate levels of potassium, calcium and magnesium |
| Middle zone | 180 | 1750 | <ul style="list-style-type: none"> • Heavy with clay • Very acidic (pH 4 to 4.5, 20 to 50% aluminum saturation) • Low levels of available phosphorous, and intermediate levels of potassium, calcium and magnesium |
| Upper zone | 240 | 2500 | <ul style="list-style-type: none"> • Light with organic matter • Slightly acidic (pH 6 to 6.5) • High levels of available phosphorous, potassium, calcium and magnesium |

^a Rainfall data collected by the Instituto Nacional de Investigación Agraria (INIA), Pucallpa, Peru.

^b Altitude and soil data collected by the World Agroforestry Centre (ICRAF), Pucallpa, Peru.

Management practices included establishment of a cover crop, application of fertilizer, branch pruning, manual weeding and a selective thinning. *Centrosema macrocarpum* Benth., a leguminous herb, was sown between rows and 5 m around the perimeter of each replication to control soil erosion, moderate soil surface temperature, improve soil fertility, reduce weed invasion, and provide farmers with a cash crop (seed for pastures). Organic compost (1 kg) and rock phosphate (200 g) were placed in each planting hole, and inorganic nitrogen, phosphorous and potassium (70 g N, 185 g P, and 100 g K) were applied around each tree 22 and 34 months after planting. Branches were pruned from the lower half of the stem 18 months after planting. One tree in each experimental plot was thinned 39 months after planting. This was a selective thinning mainly based on tree form (primarily stem bifurcations in the canopy) and growth. Farmers weeded their replications approximately every 4 weeks during the rainy season, and every 6-8 weeks during the dry season. They could do this in 2–

3 days when they had available time and labor, but it took much longer during periods of peak demand on their time and labor pool. As a result, weeding was not systematically done.

The provenance/progeny test had both research and development objectives (Weber et al. 2001), and this required some compromises in the experimental design. Farmers wanted to evaluate all 200 families in their replications, in order to select the best families and transform their replications into seed orchards. The RCB design was selected in response to this development objective. An incomplete block design with fewer families per replication would have been more efficient experimentally (Steel et al. 1997), but it would not have satisfied the farmers' objective. The relatively large replication size (around 0.3 ha) combined with farmers' weeding practices (Sotelo Montes et al. 2003) could have affected the differences among families within replications as well as the stability of families across replications.

2.4.3 Traits measured in the provenance/progeny test

Tree height and stem diameter (10 cm above ground) were measured on both trees in each experimental plot in all 15 replications at 16, 28 and 39 months. Height was measured to the nearest cm using a meter stick or telescopic measuring pole. Diameter was measured to the nearest 0.1 cm using callipers or diameter tape.

Stem diameter at breast height (Dbh) and basic density of the wood (1.3 m above ground) were measured on the thinned trees in nine replications (three in each planting zone) at 39 months. The other six replications (two in each planting zone) were excluded because mean diameter of the trees was too small to provide enough samples for analysis of wood density. Moreover, wood density was not analyzed for all trees in the nine replications due to the small Dbh of many trees, especially in the lower zone, as well as tree mortality. Dbh was measured to the nearest 0.1 cm. For wood density, one disk (10 cm thick) was taken from each tree, and stored at 4°C for 4 months. A 2-cm thick disk was then cut from the larger disk, the bark was removed, and the disk was soaked in distilled water for 48 hours. Disks with large knots or any damage were excluded. Then basic density (oven-dry mass to green volume, kg/m³) was determined using the water-displacement method (ASTM 1997).

Although the thinned trees were not randomly selected from the two trees in each experimental plot, it is unlikely that this would affect the general conclusions about the relative magnitude of variation in wood density due to provenances and families within

provenances, and the correlations between growth and wood density. There are four reasons to support this assumption. (1) Wood density was not used as a selection criterion in the thinning. (2) Means for height and diameter at 10 cm above ground (6.95 m and 9.24 cm, respectively) of the thinned trees were essentially the same as the means for all trees in the nine replications (6.83 m and 9.16 cm, respectively). Therefore, we would expect that the mean density of the thinned trees would be similar to that of all trees in the nine replications. The coefficients of variation were slightly lower for the thinned trees (36% versus 42%). (3) Analysis of variance of height and diameter of the thinned trees (using the model for analysis across zones presented in the next section) produced essentially the same results as the analysis of variance of all trees in the nine replications, and all trees in the test. This indicates that the thinned trees were a representative sample, in terms of height and diameter, of all trees in the test. (4) The frequency of trees with forks in the canopy was slightly higher among the thinned trees, compared with all trees in the nine replications (24% versus 19%). However, it is unlikely that this slight increase in the incidence of forks would produce any significant bias in wood density, in particular because wood was sampled from the stem below the canopy. The distance between the wood sampled at breast height and the start of the forks was not registered but it was at least 1 m for the smaller trees.

2.4.4 Statistical analyses

The SAS[®] statistical package, version 9.1 (SAS Institute Inc. 2002-2003), was used for all statistical analyses. Departure from the normal distribution and homogeneity of variance were tested for the residuals using statistics provided by the UNIVARIATE procedure. Data transformations were not considered necessary to satisfy the assumptions of analysis of variance and other analyses.

Analyses of variance were carried out using the GLM procedure with the Type III (partial sums of squares) estimation method to assess the relative magnitude of each source of variation. Analyses were performed across zones, and separately within each planting zone. The objective of the within-zone analyses was to determine if the relative magnitude of variation due to genetic factors was similar in planting zones with different environmental conditions. Variation in height and diameter (10 cm above ground) was assessed at each age (16, 28 and 39 months), while variation in Dbh and basic density were assessed at 39 months only. Variance of height and diameter across zones was analyzed according to a mixed linear model with the following sources of variation: zone, replication within zone [Rep(Zone)],

provenance (Prov), family within provenance [Fam(Prov)], and the interactions [Prov*Zone, Prov*Rep(Zone), Fam(Prov)*Zone, Fam(Prov)*Rep(Zone)]. Variance of Dbh and basic density across zones were analyzed with a similar model, but the interaction between family and replication did not appear in the model because only one tree per plot was assessed. Models for the analyses within zones were similar to those used across zones, except that there was no source of variation due to zone and, therefore, no interactions with zones. Zone was fixed and all other factors were random. Some F-ratios involved more than one mean square in the denominator (“quasi” F-ratios), and were tested with approximate degrees of freedom.

Individual tree heritability (h_i^2) was estimated only for traits for which variation among families was found to be significant at $\alpha \leq 0.05$ in the appropriate analyses of variance. The additive genetic variance was estimated as $3\sigma_f^2$ because, despite the sampling strategy used, we expected partial inbreeding in the populations. The terms in the denominator of h_i^2 depended on the model for the analysis of variance: Fam(Prov), Fam(Prov)*Zone, Fam(Prov)*Rep(Zone) and residual variation for tree height and diameter (10 cm above ground) across zones; Fam(Prov), Fam(Prov)*Rep and residual variation for tree height and diameter within zones; Fam(Prov), Fam(Prov)*Zone and residual variation for Dbh and basic density across zones; Fam(Prov) and residual variation for Dbh and basic density within zones. Standard errors for h_i^2 were calculated using the formula provided by Becker (1984).

Phenotypic and genetic correlations were calculated between growth traits and wood density across zones and within each zone. Correlations were assessed within zones to determine whether they were stable in different environmental conditions. Phenotypic correlations, i.e. Pearson correlation coefficients, were based on values for individual trees and were estimated using the CORR procedure. Genetic correlations were estimated only among traits for which variation among families was found to be significant at $\alpha \leq 0.05$. In order to eliminate the effect of different measurement scales when estimating genetic correlations, trait values were standardized (mean = 0, standard deviation = 1; Steel et al. 1997) for calculations across zones and within each zone. Variance components were estimated using the VARCOMP procedure with the restricted maximum likelihood method. Covariance components for variables x and y were obtained by solving the equation $\sigma_{fxy}^2 = (\sigma_{f(x+y)}^2 - \sigma_{fx}^2 - \sigma_{fy}^2)/2$. Approximate standard errors of genetic correlations were calculated using the formula provided by Falconer and Mackay (1996).

2.5 Results

Judging from the coefficients of variation (CV), there was considerable variation in growth among all trees in the test, and relatively more variation in Dbh than in basic density of the wood (Table 2.2). Moreover, there was relatively more variation in tree growth in the lower and middle zones than in the upper zone of the watershed. For example, CVs for tree height at 39 months were approximately 42%, 36% and 22% in the lower, middle and upper zones. CVs were inversely related to mean growth in the zones.

The minimum mean density was observed in the zone of slowest tree growth whereas the highest value was in the zone of intermediate growth (lower and middle zones, respectively). The difference between these zones was 8% of the overall mean.

Overall tree mortality was 16.7% at 39 months. It varied by about 6% among planting zones and provenances, and 40% among families. It was fairly evenly distributed across plots in each replication, so inter-tree competition was similar among plots. Mortality was not analyzed as a trait, but it must be considered when the best performing families are selected and the replications are transformed into seed orchards. Pearson correlations indicated that faster growing families tended to have lower mortality than slower growing families: the proportion of mortality within families was negatively correlated with mean height and diameter (10 cm above ground) of the families ($r = -0.211$ and -0.266 , respectively, $P < 0.001$, $N = 200$, proportions transformed as $\arcsin(\text{square root}[\text{proportion}])$).

2.5.1 Variation in tree height and stem diameter (10 cm above ground) at 16, 28 and 39 months

Differences in height and diameter among zones and variation due to replications within zones were significant at all ages in the analysis of variance across zones (Table 2.3). Variation due to provenances and families within provenances was also significant at all ages. Families accounted for slightly more variation than provenances but together accounted for only 7 to 11% of the total phenotypic variance (VAR). Judging from the interactions, the relative differences in mean height and diameter among provenances and families were relatively stable across zones. Similarly, provenance means were relatively stable across replications within zones, but significant variation was created by the interaction between families and replications within zones.

Table 2.2. Descriptive statistics of tree height and stem diameter (10 cm above ground) at 16, 28 and 39 months; and stem diameter at breast height (Dbh) and wood basic density at 39 months for *Calycophyllum spruceanum*. Statistics are given for all trees across zones, and separately for trees in the lower, middle and upper zones of the watershed.^{a, b}

| Trait | Across zones | | | Lower zone | | | Middle zone | | | Upper zone | | |
|--|--------------|------|-------|------------|------|-------|-------------|------|-------|------------|------|-------|
| | Mean | CV | Range | Mean | CV | Range | Mean | CV | Range | Mean | CV | Range |
| Height (m) | | | | | | | | | | | | |
| 16 months | 3.10 | 38.9 | 6.60 | 2.21 | 38.0 | 4.81 | 3.74 | 35.5 | 6.60 | 3.71 | 24.6 | 6.07 |
| 28 months | 4.85 | 46.2 | 10.52 | 2.78 | 42.9 | 6.15 | 5.20 | 36.8 | 9.27 | 6.68 | 22.2 | 10.23 |
| 39 months | 6.23 | 47.3 | 12.25 | 3.29 | 42.5 | 7.30 | 6.69 | 36.3 | 11.77 | 8.64 | 21.6 | 11.34 |
| Diameter (cm) – 10 cm above ground | | | | | | | | | | | | |
| 16 months | 4.89 | 36.1 | 9.60 | 3.67 | 35.9 | 8.65 | 5.37 | 33.1 | 9.35 | 5.75 | 24.6 | 9.15 |
| 28 months | 6.97 | 44.0 | 14.20 | 4.12 | 39.5 | 9.80 | 7.49 | 33.9 | 12.90 | 9.43 | 22.5 | 13.60 |
| 39 months | 8.43 | 44.8 | 18.60 | 4.84 | 41.6 | 11.50 | 8.97 | 34.1 | 18.10 | 11.37 | 23.6 | 17.30 |
| Dbh (cm) – 39 months | 6.08 | 40.8 | 10.50 | 3.29 | 33.9 | 5.00 | 6.40 | 30.4 | 9.30 | 7.66 | 25.5 | 10.36 |
| Basic density (kg/m ³) – 39 months | 581.5 | 8.0 | 306.0 | 552.7 | 7.4 | 270.0 | 599.6 | 7.1 | 241.0 | 585.1 | 7.5 | 285.0 |

^aCV = coefficient of variation (%).

^bNumber of trees. Across zones: height and diameter = 5360, 5278 and 4999 at 16, 28 and 39 months, respectively; Dbh = 1263; density = 1231. Lower zone: height and diameter = 1902, 1824 and 1664 at 16, 28 and 39 months, respectively; Dbh = 328; density = 326. Middle zone: height and diameter = 1700, 1695 and 1606 at 16, 28 and 39 months, respectively; Dbh = 436; density = 422. Upper zone: height and diameter = 1758, 1759 and 1729 at 16, 28 and 39 months, respectively; Dbh = 499; density = 483.

Table 2.3. Analysis of variance of tree height and stem diameter (10 cm above ground) at 16, 28 and 39 months for *Calycophyllum spruceanum*. Analyses are given for all trees across zones, and separately for trees in the lower, middle and upper zones of the watershed.^{a, b}

| Source of variation | | Height | | | | | | | | | Diameter | | | | | | | | |
|---------------------|------|-----------|------|--------|-----------|--------|------|-----------|------|--------|-----------|--------|------|-----------|------|--------|-----------|-----|--|
| | | 16 months | | | 28 months | | | 39 months | | | 16 months | | | 28 months | | | 39 months | | |
| | | DF | P>F | VAR | P>F | VAR | P>F | VAR | P>F | VAR | P>F | VAR | P>F | VAR | P>F | VAR | P>F | VAR | |
| Zone | 2 | 0.010 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | 0.014 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | | |
| Rep(Zone) | 12 | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | | |
| Prov | 6 | <0.001 | 3.1 | <0.001 | 2.9 | <0.001 | 2.2 | <0.001 | 2.2 | <0.001 | 1.9 | <0.001 | 2.6 | <0.001 | 2.6 | <0.001 | 2.3 | | |
| Fam(Prov) | 193 | <0.001 | 7.7 | <0.001 | 8.1 | <0.001 | 8.2 | <0.001 | 8.2 | <0.001 | 4.9 | <0.001 | 6.8 | <0.001 | 6.8 | <0.001 | 6.6 | | |
| Prov*Zone | 12 | 0.299 | 0.1 | 0.222 | 0.3 | 0.188 | 0.4 | 0.188 | 0.4 | 0.981 | 0.0 | 0.220 | 0.2 | 0.319 | 0.1 | 0.319 | 0.1 | | |
| Prov*Rep(Zone) | 72 | 0.424 | 0.0 | 0.187 | 0.0 | 0.336 | 0.0 | 0.336 | 0.0 | 0.134 | 0.1 | 0.179 | 0.1 | 0.399 | 0.0 | 0.399 | 0.0 | | |
| Fam(Prov)*Zone | 386 | 0.189 | 0.9 | 0.094 | 1.1 | 0.394 | 0.3 | 0.394 | 0.3 | 0.127 | 0.7 | 0.232 | 0.4 | 0.121 | 1.2 | 0.121 | 1.2 | | |
| Fam(Prov)*Rep(Zone) | 2245 | <0.001 | 32.2 | <0.001 | 34.1 | <0.001 | 30.5 | <0.001 | 30.5 | <0.001 | 32.3 | <0.001 | 25.2 | <0.001 | 24.0 | <0.001 | 24.0 | | |
| Residual | 2431 | --- | 56.0 | --- | 53.5 | --- | 58.4 | --- | 58.4 | --- | 60.1 | --- | 64.7 | --- | 65.8 | --- | 65.8 | | |
| Total | 5359 | | | | | | | | | | | | | | | | | | |

| Source of variation | | Height | | | | | | | | | Diameter | | | | | | | | |
|---------------------|------|-----------|------|--------|-----------|--------|------|-----------|------|--------|-----------|--------|------|-----------|------|--------|-----------|-----|--|
| | | 16 months | | | 28 months | | | 39 months | | | 16 months | | | 28 months | | | 39 months | | |
| | | DF | P>F | VAR | P>F | VAR | P>F | VAR | P>F | VAR | P>F | VAR | P>F | VAR | P>F | VAR | P>F | VAR | |
| Rep | 4 | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | | |
| Prov | 6 | 0.003 | 2.8 | 0.011 | 2.6 | 0.014 | 2.3 | 0.014 | 2.3 | 0.060 | 1.3 | 0.034 | 1.6 | 0.030 | 1.8 | 0.030 | 1.8 | | |
| Fam(Prov) | 193 | 0.039 | 3.4 | 0.019 | 3.7 | 0.214 | 1.7 | 0.214 | 1.7 | 0.034 | 3.4 | 0.020 | 3.9 | 0.072 | 3.1 | 0.072 | 3.1 | | |
| Prov*Rep | 24 | 0.115 | 0.7 | 0.024 | 1.7 | 0.062 | 1.8 | 0.062 | 1.8 | 0.016 | 1.8 | 0.012 | 2.0 | 0.029 | 2.1 | 0.029 | 2.1 | | |
| Fam(Prov)*Rep | 766 | <0.001 | 46.6 | <0.001 | 46.7 | <0.001 | 46.0 | <0.001 | 46.0 | <0.001 | 44.4 | <0.001 | 45.8 | <0.001 | 46.1 | <0.001 | 46.1 | | |
| Residual | 908 | --- | 46.5 | --- | 45.3 | --- | 48.2 | --- | 48.2 | --- | 49.1 | --- | 46.7 | --- | 46.9 | --- | 46.9 | | |
| Total | 1901 | | | | | | | | | | | | | | | | | | |

C. Middle zone

| Source of variation | Height | | | | | | Diameter | | | | | | |
|---------------------|-----------|--------|-----------|--------|-----------|--------|-----------|--------|-----------|--------|-----------|--------|------|
| | 16 months | | 28 months | | 39 months | | 16 months | | 28 months | | 39 months | | |
| | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | |
| Rep | 4 | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- |
| Prov | 6 | <0.001 | 4.5 | <0.001 | 4.0 | 0.001 | 3.4 | 0.002 | 2.4 | <0.001 | 3.7 | <0.001 | 3.1 |
| Fam(Prov) | 193 | <0.001 | 9.0 | <0.001 | 9.9 | <0.001 | 10.0 | <0.001 | 5.3 | <0.001 | 6.9 | <0.001 | 7.7 |
| Prov*Rep | 24 | 0.537 | 0.0 | 0.479 | 0.0 | 0.620 | 0.0 | 0.476 | 0.2 | 0.349 | 0.2 | 0.520 | 0.0 |
| Fam(Prov)*Rep | 736 | <0.001 | 28.7 | <0.001 | 30.1 | <0.001 | 31.3 | <0.001 | 29.9 | <0.001 | 25.4 | <0.001 | 25.7 |
| Residual | 736 | --- | 57.8 | --- | 56.0 | --- | 55.3 | --- | 62.2 | --- | 63.8 | --- | 63.5 |
| Total | 1699 | | | | | | | | | | | | |

D. Upper zone

| Source of variation | Height | | | | | | Diameter | | | | | | |
|---------------------|-----------|--------|-----------|--------|-----------|--------|-----------|--------|-----------|--------|-----------|--------|------|
| | 16 months | | 28 months | | 39 months | | 16 months | | 28 months | | 39 months | | |
| | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | |
| Rep | 4 | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- | <0.001 | --- |
| Prov | 6 | 0.001 | 2.4 | 0.001 | 2.6 | 0.005 | 1.9 | 0.020 | 1.3 | <0.001 | 2.8 | <0.001 | 2.2 |
| Fam(Prov) | 193 | <0.001 | 11.9 | <0.001 | 11.5 | <0.001 | 9.9 | <0.001 | 8.5 | <0.001 | 9.2 | <0.001 | 9.7 |
| Prov*Rep | 24 | 0.775 | 0.0 | 0.518 | 0.0 | 0.448 | 0.0 | 0.657 | 0.0 | 0.722 | 0.0 | 0.782 | 0.0 |
| Fam(Prov)*Rep | 743 | <0.001 | 22.5 | <0.001 | 29.3 | <0.001 | 22.2 | <0.001 | 21.0 | <0.001 | 12.4 | <0.001 | 11.2 |
| Residual | 787 | --- | 63.2 | --- | 56.6 | --- | 66.0 | --- | 69.2 | --- | 75.6 | --- | 76.9 |
| Total | 1757 | | | | | | | | | | | | |

^a DF = degrees of freedom. P > F = significance of F ratio. VAR = percentage of the total phenotypic variance explained by the variance component.

^b Due to mortality, DF decreases over time. At 39 months, DF is 2151 for Fam(Prov)*Rep(Zone) and 2164 for Residual in analysis across zones; 705 for Fam(Prov)*Rep and 731 for Residual in the lower, 712 for Fam(Prov)*Rep and 666 for Residual in the middle, and 734 for Fam(Prov)*Rep and 767 for Residual in the upper zone of the watershed.

Analyses of variance within zones generally led to the same conclusions as the analyses across zones. There was significant variation in height and diameter due to replications, provenances and families (except at 39 months in the lower zone), and the interaction between replications and families; whereas variation due to the interaction between replications and provenances generally was not significant. VAR due to provenances was very low in all zones, and VAR due to families was highest in the upper zone.

2.5.2 Variation in Dbh and basic density of wood at 39 months

There were significant differences in Dbh, but not in wood density, among planting zones (Table 2.4). However, variation due to replications within zones, provenances and families within provenances was significant for both Dbh and density in the analysis across zones. Families accounted for a larger percentage of the total phenotypic variance (VAR) than provenances, and families accounted for a larger percentage in density than in Dbh. Differences in density among provenances were relatively stable across zones, judging from the non-significant interaction between provenance and zone. However, the variation due to the interaction between provenances and zones was significant for Dbh.

Analyses within zones gave some contrasting results regarding variation due to provenances and families. Variation due to provenances and families within provenances was significant for density in all three zones. Variation due to provenances was also significant for Dbh in all three zones, but variation due to families within provenances was significant only in the upper zone.

2.5.3 Estimates of individual tree heritability (h_i^2) and correlations between tree growth and basic density of wood

Some trends were observed in the h_i^2 of tree height and stem diameter (10 cm above ground) (Table 2.5). Height generally had higher h_i^2 than diameter at all ages. The h_i^2 of both height and diameter were usually highest in the upper zone and lowest in the lower zone. In the analysis across zones, h_i^2 of both height and diameter increased slightly from 16 to 28 months and then leveled off. Time trends were not consistent, however, in the three zones.

Wood density had higher h_i^2 than Dbh at 39 months. The h_i^2 was higher in the middle and upper zones than in the lower zone, but the difference was not statistically significant based on the standards errors.

Table 2.4. Analysis of variance of stem diameter at breast height (Dbh) and wood basic density at 39 months for *Calycophyllum spruceanum*. Analyses are given for all trees across zones, and separately for trees in the lower, middle and upper zones of the watershed.^a

A. Across zones

| Source of variation | Dbh | | | Density | | |
|---------------------|------|--------|------|---------|--------|------|
| | DF | P>F | VAR | DF | P>F | VAR |
| Zone | 2 | 0.002 | --- | 2 | 0.067 | --- |
| Rep(Zone) | 6 | <0.001 | --- | 6 | <0.001 | --- |
| Prov | 6 | 0.002 | 3.6 | 6 | <0.001 | 6.0 |
| Fam(Prov) | 193 | <0.001 | 10.0 | 193 | <0.001 | 17.7 |
| Prov*Zone | 12 | 0.017 | 0.2 | 12 | 0.945 | 0.0 |
| Prov*Rep(Zone) | 36 | 0.997 | 0.0 | 36 | 0.601 | 0.0 |
| Fam(Prov)*Zone | 355 | 0.985 | 0.0 | 353 | 0.314 | 1.2 |
| Residual | 652 | --- | 86.2 | 622 | --- | 81.1 |
| Total | 1262 | | | 1230 | | |

B. Lower zone

| Source of variation | Dbh | | | Density | | |
|---------------------|-----|--------|------|---------|-------|------|
| | DF | P>F | VAR | DF | P>F | VAR |
| Rep | 2 | <0.001 | --- | 2 | 0.002 | --- |
| Prov | 6 | 0.002 | 4.5 | 6 | 0.027 | 5.3 |
| Fam(Prov) | 170 | 0.346 | 6.1 | 169 | 0.024 | 15.1 |
| Prov*Rep | 12 | 0.994 | 0.0 | 12 | 0.637 | 0.0 |
| Residual | 137 | --- | 89.4 | 136 | --- | 79.6 |
| Total | 327 | | | 325 | | |

C. Middle zone

| Source of variation | Dbh | | | Density | | |
|---------------------|-----|--------|------|---------|--------|------|
| | DF | P>F | VAR | DF | P>F | VAR |
| Rep | 2 | <0.001 | --- | 2 | <0.001 | --- |
| Prov | 6 | 0.028 | 3.7 | 6 | 0.009 | 5.5 |
| Fam(Prov) | 188 | 0.094 | 7.3 | 187 | <0.001 | 19.1 |
| Prov*Rep | 12 | 0.621 | 0.0 | 12 | 0.436 | 0.0 |
| Residual | 227 | --- | 89.0 | 214 | --- | 75.4 |
| Total | 435 | | | 421 | | |

D. Upper zone

| Source of variation | Dbh | | | Density | | |
|---------------------|-----|--------|------|---------|--------|------|
| | DF | P>F | VAR | DF | P>F | VAR |
| Rep | 2 | <0.001 | --- | 2 | <0.001 | --- |
| Prov | 6 | <0.001 | 4.7 | 6 | 0.003 | 5.3 |
| Fam(Prov) | 190 | 0.045 | 8.7 | 190 | <0.001 | 18.8 |
| Prov*Rep | 12 | 0.976 | 0.0 | 12 | 0.491 | 0.4 |
| Residual | 288 | --- | 86.6 | 272 | --- | 75.5 |
| Total | 498 | | | 482 | | |

^a DF = degrees of freedom. P > F = significance of F ratio. VAR = percentage of the total phenotypic variance explained by the variance component.

Table 2.5. Heritability of tree height and stem diameter (10 cm above ground) at 16, 28 and 39 months; and stem diameter at breast height (Dbh) and wood basic density at 39 months for *Calycophyllum spruceanum*. Heritability is given for all trees across zones, and separately for trees in the lower, middle and upper zones of the watershed. The standard error is given in parentheses, followed by the number of trees involved in the calculation.^a

| Trait | Across zones | Lower zone | Middle zone | Upper zone |
|--|---------------------|---------------------|---------------------|---------------------|
| Height (m) | | | | |
| 16 months | 0.24 (0.04) 5360 | 0.10 (0.06) 1902 | 0.28 (0.08) 1700 | 0.37 (0.09) 1758 |
| 28 months | 0.25 (0.05) 5278 | 0.11 (0.06) 1824 | 0.31 (0.08) 1695 | 0.35 (0.08) 1759 |
| 39 months | 0.25 (0.05) 4999 | NSF | 0.31 (0.09) 1606 | 0.30 (0.08) 1729 |
| Diameter (cm) 10 cm above ground | | | | |
| 16 months | 0.15 (0.03) 5360 | 0.11 (0.06) 1902 | 0.16 (0.07) 1700 | 0.26 (0.08) 1758 |
| 28 months | 0.21 (0.04) 5278 | 0.12 (0.06) 1824 | 0.22 (0.08) 1695 | 0.28 (0.08) 1759 |
| 39 months | 0.20 (0.04) 4999 | NSF | 0.24 (0.08) 1606 | 0.30 (0.08) 1729 |
| Dbh (cm) 39 months | 0.31 (0.10) 1263 | NSF | NSF | 0.27 (0.21) 499 |
| Basic density (kg/m ³) 39 months | 0.53 (0.12) 1231 | 0.48 (0.32) 326 | 0.61 (0.25) 422 | 0.60 (0.22) 483 |

^aNSF = Family within provenance was not significant ($P>0.05$) in analysis of variance, so heritability was not calculated.

The phenotypic (Pearson) and genetic correlations indicated that larger trees (i.e., trees with greater height and Dbh) tended to have denser wood (Table 2.6). The standard errors of genetic correlations were generally less than 33% of the estimated correlation.

Table 2.6. Pearson and genetic correlations among tree height, stem diameter at breast height (Dbh) and wood basic density at 39 months for *Calycophyllum spruceanum*. Correlations are given for all trees across zones, and separately for trees in the lower, middle and upper zones of the watershed. The significance (for Pearson r) or standard error (for genetic correlation) is given in parentheses, followed by the number of trees involved in the calculation.^a

| Trait | Across zones | | Lower zone | | Middle zone | | Upper zone | |
|---------|--------------------------|--------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|
| | Height | Dbh | Height | Dbh | Height | Dbh | Height | Dbh |
| Dbh | 0.93 (<0.001) 1254 | --- | 0.89 (<0.001) 326 | --- | 0.88 (<0.001) 432 | --- | 0.82 (<0.001) 496 | --- |
| Density | 0.53 (<0.001) 1222 | 0.51 (<0.001) 1231 | 0.39 (<0.001) 324 | 0.39 (<0.001) 326 | 0.56 (<0.001) 418 | 0.55 (<0.001) 422 | 0.40 (<0.001) 480 | 0.41 (<0.001) 483 |

| Trait | Across zones | | Lower zone | | Middle zone | | Upper zone | |
|---------|------------------------|------------------------|------------|-----|-----------------------|-----|-----------------------|-----------------------|
| | Height | Dbh | Height | Dbh | Height | Dbh | Height | Dbh |
| Dbh | 0.91 (0.04) 1222 | --- | NSF | --- | NSF | --- | 0.89 (0.09) 480 | --- |
| Density | 0.44 (0.15) 1222 | 0.46 (0.15) 1222 | NSF | NSF | 0.91 (0.07) 418 | NSF | 0.74 (0.13) 480 | 0.73 (0.17) 480 |

^a NSF = Family within provenance was not significant ($P > 0.05$) for one or both variables in analysis of variance, so genetic correlation was not calculated.

2.6 Discussion

2.6.1 Variation in tree growth

Mean growth of *Calycophyllum spruceanum* at 16 and 39 months was similar to values observed at 18 and 42 months in another test of this species conducted in the same watershed, but with a different set of provenances (Sotelo Montes et al. 2003; Weber and Sotelo Montes 2005). Also, its growth was similar to other tropical hardwoods of comparable age in plantations in Latin America [e.g. *Alnus acuminata* Kunth. in Costa Rica (Cornelius et al. 1996); *Carapa guianensis* Aubl. (Bauch and Dünisch 2000) in Brazil; *Sterculia apetala* (Jacq.) Karst in Colombia (Dvorak et al. 1998)].

Results confirm that there is a potential to increase plantation yield by selecting fast-growing families and provenances of *C. spruceanum* at an early age. Provenances and especially families within provenances accounted for significant variation in tree height and stem diameter (10 cm above ground) at 16, 28 and 39 months, and in diameter at breast height (Dbh) at 39 months in the analysis across planting zones. Moreover, provenance means for height and diameter (but not Dbh), and family means for height, diameter and Dbh were relatively stable across zones. Significant variation in tree growth due to provenances and/or families has also been detected at early ages in several tropical hardwoods tested in Latin America [e.g., *Alnus acuminata* Kunth. (Cornelius et al. 1996); *Bombacopsis quinata* (Jacq.) Dugand (Hodge et al. 2002); *Gmelina arborea* Roxb. (Osorio 2004); *Grevillea robusta* Cunn. (Shimizu et al. 2002); *Guazuma crinita* Mart. (Rochon 2004); *Vochysia guatemalensis* Sm., J.D. (Cornelius and Mesén 1997)].

These results are noteworthy because the provenances/families were sampled from a small region in one watershed; replication size was relatively large, which probably increased the environmental variation within the replications; and farmers' erratic weeding practices produced considerable variation within and among replications. The latter two factors would tend to increase the residual variation and the family by replication interaction, making it more difficult to detect statistically significant variation due to families. The large residual variation is probably the major reason why variation due to families was not significant for diameter (at 10 cm above ground) and Dbh in all planting zones. In addition, estimates for mean Dbh of families and most provenances were based on small sample sizes, especially

within zones. This produced large standard errors, which also made it more difficult to detect statistically significant variation due to provenances and families.

Planting zones generally produced larger differences in tree growth, compared with families and provenances. For example, the range in mean height, diameter (10 cm above ground) and Dbh, respectively, at 39 months was 5.35 m, 6.53 cm and 4.37 cm among planting zones; 4.09 m, 5.23 cm and 6.30 cm among families; and only 0.70 m, 1.08 cm and 0.69 cm among provenances. Therefore, the greatest gains in plantation yield can be realized first by selecting the best planting zone, and then selecting the fastest growing and best adapted families for that zone. Although provenances did not account for much variation, additional gain could be achieved by selecting the best provenances.

The coefficients of variation indicated that there was relatively more variation in growth among trees in the planting zones with lower rainfall and less fertile soils (lower and middle zones) than in the zone with the highest rainfall and most fertile soils (upper zone). This could reflect two interacting factors (Weber and Sotelo Montes 2005). First, farmers' erratic weeding practices undoubtedly produced considerable spatial and temporal variation in soil moisture, temperature and fertility within the replications. One would expect this micro-environmental variation to produce greater differences in growth among neighboring trees in a zone of low rainfall and infertile soils than in a zone of high rainfall and fertile soils. Second, if there is phenotypic variation in drought-tolerance mechanisms such as leaf abscission, one would expect greater variation to be expressed among trees planted in the drier planting zones. In the upper zone, partial leaf abscission in the upper canopy was rarely observed among trees in the replications during the dry season. But in the lower and middle zones, neighboring trees within the replications varied from partial to complete leaf abscission during the dry season. Since leaf abscission reduces the photosynthetic surface, variation in leaf abscission among neighboring trees could produce substantial variation in growth rates (e.g., Dvorak et al. 1998).

2.6.2 Variation in basic density of juvenile wood

Mean basic density of *C. spruceanum* wood at 39 months (581 kg/m^3 , measured at 1.3 m above ground) was slightly higher than the value at 32 months observed in another test of this species (563 kg/m^3 , measured from 35 to 65 cm above ground; Weber and Sotelo Montes 2005). The coefficient of variation (8% among all trees) was slightly greater than the values

reported (around 5%) for other tropical hardwoods at 5-9 years of age in plantations (Miranda et al. 2001a; Raymond and Muneri 2001; Santos et al. 2004).

Like the growth traits, there was significant variation in basic density due to provenances and especially families within provenances, and means for both provenances and families were relatively stable across zones. As mentioned above for Dbh, this is noteworthy because means for families and most provenances were estimated from a small number of trees, especially within zones, and this resulted in large standard errors that made it difficult to detect statistically significant variation due to provenances and families. Families accounted for much more variation than did provenances: the range in mean density was 148 kg/m³ among families, but only 33 kg/m³ among provenances. Therefore, greater gains in density could be obtained by selecting the best families rather than the best provenances. Nevertheless, average wood density could also be improved by selecting the best provenances.

The significant variation observed in the present study is interesting considering that variation due to provenances was not significant for wood density in another test of *C. spruceanum* at 32 months (Weber and Sotelo Montes 2005). The lack of significance in the earlier study was probably due to the fact that provenances originated from a region closer to the equator and with relatively homogenous climatic conditions.

There has been little research on genetic variation in wood density at an early age in tropical hardwood plantations. Khasa et al. (1995) reported significant differences in density at 21 months among provenances of *Racosperma auriculiformis* Cunn. ex. Benth. and *R. mangium* Willd. that were sampled from a broad range of environments in Australia and tested in Zaire. Other reports of significant variation due to provenances and/or families are based on older trees [e.g., *Eucalyptus dunnii* Maiden at 6½ years (Arnold et al. 2004); *E. globulus* Labill. at 9 years (Miranda et al. 2001b); *E. grandis* (Hill ex Maiden) at 8 years (Santos et al. 2004); and *Sterculia apetala* (Jacq.) Karst at 10 years (Dvorak et al. 1998)].

In contrast to the growth traits, wood density did not differ significantly among the three planting zones in the present study. Weber and Sotelo Montes (2005) reported similar results for density in the lower stem in another provenance test of *C. spruceanum* established in the same planting zones. Apparently the environmental differences among zones were not large enough to produce a significant difference in density. Nevertheless, in the present study mean

density was lowest in the zone of slowest tree growth (lower zone) and the range in mean density among the zones was relatively large (47 kg/m³). Therefore the environmental conditions of different planting zones should be assessed before deciding to establish plantations in the zones.

2.6.3 Heritability of tree growth and basic density of juvenile wood

Estimates of individual tree heritability (h_i^2) for growth traits of *C. spruceanum* were within the range of values reported for other tropical hardwoods at an early age (e.g., Cornelius et al. 1996; Greaves et al. 1997; Shimizu et al. 2002). The estimated h_i^2 was slightly higher for tree height than stem diameter at 10 cm above ground: h_i^2 across zones, averaged over ages, was 0.25 for height and 0.19 for diameter (Table 2.5). A similar result was reported for other tropical hardwoods (Pinyopusarerk et al. 1996; Hodge et al. 2002).

In general, estimates of h_i^2 for both height and diameter suggest that selection of trees at 16 months would be about as efficient as selection at 28 or 39 months. For example, in the analysis across zones, h_i^2 for both height and diameter did not change significantly from 16 to 39 months. The h_i^2 for growth of *Sterculia apetala* (Jacq.) also did not change significantly from 3 to 8 years of age (Dvorak et al. 1998).

The h_i^2 for height and diameter were highest in the planting zone where growth rate was highest and lowest in the zone where growth rate was lowest (upper and lower zones, respectively). This is consistent with Campbell and Sorensen's (1978) hypothesis that the expression of genetic variation in growth traits will be lower in test environments where trees grow slowly compared with environments where trees grow more rapidly. Similar results were reported for *Eucalyptus* spp. (MacDonald et al. 1997; Ginwal et al. 2004).

As expected, wood density had a higher h_i^2 than diameter at breast height (Dbh) at 39 months. Standard errors were relatively large, especially within zones, due to the small number of trees per family. As far as we know, h_i^2 of wood density has not been assessed at a very early age in other tropical hardwoods, but these results are consistent with studies of tropical hardwoods evaluated at older ages (e.g., Wei and Borralho 1997; Raymond 2002; Arnold et al. 2004), and with many temperate zone tree species (Zobel and Jett 1995).

2.6.4 Phenotypic and genetic correlations between tree growth and basic density of juvenile wood

Phenotypic and genetic correlations may differ in magnitude and even in sign among test environments and populations of the same species (Falconer and Mackay 1996), and due to silvicultural manipulation (Zhang 1995). In general, the diffuse-porous hardwoods show little or no relationship between tree growth and wood density (Zobel and Jett 1995). Most studies have looked at the relationship between density and radial growth or ring width rather than the relationship with height growth (Zhang 1995).

The relationship between growth rate and wood density in the hardwoods is controversial. For example, among young trees of *Eucalyptus nitens* in Australia, phenotypic correlations between density and growth (tree height, stem diameter) were not significant, but the genetic correlation between density and stem diameter (but not tree height) was negative and significant (Greaves et al. 1997). For *Eucalyptus globulus* and *E. nitens*, the correlations were generally very small and the sign of the coefficient varied across sites, indicating no systematic relationships of density with tree size (Raymond and Muneri 2001).

In the present study, phenotypic correlations between tree growth and wood density at breast height were positive and relatively strong in all planting zones at 39 months. However, in another test of this species, carried out in the same watershed but with provenances from different watersheds (Weber and Sotelo Montes 2005), the phenotypic correlation between stem diameter and density in the lower stem varied in magnitude and sign among planting zones at 32 months. In that study, the variance/covariance structure among traits in the “foreign” seed sources was apparently strongly affected by the environmental differences among the planting zones. In other words, the genotypes did not respond in the same way to the environmental differences (Falconer and Mackay 1996). In the present study, genotypes of the “local” seed sources tended to respond in the same way to the environmental differences among planting zones. The difference in results appears to reflect the combined effects of different genetic material (“foreign” versus “local” seed sources) and their potential interactions with different environmental conditions, but this hypothesis needs to be tested.

Genetic correlations between tree growth and wood density were positive in the middle and upper zones. The genetic correlation was not calculated in the lower zone, where tree growth was slowest, because variation in tree growth due to families was not significant in the analysis of variance. This is consistent with Campbell and Sorensen’s (1978) hypothesis

mentioned earlier. Based on the genetic correlation, selection of faster growing trees should favor an increase in wood density in planting zones where trees grow relatively rapidly (like the middle and upper zones), and have little or no effect on density in zones where trees grow slowly (like the lower zone) for reasons explained in the following paragraph. However, estimates are needed from other tree populations and test environments in order to make a general conclusion about the genetic correlation between growth and density in this species. Standard errors were reasonably small, even though the genetic correlations were based on a small number of trees per family (especially for Dbh and wood density). Nevertheless, larger numbers of trees per family should be used in future studies.

Since there is a positive genetic correlation between wood density and tree growth of *C. spruceanum*, and density is considered as the most important predictor of wood properties (Panshin and de Zeeuw 1980), one would expect a correlation between tree growth and other wood properties in this species. Results from another study in the same provenance/progeny test at 39 months indicated that selecting faster-growing trees and/or trees with denser wood of *C. spruceanum* would have a positive effect on some mechanical properties (Sotelo Montes et al. 2006d, chapter 5).

A positive genetic correlation between tree growth and wood density at breast height could be explained in terms of the mechanical design of trees. Mosbrugger (1990) notes that the base of the tree has the highest bending stress and this stress can be reduced by increasing the strength of supporting tissue at the base of the tree. Strength could be increased by producing denser wood, which has a greater modulus of elasticity (Niklas 1997b). This hypothesis is consistent with results reported for other tropical, hardwood pioneer species (Wiemann and Williamson 1989a; Woodcock and Shier 2002).

Data are not available to estimate age-age correlations between tree growth and wood density in *C. spruceanum*. A study of age-age correlations that considers the rotation ages for construction poles (minimum of 2 to 3 years) and sawn timber (15 to 20 years) would be very useful. However, studies on other hardwood species indicate that early selection for density and tree growth should be possible (Dvorak et al. 1998; Hodge et al. 2002).

2.7 Conclusions

This study demonstrates that there is considerable genetic variation in tree growth and basic wood density of *C. spruceanum* at an early age. A greater proportion of this variation occurs within provenances rather than among provenances. The positive genetic correlation between growth and density offers the opportunity to select faster growing trees with denser wood, and this would be more effective in zones where trees grow relatively rapidly. Estimates of h_i^2 for the traits assessed in this study are similar to those reported for other tropical hardwoods. Based on estimates of h_i^2 and genetic correlations, we recommend that tree improvement programs should use both tree growth and wood density as selection criteria for this species at an early age. For example, tree breeders could first select the fastest growing and best adapted provenances based on Dbh, and then select the families that have the highest wood density within these provenances. If all provenances are equally adapted to the planting zone, then tree breeders could consider that all families are from the same population. In this case, they could select the best families based on both Dbh and wood density. Due to the lower performance in tree growth in the planting zone with low rainfall and infertile soils, plantations in similar environments should be avoided. Relationships between tree growth, wood density and other juvenile-wood properties should be investigated: these studies are underway for *C. spruceanum*, and will allow us to make some general recommendations about planting zones for different wood products of this species. In addition, research should be conducted on changes in genetic correlations between tree growth and wood properties over time, age-age correlations for growth and wood traits, and early-selection efficiency for this species.

Chapitre 3 Genetic variation in wood color and its correlations with tree growth and wood density of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon

3.1 Résumé

Calycophyllum spruceanum (Benth.) Hook. f. ex K. Shum. est une espèce importante croissant dans le bassin de l'amazone péruvienne. Actuellement, les marchés préfèrent le bois avec une couleur jaune uniforme, mais ces préférences peuvent changer dans le futur. Du fait que les agriculteurs et l'industrie utilisent du bois provenant des jeunes arbres, les programmes d'amélioration devraient se pencher sur la variation génétique des propriétés du bois juvénile, afin de faire des ajustements éventuels à des nouvelles préférences du marché. Un essai de provenance/descendance a été effectué afin d'évaluer la variation génétique, de la croissance et des propriétés du bois de jeunes arbres, la force de leur contrôle génétique, ainsi que leurs relations au niveau génétique et phénotypique, dans différentes zones de plantation. Cet article présente des résultats des analyses sur la variation des caractéristiques de la couleur du bois à l'âge de 39 mois et leur corrélation avec la croissance de l'arbre et la masse volumique basale du bois. Nous avons trouvé des variations génétiques significatives dues aux provenances et particulièrement dues aux familles à l'intérieur des provenances dans quelques caractéristiques de couleur. En outre, nous avons aussi trouvé des différences significatives pour quelques caractéristiques de couleur entre les zones de plantation. Les corrélations génétiques significatives indiquent qu'en général, la sélection d'arbres à croissance plus rapide et/ou des arbres avec du bois plus dense aurait peu d'effet sur la couleur du bois et son uniformité. En général, la couleur du bois a une héritabilité moins élevée, mais le contrôle génétique de la couleur était plus élevé dans les zones de plantation où les arbres croissaient plus rapidement. Nos résultats suggèrent que la sélection basée sur la couleur du bois serait plus effective dans les zones comportant un sol plus fertile et une plus grande pluviosité.

3.2 Abstract

Calycophyllum spruceanum (Benth.) Hook. f. ex K. Shum. is an important timber-tree species in the Peruvian Amazon Basin. Markets currently prefer wood with a uniform, light yellow color, but these preferences may change in the future. As farmers and industry commonly use wood from young trees, it is important to investigate genetic and environmental variation in juvenile-wood properties to assess whether tree improvement programs could make adjustments to changing preferences. A provenance/progeny test was established to evaluate genetic variation in growth and wood properties of young trees, the strength of their genetic control as well as their interrelationships both at the genetic and the phenotypic level in different planting zones. This paper presents analyses of variation in wood color characteristics at 39 months, and their correlations with tree growth and wood basic density. Significant variation due to provenances and especially due to families within provenances was found in some wood color characteristics, and some color characteristics also differed significantly among planting zones. Genetic correlations indicate that, in general, selection of faster growing trees and/or trees with denser wood would have little effect on wood color and its uniformity. In general, wood color had low heritability but genetic control of color was highest in the planting zone where trees grew most rapidly. Results suggest that selection based on wood color would be more effective in zones with more fertile soils and higher rainfall.

3.3 Introduction

The Peruvian Amazon has many valuable timber-tree species, but there has been little research on genetic variation of commercial traits in these species. Farmers rank *Calycophyllum spruceanum* (Bentham) Hooker f. ex Shumann (Rubiaceae family) as one of the best species for lumber, poles, firewood and charcoal in agroforestry systems (Sotelo Montes and Weber 1997). *C. spruceanum* is a pioneer species that colonizes the floodplain and disturbed forests in the Amazon of Peru, Brazil, Ecuador and Colombia (Linares et al. 1992). Trees can attain heights of 35 m with stem diameters of 1.8 m at breast height (Sears 2003). The wood is diffuse-porous, with a basic density at breast height (1.3 m above ground) of 740 kg/m³ for mature wood in natural stands (Keenan and Tejada 1984) and 563 kg/m³ in the lower stem (Weber and Sotelo

Montes 2005) at 32 months of age in plantations. Stems can be harvested for construction poles after 2 to 3 years, or sawn timber after 15 to 20 years, and then coppiced for successive harvests.

National and international markets currently prefer *C. spruceanum* wood with a uniform, yellow color for furniture, wall paneling and parquet floors (Toledo and Rincón 1996), but preferences may change in the future. Therefore, it is important for tree improvement programs to respond to the current market and also prepare for potential changes. Farmers and industry commonly use wood of young trees of this species, and they will probably use it even more in the future with the promotion of agroforestry and small-scale plantation forestry. Tree improvement programs, therefore, should initiate research on genetic variation in properties of juvenile wood to see whether it is possible to improve them through breeding work and to measure the impact of selection for one trait on other traits (Zobel and Sprague 1998).

Wood color is influenced by both genetic and environmental factors (Phelps et al. 1983; Janin 1987; Rink and Phelps 1989; Wilkins and Stamp 1990; Mosedale et al. 1996; Zobel and Sprague 1998; Gierlinger et al. 2004; Hannrup et al. 2004). In addition, site differences can affect wood color (Rink 1987; Wilkins and Stamp 1990; Klumpers et al. 1993), density and tree growth (Zobel and Jett 1995), so one might expect that wood color is to some extent correlated with wood density and tree growth, at least in some sites.

Heritability estimates are needed to assess the potential genetic gain that can be realized by selection. Genetic control of wood color has not been investigated in *C. spruceanum*, but observations suggest that it varies among trees and planting zones. If there is genetic variation in wood color then tree improvement programs may help to respond to potential changes in market preferences. In addition, estimates of genetic correlations are necessary to assess if selection based on tree growth and/or other commercially important traits would significantly affect wood color. Since heritabilities and genetic correlations depend on the specific test environment and population of trees (Falconer and Mackay 1996), they should be evaluated in contrasting environments and in different populations to better know the range of potential genetic gains.

A provenance/progeny test of *C. spruceanum* was established in the Peruvian Amazon Basin. Results from the test at 39 months demonstrate that (a) there is considerable genetic variation in

tree growth and juvenile wood density; (b) a greater proportion of this variation occurs among families within provenances rather than among provenances; (c) wood density is under stronger genetic control than tree growth; and (d) it is possible to select faster growing trees with denser wood (Sotelo Montes et al. 2006a, chapter 2).

This paper presents additional results from the provenance/progeny test at 39 months. The objectives were to (a) determine the relative magnitude of variation in wood color at an early age that is due to provenances and families within provenances, (b) evaluate phenotypic and genetic correlations between wood color and tree growth and wood density, and the heritability of wood color in two different planting zones. The major results are compared with other tropical hardwoods, and some practical implications are discussed.

3.4 Materials and methods

3.4.1 Sample region, study area, experimental design and management of the provenance/progeny test

The sample region is located in the Aguaytía watershed of the western Peruvian Amazon (Figure 2.1, chapter 2). Open-pollinated seeds were collected in September-October 1998 from 200 mother trees of *Calycophyllum spruceanum* growing in seven geographic locations (provenances) in the lower, middle and upper parts of the watershed. Farmers selected the trees primarily from those that had good bole form and no external diseases. To reduce the chance of sampling siblings, a distance of at least 100 m was maintained between any two selected trees. Selection intensity was only about 20%, so there is probably little difference between the selected trees and the entire population in each provenance. The number of selected trees was roughly proportional to the total number in the provenance (13, 20, 47, 47, 10, 47 and 16 for provenance codes 1 to 7, respectively).

The provenance/progeny test was established in the lower, middle and upper parts of the Aguaytía watershed, but restricted to upland, non-alluvial soils (Figure 2.1, chapter 2). Soil fertility and mean annual precipitation increase, in general, from the lower to the upper parts of the watershed. Details about climate and soils are given elsewhere (Sotelo Montes et al. 2006a, chapter 2).

Seedlings of the 200 families were grown in a nursery for 15 months and transplanted into the experimental sites in February 2000. The experimental design was a randomized complete block: five replications were established on different farms in each of the lower, middle and upper parts of the watershed (hereafter called planting zones). In each replication, the 200 families were randomly assigned to 200 experimental plots. Experimental plots consisted of two trees of the same family. Spacing was 2.5 by 2.5 meters within and between rows. Two rows of border trees surrounded the experimental design on each site. Dead trees were replaced during the first dry season, but data collected on replants were not included in the analyses.

Management practices included a cover crop, fertilizer application, branch pruning, manual weeding and a selective thinning. Details about the cover crop, pruning and weeding are given elsewhere (Sotelo Montes et al. 2006a, chapter 2). Organic compost (1 kg) and rock phosphate (200 g) were placed in each planting hole, and inorganic nitrogen, phosphorous and potassium (70 g N, 185 g P, and 100 g K) were applied around each tree 22 and 34 months after planting. One tree in each experimental plot was thinned 39 months after planting. This was a selective thinning mainly based on tree form (primarily stem bifurcations in the canopy) and growth.

3.4.2 Traits measured in the provenance/progeny test

Measurements were made on the thinned trees in six replications: three each in the middle and upper zones of the watershed at 39 months. The other nine replications (two each in the middle and upper zones, and five from the lower zone) were excluded because mean diameter of trees was too small to provide samples of sufficient size for analysis of wood color. Although the thinned trees were not randomly selected from the two trees in each experimental plot, it is unlikely that this would affect the general conclusions about the relative magnitude of variation in wood properties due to provenances and families within provenances, and the correlations between tree growth and wood properties. Three reasons support this assumption. (1) Wood properties (including color) were not used as selection criteria in the thinning. (2) Mean height of the thinned trees was only slightly lower than the mean height of all trees in the six replications (7.3 m and 7.8 m, respectively). (3) Wood samples were obtained from the lower stem, well below the stem bifurcations in the canopy.

Wood samples (approximately 2.5 x 2.5 x 45 cm) were collected in the south-facing quadrat of the stem, between pith and bark, from 0.75 to 1.2 m above the ground. Samples were stored under controlled conditions (60% relative humidity, 20°C) for approximately 6 months to attain equilibrium moisture content (mean = 12.2% ± 0.4%) before processing. Color was then measured using the CIELAB color system (BYK-Gardner 2004). Color was determined on the tangential surface of each sample, using a portable spectrophotometer (color-guide 20 mm with white standard; employing illuminant D₆₅, 10° CIE observer and the measurement geometry 45°/0° incidence/observer as conditions of measurement). The CIELAB color system estimates the value of three variables: L* = lightness ranging from black (0) to white (100), a* = green (-) to red (+) hues, and b* = blue (-) to yellow (+) hues. Measurements were taken at eight equidistant points along each wood sample: if a point fell on a branch trace, the measurement was taken as close as possible to the original point, but outside the branch trace on clear wood.

Seven variables describing mean color and variability in color were computed for each wood sample. Mean values for L*, a* and b* (Mean-L*, Mean-a*, Mean-b*) were calculated from the eight measurements. Variability in each of the three color variables (Var-L*, Var-a*, Var-b*) within each sample was estimated by computing the difference between each pair of values (i.e., 28 pairs for each variable), and summing the absolute values of the differences. A combined estimate of variability in wood color (DeltaE) was estimated in the following way. For each of the seven neighboring measurement points (i.e., point 1 with 2, 2 with 3, etc.), we calculated three squared differences (i.e., between L*, a* and b*), summed these squared differences, and then took the square root of this sum. The seven values were then summed to derive DeltaE values. Measures of variability in color were adapted from indices used in mathematical ecology (Pielou 1977).

Tree height was measured to the nearest cm using a meter stick or a telescopic measuring pole. Stem diameter at breast height (Dbh, 1.3 m above ground) was measured to the nearest 0.1 cm using callipers for small trees and diameter tape for larger trees. Basic density (oven-dry mass to green volume, kg/m³) of wood disks (2 cm thick, sampled at breast height) was determined using the water-displacement method (ASTM 1997).

3.4.3 Statistical analyses

The SAS[®] statistical package, version 8 (SAS Institute Inc. 2002-2003), was used for all statistical analyses. Departure from the normal distribution and homogeneity of variance was tested for the residuals using statistics provided by the UNIVARIATE procedure. Data transformations were not considered necessary to satisfy the assumptions of analysis of variance and other analyses.

Analyses of variance of wood color variables were carried out using the GLM procedure with the Type III (partial sums of squares) estimation method to assess the relative magnitude of each source of variation. Analyses were performed across zones, and separately within each planting zone. The objective of the within-zone analyses was to determine if the relative magnitude of variation due to genetic factors was similar in planting zones with different environmental conditions. Variance of each variable across zones was analyzed according to a mixed linear model with the following sources of variation: zone (Z), replication nested in zone [R(Z)], provenance (P), family nested in provenance [F(P)], and the interactions [P*Z, P*R(Z), F(P)*Z]. The model for the analysis within zones was similar to that used across zones, except that there was no source of variation due to zone and, therefore, no interactions with zones. Zone was fixed and all other factors were random. Some F-ratios involved more than one mean square in the denominator (“quasi” F-ratios), and were tested with approximate degrees of freedom using the RANDOM statement.

Phenotypic and genetic correlations were calculated between the wood color variables and tree height, Dbh and basic density of the wood. Correlations were assessed across zones, and also within zones to determine whether they were stable in different environmental conditions. Phenotypic correlations, i.e. Pearson correlation coefficients, were based on values for individual trees and were estimated using the CORR procedure. Genetic correlations were estimated only among traits for which variation among families was found to be significant at $\alpha \leq 0.05$. In order to eliminate the effect of different measurement scales when estimating genetic correlations, trait values were standardized (mean = 0, standard deviation = 1; Steel et al. 1997) for calculations across zones and within each zone. Variance components were estimated using the VARCOMP procedure with the restricted maximum likelihood method. Covariance components for variables

x and y were obtained by solving the equation $\sigma^2_{f_{xy}} = (\sigma^2_{f_{(x+y)}} - \sigma^2_{f_x} - \sigma^2_{f_y})/2$. Approximate standard errors of genetic correlations were calculated using the formula provided by Falconer and Mackay (1996).

Individual tree heritability (h_i^2) was estimated only for traits for which variation among families was found to be significant at $\alpha \leq 0.05$ in the appropriate analyses of variance. The additive genetic variance was estimated as $3\sigma^2_f$ because, despite the sampling strategy used, we expected partial inbreeding in the populations. Standard errors for h_i^2 were calculated using the formula provided by Becker (1984).

3.5 Results and discussion

Wood color of *Calycophyllum spruceanum* at 39 months was within the range reported for other tropical hardwoods with diffuse porous wood. In general, most species with lower density (400 – 550 kg/m³) tend to have lighter wood ($L^* > 54$) with a yellowish hue, while most with higher density (750 – 950 kg/m³) tend to have darker wood ($L^* < 54$) with a reddish hue (Rodríguez and Sibille 1996; Nishino et al. 1998; Janin et al. 2001; Kishino and Nakano 2004). In the present study, *C. spruceanum* wood at 39 months falls within the first category (Table 3.1: Mean- $L^* = 67.6$, Mean- $a^* = 5.3$, Mean- $b^* = 22.1$): the wood had relatively large means for L^* and b^* values, reflecting its light, yellow appearance; and basic density of 592 kg/m³ (not tabled). The variability in lightness (Var- L^*) was notably greater than the variability in the reddish and yellowish hues (Var- a^* and Var- b^* , respectively). As others have noted (Klumpers et al. 1993; Nishino et al. 1998), lightness tends to be a more important criterion than hue, in terms of variability within a species.

For purposes of comparison in the following sections, trees grew more rapidly in the upper than in the middle zone of the watershed. Mean tree height was 7.8 and 9.1 m in the middle and upper zones, respectively (Sotelo Montes et al. 2006a, chapter 2).

Table 3.1. Descriptive statistics of wood color for *Calycophyllum spruceanum* at 39 months. Statistics are given for all trees across zones, and separately for trees in the middle and upper zones of the watershed.^a

A. Across zones (N = 684)

| Trait | Mean | St. dev. | CV | Minimum | Maximum |
|---------------------------------------|-------|----------|------|---------|---------|
| Mean-L* = black (0) to white (100) | 67.63 | 2.68 | 4.0 | 57.88 | 77.24 |
| Mean-a* = green (-) to red (+) hues | 5.34 | 1.11 | 20.9 | 1.36 | 9.09 |
| Mean-b* = blue (-) to yellow (+) hues | 22.12 | 1.15 | 5.2 | 18.32 | 25.99 |
| Var-L* | 45.89 | 21.27 | 46.4 | 10.11 | 148.15 |
| Var-a* | 26.86 | 11.24 | 41.9 | 5.19 | 79.55 |
| Var-b* | 27.45 | 11.13 | 40.6 | 5.95 | 96.89 |
| DeltaE | 13.70 | 4.74 | 34.6 | 4.59 | 34.16 |

B. Middle zone (N = 287)

| Trait | Mean | St. dev. | CV | Minimum | Maximum |
|---------------------------------------|-------|----------|------|---------|---------|
| Mean-L* = black (0) to white (100) | 66.76 | 2.45 | 3.7 | 57.88 | 77.24 |
| Mean-a* = green (-) to red (+) hues | 5.82 | 1.07 | 18.3 | 2.50 | 9.09 |
| Mean-b* = blue (-) to yellow (+) hues | 21.85 | 1.04 | 4.8 | 18.32 | 24.76 |
| Var-L* | 44.49 | 22.52 | 50.6 | 10.11 | 148.15 |
| Var-a* | 26.24 | 11.16 | 42.5 | 8.25 | 79.55 |
| Var-b* | 27.04 | 10.83 | 40.1 | 7.76 | 75.98 |
| DeltaE | 13.53 | 5.03 | 37.2 | 5.20 | 34.16 |

C. Upper zone (N = 397)

| Trait | Mean | St. dev. | CV | Minimum | Maximum |
|---------------------------------------|-------|----------|------|---------|---------|
| Mean-L* = black (0) to white (100) | 68.26 | 2.66 | 3.9 | 59.21 | 76.70 |
| Mean-a* = green (-) to red (+) hues | 4.99 | 1.01 | 20.3 | 1.36 | 0.01 |
| Mean-b* = blue (-) to yellow (+) hues | 22.31 | 1.18 | 5.3 | 18.70 | 25.99 |
| Var-L* | 46.90 | 20.29 | 43.3 | 13.20 | 139.31 |
| Var-a* | 27.30 | 11.29 | 41.4 | 5.19 | 60.81 |
| Var-b* | 27.75 | 11.35 | 40.9 | 5.95 | 96.89 |
| DeltaE | 13.83 | 4.52 | 32.7 | 4.59 | 31.13 |

^a CV= coefficient of variation (%).

3.5.1 Environmental and genetic variation in juvenile-wood color

Soil chemical and physical properties may produce differences in wood color among sites (Wilkins and Stamp 1990) and within sites (Phelps et al. 1983). In the present study, there were significant differences only in the reddish hue (Mean-a*) due to planting zones (Table 3.2): the wood was slightly redder in the middle than in the upper zone of the watershed (Table 3.1). Since current markets prefer yellowish color of *C. spruceanum*, this suggests that zones where trees grow more rapidly (like the upper zone of the watershed) would be better for producing wood with the desired hue. However, lightness (Mean-L*) and the reddish (Mean-a*) and yellowish (Mean-b*) hues also varied significantly due to replications within zones (Table 3.2), presumably reflecting environmental differences in soil fertility, soil moisture, etc. among replications as well as differences produced by farmers' inconsistent weeding practices (Sotelo Montes et al. 2003). However, these effects are confounded with many other environmental and human factors, and cannot be separated. Rink (1987) also reported that the lightness of *Juglans nigra* L. wood differed significantly among replications.

To our knowledge, genetic variation in wood color has not been investigated for any tropical hardwood at an early age. In the present study, there was significant genetic variation in some wood color traits at 39 months (Table 3.2). Analysis of variance across zones showed the presence of significant variation in the yellowish hue (Mean-b*) due to provenances and in lightness (Mean-L*) due to families within provenances. Moreover, differences among provenances and families were relatively stable across zones, judging from their non-significant interactions with zones. There was relatively more variation among families within provenances than among provenances: for example, the ranges in Mean-L*, Mean-a* and Mean-b* were 9.7, 4.5 and 5.3, respectively among families, but only 0.8, 0.3 and 0.7, respectively among provenances. The variation among families is particularly interesting, because it indicates that families with lighter colored wood (preferred in current markets) can be identified at an early age for tree improvement programs and, if market preferences change in the future, there is an opportunity to identify families with darker wood.

Table 3.2. Analysis of variance of wood color for *Calycophyllum spruceanum* at 39 months. Analyses are given for all trees across zones, and separately for trees in the middle and upper zones of the watershed.^{a, b, c}

| Source of variation | Across zones ^d | | | | | | Middle zone ^e | | | | | | Upper zone ^f | | | | | | |
|---------------------|---------------------------|------|-------|---------|-------|------|--------------------------|-------|-------|---------|-------|-------|-------------------------|-------|-------|---------|-------|-------|-------|
| | Mean-L* | | | Mean-b* | | | Mean-L* | | | Mean-b* | | | Mean-L* | | | Mean-b* | | | |
| | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | |
| Z | 0.072 | --- | 0.026 | --- | 0.138 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| R(Z) | 0.031 | --- | 0.005 | --- | 0.029 | --- | R | 0.503 | --- | 0.037 | --- | --- | --- | 0.002 | --- | 0.015 | --- | --- | 0.091 |
| P | 0.822 | 0.0 | 0.384 | 0.6 | 0.020 | 2.1 | P | 0.823 | 0.0 | 0.606 | 0.1 | 0.175 | 2.2 | 0.162 | 1.8 | 0.051 | 1.3 | 0.066 | 0.0 |
| F(P) | 0.005 | 10.1 | 0.080 | 5.9 | 0.265 | 3.3 | F(P) | 0.123 | 7.9 | 0.620 | 0.7 | 0.576 | 0.0 | 0.140 | 10.6 | 0.023 | 15.8 | 0.013 | 17.4 |
| P*Z | 0.379 | 0.6 | 0.394 | 0.0 | 0.852 | 0.0 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| P*R(Z) | 0.034 | 1.8 | 0.622 | 0.0 | 0.681 | 0.0 | P*R | 0.003 | 1.8 | 0.357 | 0.0 | 0.321 | 0.0 | 0.632 | 0.7 | 0.874 | 0.0 | 0.852 | 0.0 |
| F(P)*Z | 0.778 | 0.0 | 0.500 | 4.0 | 0.297 | 6.8 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Res. | --- | 87.5 | --- | 89.5 | --- | 87.8 | Res. | --- | 90.3 | --- | 99.2 | --- | 97.8 | --- | 86.9 | --- | 82.9 | --- | 82.6 |

^a Sources of variation: Z = zone, R = replication, R(Z) = replication in zone, P = provenance, F(P) = family in provenance, interactions [P*Z, P*R(Z), F(P)*Z], Res. = residual.

^b P > F = significance of F ratio. VAR = percentage of the total phenotypic variance explained by the variance component.

^c Variables describing variability in wood color (Var-L*, Var-a*, Var-b*, DeltaE) are not tabled: Var-a*, Var-b* and DeltaE did not vary significantly due to any source of variation; Var-L* varied significantly due to F(P) only in the middle zone of the watershed (P > F = 0.034, VAR = 14.6).

^d Degrees of freedom: Z = 1, R(Z) = 4, P = 6, F(P) = 189, P*Z = 6, P*R(Z) = 23, F(P)*Z = 155, Res. = 298, Total = 682. One provenance is not represented in one replication in middle part of watershed, so there is no interaction for this provenance in that replication.

^e Degrees of freedom: R = 2, P = 6, F(P) = 160, P*R = 11, Res. = 106, Total = 285.

^f Degrees of freedom: R = 2, P = 6, F(P) = 184, P*R = 12, Res. = 192, Total = 396.

However, the statement mentioned early is valid for products from juvenile wood, and we cannot extrapolate to mature wood because juvenile-mature correlations have not been investigated in this species. Therefore, we do not really know if the color will change over time.

Analyses within zones gave some contrasting results, compared with the analysis across zones. For example, variation due to families was significant for Mean-a* and Mean-b* in the upper zone but not in the middle zone of the watershed. Since the expression of genetic variation depends on the environmental conditions of the test environment (Campbell and Sorensen 1978; Sotelo Montes et al. 2003), this result probably reflects the differences in soil fertility and moisture between the two planting zones (more fertile and higher precipitation in the upper zone of the watershed). The effect of soil fertility and moisture on wood color has been reported by other researchers. For example, Klumpers et al. (1993) observed that the amount of available soil moisture was the major soil factor influencing wood color of *Quercus robur* L, and Luostarinen et al. (2002) found that wood color of *Betula pendula* Roth was lighter and also less red/yellow in a more fertile site.

Uniformity in wood color is an important practical concern, because variability in color reduces the aesthetic value of the wood. Janin et al. (2001) noted that precise color determination can provide a useful means to classify, match and join pieces of wood in parquet floors, joinery and furniture manufacturing.

In the present study, the four measures of variability in wood color (Var-L*, Var-a*, Var-b*, DeltaE) generally did not vary significantly due to any source of variation in the analyses of variance across and within zones (exception: Var-L* in the middle zone of the watershed). This indicates that the level of the variation in wood color is similar among samples. However, wood samples were relatively short (45 cm long) and obtained only from the lower part of the stem. Additional research is necessary to evaluate variability in wood color related to the vertical and radial position in the stem.

Changes in wood color are generally associated with the deposition of extractives in the heartwood during the process of wood maturation (Burtin et al. 1998). The natural color of wood depends of biological factors including the age of the wood and the tree (Klumpers et al. 1993),

anatomical and structural properties of the wood (Mosedale et al. 1996) and the chemical composition of the constituents of the cell wall (Janin 1987). Color also depends on whether the wood was cut in the tangential or radial plane, as well as the light source and orientation of the wood surface in relation to the light source (Janin 1987). Moreover, wood color can change with thermal treatments, drying and exposure to ultraviolet radiation (Luostarinen et al. 2002, Kishino and Nakano 2004, Pastore et al. 2004). Further research is necessary to evaluate the effect of these factors on variability in wood color of *C. spruceanum*.

3.5.2 Phenotypic and genetic correlations between juvenile wood color and the tree's growth and wood density

Phenotypic correlations (Pearson r) with wood color were generally weak at 39 months (Table 3.3A). Using data of individual trees across the two zones, the correlations indicated that the wood of larger trees (i.e., trees with greater height and Dbh) tended to have a yellower hue (larger Mean-b*). Height was negatively correlated with Var-b*, suggesting that wood of taller trees had less variability in the yellow hue. Correlations between basic density and color indicated that denser wood tended to be darker (smaller Mean-L*) and had a redder/yellower hue (larger Mean-a* and Mean-b*, respectively). The correlation between density and lightness is consistent with the general pattern (denser wood tends to be darker) observed from comparisons of density and lightness for a broad range of tropical hardwoods (Rodríguez and Sibille 1996; Nishino et al. 1998; Janin et al. 2001; Kishino and Nakano 2004).

Phenotypic correlations within each zone suggest that there may be a trade-off in some planting zones if we wish to produce fast growing trees, with light yellow-colored wood and high wood density (Table 3.3A). For example, larger trees tended to have redder/yellower wood (larger Mean-a* and Mean-b*, respectively) in the middle zone of the watershed, but in the upper zone of the watershed only Dbh was positively correlated with Mean-a*. In addition, larger trees in the upper zone of the watershed tended to have darker wood (smaller Mean-L*) with a more uniform yellow hue (smaller Var-b*), but these correlations were not significant in the middle zone of the watershed. Denser wood tended to have a redder/yellower color in both zones of the watershed, and it was also slightly darker in the middle zone of the watershed.

Table 3.3. Pearson and genetic correlations between wood color and the tree's height, diameter at breast height (Dbh) and wood basic density for *Calycophyllum spruceanum* at 39 months. Correlations are given for all trees across zones, and separately for trees in the middle and upper zones of the watershed. The significance (for Pearson r) or standard error (for genetic correlation) is given in parentheses, followed by the number of trees involved in the calculation.

A. Pearson correlations ^{a, b}

| | Across zones | | | Middle zone | | | Upper zone | | |
|--|-------------------------|-------------------------|-------------------------|------------------------|------------------------|-------------------------|-------------------------|--------------------------|-------------------------|
| | Height | Dbh | Density | Height | Dbh | Density | Height | Dbh | Density |
| Mean-L* black (0) to white (100) | NS | NS | -0.13 (0.001) 657 | NS | NS | -0.16 (0.007) 276 | -0.10 (0.038) 397 | -0.18 (<0.001) 397 | NS |
| Mean-a* green (-) to red (+) hues | NS | NS | 0.47 (<0.001) 657 | 0.19 (0.001) 285 | 0.16 (0.008) 287 | 0.45 (<0.001) 276 | NS | 0.13 (0.011) 397 | 0.38 (<0.001) 381 |
| Mean-b* blue (-) to yellow (+) hues | 0.15 (<0.001) 682 | 0.18 (<0.001) 684 | 0.13 (<0.001) 657 | 0.19 (0.002) 285 | 0.17 (0.004) 287 | 0.23 (<0.001) 276 | NS | NS | 0.18 (<0.001) 381 |
| Var-b* | -0.08 (0.034) 682 | NS | NS | NS | NS | NS | -0.11 (0.029) 397 | -0.16 (0.002) 397 | NS |

^a NS = correlation not significant ($P > 0.05$).

^b Correlations with Var-L*, Var-a* and DeltaE are not listed because they were not significant.

B. Genetic correlations ^{c, d, e}

| | Across zones | | | Middle zone | | | Upper zone | | |
|--|------------------------|------------------------|------------------------|-------------|-----|---------|------------------------|------------------------|-----------------------|
| | Height | Dbh | Density | Height | Dbh | Density | Height | Dbh | Density |
| Mean-L* black (0) to white (100) | -0.25 (0.40) 655 | -0.05 (0.38) 655 | -0.17 (0.36) 655 | NSF | NSF | NSF | NSF | NSF | NSF |
| Mean-a* Green (-) to red (+) hues | NSF | NSF | NSF | NSF | NSF | NSF | -0.02 (0.35) 381 | -0.02 (0.39) 381 | 0.24 (0.30) 381 |
| Mean-b* Blue (-) to yellow (+) hues | NSF | NSF | NSF | NSF | NSF | NSF | -0.39 (0.31) 381 | -0.37 (0.35) 381 | 0.27 (0.31) 381 |
| Var-L* | NSF | NSF | NSF | NSF | NSF | NSF | 0.60 (0.70) 274 | NSF | 0.10 (0.72) 274 |

^c NSF = Family within provenance was not significant ($P > 0.05$) for one or both variables in analysis of variance, so genetic correlation was not calculated.

^d NSF for Var-a*, Var-b* and DeltaE.

^e Correlations considered statistically significant are underlined.

Similar results have been reported elsewhere, but the relationships probably depend on several factors, including the species, population, age, sample position, environment and the fertilizers added. For example, Wilkins and Stamp (1990) reported that faster growing trees of *Eucalyptus grandis* Hill (Maiden) at 9.5 years produced redder heartwood. Klumpers et al. (1993) found that in *Quercus robur* L. (a) a darker, redder wood was produced in sites where soil water was more abundant in the spring, (b) the color became increasingly darker and redder from bark to pith, and (c) the heartwood became increasingly redder with the age of the trees. Rink (1987), however, found that faster growing trees of *Juglans nigra* L. produced lighter colored heartwood at 10 years. In the same test of *J. nigra*, Rink and Phelps (1989) reported that taller trees had denser and darker colored heartwood. Several researchers studied the relationship between extractive content and wood color using mature-wood samples from older trees. Klumpers et al. (1993) found that there was a significant correlation between color and extractive content in the outer heartwood, but not in the inner heartwood of both *Quercus petraea* Liebl. and *Q. robur* L. Mosedale et al. (1996) found a relationship between color and heartwood extractives but not sapwood extractives in *Q. petraea* Liebl. Gierlinger et al. (2004) found a strong relationship between color and heartwood extractives in different species of *Larix*, but Hannrup et al. (2004) did not find any significant relationship between color and extractives in *Picea abies* (L.) Karst. One would not expect to find a relation between wood color and extractives in juvenile wood of *C. spruceanum* prior to heartwood formation, but this question should be investigated in future research.

Most genetic correlations with wood color were low in magnitude, and not considered to be statistically significant because the standard errors were larger than the estimated correlations (Table 3.3B). Only two correlations with tree height and Dbh could be considered significant: At the family level, larger trees had wood with a less yellowish hue (smaller Mean-b*) in the upper zone of the watershed.

Considering the magnitude of the genetic correlations and their standard errors, selecting fast-growing trees and/or trees with denser wood would likely have little effect on juvenile-wood color. The significant correlations suggest that if we select larger trees in the upper zone of the watershed and plant their progeny in that zone of the watershed, the juvenile wood would have a

slightly less yellowish hue. Further research is necessary to explore this relation in trees at different ages and in different environmental conditions.

Genetic correlations with wood color have not been reported for other tropical hardwood species at an early age. Hannrup et al. (2004) reported some significant genetic correlations with growth and wood density in *Picea abies* (L.) Karst.: Dbh was negatively correlated with a^* (i.e., wood of larger-diameter trees had a greener hue); both earlywood and latewood density were positively correlated with a^* (i.e., denser wood had a redder hue); and latewood density was also positively correlated with b^* (i.e., denser wood had a yellower hue). However these results are based on conifer wood and cannot be generalized to hardwood species such as *C. spruceanum*.

Phenotypic and genetic correlations may differ in magnitude and even in sign among test environments and also among populations of the same species (Falconer and Mackay 1996). This reflects the fact that the phenotypic correlation is the result of both the genetic and environmental correlations between the traits. In the present study, most of the phenotypic correlations were weak (but significant), while the corresponding genetic correlations were essentially zero. Since genetic control (i.e. heritability) was relatively low for both the growth traits (Sotelo Montes et al. 2006a, chapter 2) and color traits (discussed below), the magnitude and sign of the phenotypic correlation was primarily due to the environmental correlation between the traits.

3.5.3 Estimates of individual tree heritability (h_i^2) for juvenile wood color

The h_i^2 of most wood color traits at 39 months was not significantly different from zero (Table 3.4). The only significant values were for lightness (Mean- L^*) across zones, for variability in lightness (Var- L^*) in the middle zone of the watershed, and for the reddish (Mean- a^*) and yellowish (Mean- b^*) hues in the upper zone of the watershed. Results suggest that early selection based on wood-color would be most effective in zones with more fertile soils and higher rainfall (the upper zone of the watershed in the present study). However, the selection would produce relatively small genetic gains because there was relatively little phenotypic variation in wood color traits (low standard deviations, Table 3.1) and only moderately high h_i^2 for Mean- a^* and Mean- b^* .

Table 3.4. Heritability of wood color for *Calycophyllum spruceanum* at 39 months. Heritability is given for all trees across zones, and separately for trees in the middle and upper zones of the watershed. The standard error (in parentheses), and number of trees involved in the calculation are given after the heritability.^a

| Trait | Across zones | Middle zone | Upper zone |
|---|-----------------|-----------------|-----------------|
| Mean-L* black (0) to white (100) | 0.31 (0.17) 684 | NSF | NSF |
| Mean-a* green (-) to red (+) hues | NSF | NSF | 0.48 (0.27) 397 |
| Mean-b* blue (-) to yellow (+) hues | NSF | NSF | 0.52 (0.27) 397 |
| Var-L* | NSF | 0.44 (0.36) 287 | NSF |

^a NSF = Family within provenance was not significant ($P > 0.05$) in analysis of variance, so heritability was not calculated.

Wood color had a lower h_i^2 than basic density of the wood at 39 months in this test ($h_i^2 = 0.53$ for basic density across zones; Sotelo Montes et al. 2006a, chapter 2). Although no estimates are available for other tropical hardwoods at an early age, this agrees with results of studies of temperate conifers and hardwoods. For example, Hannrup et al. (2004) found that wood color had a lower h_i^2 than latewood density for *Picea abies* (L.) Karst., Mosedale et al. (1996) suggested that wood density was under stronger genetic control than wood color for *Quercus petraea* Liebl, and Rink (1987) reported that heartwood color was controlled more by environmental than by genetic factors for *Juglans nigra* L.

3.6 Conclusions

There is genetic variation in some wood color traits of *C. spruceanum* at an early age, and a greater proportion of this variation occurs among families within provenances rather than among provenances. There is potential, therefore, to select families with slightly different wood colors in response to current and future market preferences. Genetic correlations with wood color indicate that, in general, selection of faster growing trees and/or trees with denser wood would have little effect on wood color and its uniformity. The estimates of individual tree heritability for color

suggest that *C. spruceanum* is similar to other tropical species in terms of the magnitude of additive genetic variance.

Chapitre 4 Genetic variation in wood shrinkage, and its correlations with tree growth and wood density of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon

4.1 Résumé

Calycophyllum spruceanum (Benth.) Hook. f. ex Shum. est une espèce importante dans le bassin de l'Amazonie péruvienne. Du fait que les fermiers et l'industrie utilisent du bois provenant des jeunes arbres, les généticiens devraient étudier la variation génétique des propriétés du bois juvénile pour connaître son potentiel d'amélioration. Une étude précédente employant le même essai de provenance/descendance a montré qu'il y avait variation génétique significative de la croissance de l'arbre et de la masse volumique du bois, que l'héritabilité était plus élevée pour la masse volumique que pour la croissance, et que la masse volumique et la croissance étaient corrélées positivement à 39 mois. Cet article présente des résultats pour le retrait du bois à 39 mois, et leurs corrélations avec la croissance de l'arbre et la masse volumique du bois. Les données provenaient d'arbres récoltés lors d'une éclaircie. Le retrait fut relativement faible si l'on tient compte de sa masse volumique. La variation génétique du retrait due aux familles dans les provenances fut significative, tandis que celle due aux provenances, ne le fut que dans certains cas. L'héritabilité était modérément élevée pour le retrait linéaire et volumétrique (0.37 to 0.50), et faible pour le rapport T/R (0.21 to 0.29). Les corrélations génétiques qui ont été considérées significatives étaient entre 0.30 et 0.80. En général, les corrélations génétiques suggèrent que la sélection des arbres à croissance plus rapide et/ou avec une masse volumique du bois plus élevée, aura comme conséquence un bois avec un plus grand retrait et un plus grand rapport retrait tangentiel/radial (T/R).

4.2 Abstract

Calycophyllum spruceanum (Benth.) Hook. f. ex Shum. is an important timber-tree species in the Peruvian Amazon Basin. Farmers and industry use wood from young trees of this species, so tree breeders should investigate genetic variation in juvenile-wood properties to verify whether they can be improved. A previous study using the same provenance/progeny test showed that there

was significant genetic variation in tree growth and wood density, that heritability was higher for density than for growth, and that density and growth were positively correlated at 39 months. This paper presents results for wood shrinkage at 39 months, and their correlations with tree growth and wood density. Data were collected on thinned trees. Shrinkage values were relatively low when considering wood density of this species. There was significant genetic variation in wood shrinkage due to families within provenances and, in some cases, due to provenances. Heritability estimates were moderately high for linear and volumetric shrinkage (0.37 to 0.50) and lower for the T/R ratio (0.21 to 0.29) across zones. The genetic correlations that were considered significant ranged from 0.30 to 0.80. In general, genetic correlations suggest that selection of faster-growing trees with higher wood density would result in wood with greater shrinkage and a larger tangential/radial shrinkage (T/R) ratio.

4.3 Introduction

Plantation forestry is an attractive management option in the tropics because the rotation period can be significantly shorter than in natural stands. However, wood properties are likely to be affected because trees grown in plantations have a higher volume of juvenile wood compared with trees in natural stands (Skaar 1988; Trockenbrodt et al. 1999; Ofori and Brentuo 2005). The juvenile zone is the area where rapid radial changes in wood properties occur within the stem. Since juvenile wood will be used increasingly in the future, there is a need for research on genetic variation in juvenile-wood properties, their correlations with tree growth, and their impact on end-use products (Zobel and Sprague 1998).

Shrinkage is one of the most important properties of dimensional stability of wood (Skaar 1988; Pliura et al. 2005), and this property is influenced by genetic and environmental factors (Nepveu et al. 1978; Nepveu and Velling 1983; Nepveu 1984; Yang et al. 2002; Pliura et al. 2005). In theory, there is a positive relationship between shrinkage (tangential, radial, volumetric) and wood density (Tsoumis 1991), but this relationship varies among species (Siau 1984; Skaar 1988; Shupe et al. 1995a; Koubaa et al. 1998; Ofori and Brentuo 2005). Juvenile wood tends to have less transversal shrinkage than mature wood because it has lower density (Bowyer et al. 2003). However, there have been relatively few studies looking at the relationship between tree growth

and wood shrinkage in hardwood species (Nepveu and Velling 1983; Koubaa et al. 1998; Pliura et al. 2005), especially in tropical hardwoods.

Calycophyllum spruceanum (Bentham) Hooker f. ex Shumann (Rubiaceae family) is an important timber tree species for farming communities in the Peruvian Amazon (Sotelo Montes and Weber 1997), with demand in national and international markets for furniture, wall paneling and parquet floors (Toledo and Rincón 1996). It is a pioneer species that colonizes the floodplain and disturbed forests in the Amazon of Peru, Brazil, Ecuador and Colombia (Linares et al. 1992). Trees can attain heights of 35 m with stem diameters of 1.8 m at breast height (Sears 2003). The wood is diffuse-porous, with a basic density at breast height (1.3 m above ground) of about 740 kg/m³ for mature wood in natural stands (Keenan and Tejada 1984) and close to 600 kg/m³ at 39 months of age in plantations (Sotelo Montes et al. 2006a, chapter 2). Farmers and industry commonly use juvenile wood of this species, and the demand for it will increase in the future with the promotion of agroforestry and small-scale plantation forestry.

A provenance/progeny test of *C. spruceanum* was established in a watershed of the Peruvian Amazon Basin and evaluated at 39 months. Results indicated that there was significant variation in tree growth and wood density due to provenances and families within provenances, that wood density had a higher heritability than growth, and that these variables were positively correlated at the genetic and phenotypic levels (Sotelo Montes et al. 2006a, chapter 2). This paper presents additional results of wood properties from the same provenance/progeny test. The objectives were to (a) determine the relative magnitude of variation in juvenile-wood shrinkage among provenances and families within provenances, (b) evaluate phenotypic and genetic correlations between wood shrinkage and the tree's growth and wood density, as well as the heritability of wood shrinkage in two planting zones. Genetic variation and heritability of basic density were also assessed for comparison with shrinkage properties. Results are compared with other hardwood species, and some practical implications are discussed.

4.4 Materials and methods

4.4.1 Sample region, study area, experimental design and management of the provenance/progeny test

The sample region is located in the Aguaytía watershed of the Peruvian Amazon (Figure 1). Large natural stands of *C. spruceanum* occur along the rivers in the lower, middle and upper parts of the watershed, and on upland soils in the latter; whereas smaller stands occur on upland soils in the lower and middle parts of the watershed. Trees are also scattered throughout most of the watershed, so it is assumed that the stands are not genetically isolated and are subpopulations of an extensive natural population. The breeding system of *C. spruceanum* has not been studied, but we assume that some inbreeding has occurred and continues to occur in these subpopulations and open-pollinated families are not pure half-sibs as others have assumed (Hodge et al. 2002, Hodge and Dvorak 2004).

Open-pollinated seeds were collected from 200 selected mother trees (families) growing in seven geographic locations (provenances) distributed in the lower, middle and upper parts of the watershed. To reduce the chance of sampling siblings, at least 100 m was maintained between any two selected trees. Selection intensity was only about 20%, so there was little if any effect due to selection. The number of selected trees (13, 20, 47, 47, 10, 47 and 16 for provenance codes 1 to 7, respectively) was roughly proportional to the total number in each provenance. The test was established in the lower, middle and upper parts of the watershed, but restricted to upland, non-alluvial soils due to logistic and economical considerations as well as market access. In general, soil fertility and mean annual rainfall increase from the lower to the upper part of the watershed. Details about sampling procedures and tree selection criteria in the provenances, and the climate and soils in the sample region and study area are given elsewhere (Sotelo Montes et al. 2006a, chapter 2).

The experimental design was a randomized complete block with 15 replications in total: five were established on different farms in each of the lower, middle and upper parts of the watershed (hereafter called planting zones). In each replication, the 200 families were randomly assigned to 200 experimental plots, with two trees per plot. Spacing was 2.5 by 2.5 meters within and between rows. Two rows of trees surrounded the experimental design on each site to avoid border

effects. Dead trees were replaced during the first dry season, but data collected on replants were not retained for the analyses.

Overall tree mortality was 16.7% at 39 months. It varied by about 6% among planting zones and provenances, and 40% among families. It was fairly evenly distributed across plots in each replication, so inter-tree competition was similar among plots. Tending practices included a cover crop, fertilizer application, branch pruning and manual weeding, and are described elsewhere (Sotelo Montes et al. 2006a, chapter2). Thirty-nine months after planting, one tree in each experimental plot was selectively thinned, based on tree form (primarily stem bifurcations in the canopy) and growth.

4.4.2 Traits measured in the provenance/progeny test

Measurements were made on the thinned trees of six of the 15 replications: three each in the middle and upper zones of the watershed. The other nine replications (two each in the middle and upper zones, and the five in the lower zone) were excluded because mean diameter of the trees was too small to provide enough samples of sufficient size for analysis of wood shrinkage. Tree height was measured to the nearest cm using a meter stick or a telescopic measuring pole. Stem diameter at breast height (Dbh, 1.3 m above ground level, without bark) was measured to the nearest 0.1 cm using callipers for small trees and diameter tapes for larger trees.

Although the thinned trees were not randomly selected from the two trees in each experimental plot, it is unlikely that the results of this study would not apply to the species as a whole (Sotelo Montes et al. 2006a, chapter 2). The following reasons can be advanced to support this assumption. (1) Wood properties were not used as selection criteria in the thinning. (2) Wood samples were obtained from the lower stem, well below the stem bifurcations in the canopy. (3) Mean height of the thinned trees (8.6 m) was essentially the same as the mean height of all trees in the six replications (8.4 m).

Shrinkage and basic density were determined for 767 trees (335 and 432 in the middle and upper zones, respectively), using one wood sample per tree. Two sizes were used for measurements: 8 x 2 x 2 cm for the larger trees, and 6 x 1.5 x 1.5 cm for the smaller trees. This was done in order to sample a maximum number of trees in each planting zone, and to have the last two growing

seasons represented in the samples. This sampling procedure could have produced a slight difference in wood density and shrinkage between the two samples because of the relationships between growth, wood density and shrinkage mentioned in the introduction. Therefore, the data were adjusted for dimension of the samples for the statistical analyses.

Sampling involved two steps. First, a 45-cm long stick was prepared from the green log: this was located close to the bark, in the south-facing quadrant of the stem, between 30 and 75 cm above ground level. Cross-sections of the sticks were 2.5 x 2.5 cm for the larger trees (greater than approximately 7.0 cm in Dbh), and 2.0 x 2.0 cm for the smaller trees (less than approximately 7.0 cm in Dbh). The cut ends of the sticks were treated with paraffin to prevent water loss, stored in a moisture-saturated environment for 1 month, and then stored at 4°C for approximately 6 months. One small clear sample without defects was then prepared from each stick, and immediately soaked in distilled water for 72 hours to ensure a moisture content above the fiber saturation point (FSP) prior to measurement.

Shrinkage and basic density were measured using standard procedures (ASTM 1994), except for the sample dimensions. The saturated mass of the small clear sample was determined to the nearest 0.001 g using a digital balance, and the three principal dimensions were measured to the nearest 0.001 mm with a digital micrometer. Saturated volume was measured to the nearest 0.001 cm³ using the water displacement method. Samples were then stored under controlled conditions (20°C, 60% RH) for 120 days to attain the equilibrium moisture content (EMC) at the air-dry condition (EMC average = 12.68%, standard error = 0.01%). Dimensions and masses of the samples were then recorded in the air-dry condition. Finally, the samples were progressively oven-dried for 7 days at gradually increasing temperatures up to 103°C. Dimensions and masses of the oven-dry samples were then recorded, after allowing them to cool down to room temperature over phosphorous pentoxide to prevent moisture adsorption. Dimensional differences of samples were used to estimate partial and total shrinkage. Partial shrinkage [$\{(\text{saturated} - \text{air-dry dimension})/\text{saturated dimension}\} \times 100$], was estimated in the lineal directions [radial (β_{RH}), tangential (β_{TH}), longitudinal (β_{LH})], and these values were used to calculate the partial coefficient of anisotropy (T/R ratio = β_{TH}/β_{RH}) and partial volumetric shrinkage [$\beta_{RH} + \beta_{TH} + \beta_{LH} - 0.01(\beta_{RH} \times \beta_{TH})$]. Total shrinkage [$\{(\text{saturated} - \text{oven-dry dimension})/\text{saturated dimension}\} \times 100$] was also estimated in the lineal directions, and used to calculate the total

coefficient of anisotropy and total volumetric shrinkage. Basic density (BD) is reported as the ratio of oven-dry mass to saturated volume (kg/m^3).

4.4.3 Statistical analyses

The SAS[®] statistical package, version 9.1 (SAS Institute Inc. 2002-2003), was used for all statistical analyses. Data transformations were not required to satisfy the assumptions of analysis of variance and other analyses. Analyses of tree height and stem diameter were reported elsewhere (Sotelo Montes et al. 2006a, chapter 2).

Analyses of covariance were carried out across planting zones and separately within each zone using mixed linear models (GLM procedure, partial sums of squares estimation method). Dimension (Dim) and equilibrium moisture content (EMC) of the wood samples were covariates. Basic density and total shrinkage parameters were adjusted for Dim. Partial shrinkage parameters were adjusted for Dim and EMC. The model for the analysis across zones included the following sources of variation: zone (Z), replication within zone [R(Z)], provenance (P), family within provenance [F(P)], the interactions [P*Z, P*R(Z), F(P)*Z], Dim and EMC. Zone was treated as fixed factor and the others as random factors. Some F-ratios involved more than one mean square in the denominator (“quasi” F-ratios), and were tested with approximate degrees of freedom. The model for the analysis within zones was similar to that used across zones except that there was no source of variation due to zone and, therefore, no interactions with zone.

To estimate variance components, data were adjusted across zones and separately within each zone, and then analyzed using the VARCOMP procedure with the restricted maximum likelihood method. Phenotypic correlations (Pearson r) were calculated at the tree level (CORR procedure) also using adjusted data. Individual tree heritability (h_i^2), genetic correlations and their standard errors (Becker 1984; Falconer and Mackay 1996) were estimated only for traits that had significant ($\alpha \leq 0.05$) variation due to families within provenances in the appropriate analysis of variance. Trait values were standardized (Steel et al. 1997) for calculation of genetic correlations. We assumed partial inbreeding and estimated additive genetic variance as $3\sigma_f^2$, as others have done for other tropical hardwood species (Hodge et al. 2002; Hodge and Dvorak 2004), in order

to provide a conservative estimate of h_i^2 . Variance components were also expressed as a percentage (VAR) of the total phenotypic variance explained by the variance component.

4.5 Results and discussion

4.5.1 Means and coefficients of variation of shrinkage properties and basic density

Mean basic density of all trees in the middle and upper zones of the watershed (594 kg/m^3) was very similar to that obtained using disks sampled at breast height in the same provenance/progeny test (592 kg/m^3 ; Sotelo Montes et al. 2006a, chapter 2), and was higher than that observed for disks sampled between 30 cm and 65 cm above ground in another test of this species established in the same planting zones (563 kg/m^3 ; Weber and Sotelo Montes 2005). The coefficient of variation for basic density in the present study (6% for all trees) was slightly smaller than those reported earlier (around 8% for all trees: Weber and Sotelo Montes 2005; Sotelo Montes et al. 2006a, chapter 2). Moreover, it was previously reported that trees grew more rapidly in the upper than in the middle zone of the watershed. For example, mean tree height at 39 months was 6.7 and 8.6 m among all replications in the middle and upper zones of the watershed, respectively (Sotelo Montes et al. 2006a, chapter 2).

Estimates of shrinkage and basic density of juvenile wood of *Calycophyllum spruceanum* in the present study (Table 4.1) were lower than those reported by Keenan and Tejada (1984) for mature wood from ten trees sampled in natural stands. These differences between juvenile and mature wood are consistent with those observed in many other species (Tsoumis 1991; Bowyer et al. 2003). However, the ratio of volumetric shrinkage to basic density was similar in both studies (around 19). For temperate woods, the mean value of this ratio is usually close to the FSP, which is between 25% and 30% (Skaar 1988). The lower ratio obtained in the present study could be due to the fact that FSPs are lower for tropical than for temperate woods (Wangaard 1951) and/or that shrinkage in tropical woods is lower due to the presence of extractives (Choong and Achmadi 1991). For *C. spruceanum* the latter alternative appears more plausible given that the FSP estimated by the volumetric shrinkage intersection method (Skaar 1988) gave a value of about 27%. Thus, considering its density, *C. spruceanum* exhibits a low degree of shrinkage.

Table 4.1. Descriptive statistics of wood shrinkage properties and basic density for *Calycophyllum spruceanum* at 39 months. Statistics are given for all trees across zones, and separately for trees in the middle and upper zones of the watershed.^{a, b}

| Trait | Across zones (N= 767) | | | Middle zone (N = 335) | | | Upper zone (N = 432) | | |
|------------------------------------|-----------------------|----------|------|-----------------------|----------|------|----------------------|----------|------|
| | Mean | St. dev. | CV | Mean | St. dev. | CV | Mean | St. dev. | CV |
| Partial shrinkage | | | | | | | | | |
| R (%) | 1.62 | 0.27 | 16.7 | 1.59 | 0.28 | 17.6 | 1.64 | 0.26 | 15.9 |
| T (%) | 4.17 | 0.69 | 16.5 | 3.98 | 0.68 | 17.0 | 4.31 | 0.66 | 15.3 |
| V (%) | 5.87 | 0.82 | 13.9 | 5.64 | 0.81 | 14.4 | 6.05 | 0.77 | 12.8 |
| T/R ratio | 2.61 | 0.40 | 15.2 | 2.54 | 0.41 | 16.2 | 2.67 | 0.38 | 14.3 |
| Total shrinkage | | | | | | | | | |
| R (%) | 3.48 | 0.56 | 16.2 | 3.37 | 0.56 | 16.5 | 3.57 | 0.55 | 15.5 |
| T (%) | 7.50 | 1.07 | 14.2 | 7.18 | 1.06 | 14.8 | 7.74 | 1.00 | 12.9 |
| V (%) | 11.19 | 1.34 | 12.0 | 10.76 | 1.33 | 12.4 | 11.52 | 1.25 | 10.8 |
| T/R ratio | 2.18 | 0.28 | 12.7 | 2.16 | 0.29 | 13.7 | 2.19 | 0.26 | 11.8 |
| Basic density (kg/m ³) | 594.4 | 34.8 | 5.9 | 600.7 | 32.8 | 5.5 | 589.5 | 35.6 | 6.0 |

^a Data for partial shrinkage are adjusted for dimension and equilibrium moisture content of the wood sample. Data for total shrinkage and density are adjusted for dimension only.

^b CV = coefficient of variation (%).

N = Number of trees.

The ratio of volumetric shrinkage to basic density of *C. spruceanum* in the present study was within the range of values reported for juvenile wood of other tropical hardwoods of lower density grown in plantations. For example, this ratio (with basic density in parentheses) was 20 (500 kg/m³) for *Tectona grandis*, 14 (580 kg/m³) for *Hevea brasiliensis* and 12 (553 kg/m³) for *Hyeronima alchorneoides* (Moya and Arce 2003; Matan and Kyokong 2003; Solís and Moya 2006). Differences among species probably reflect the variation in FSP and the effect of extractives on wood shrinkage, as explained above.

The coefficient of anisotropy (T/R ratio) was approximately 2.6 and 2.2 for the partial and total shrinkage, respectively (Table 4.1). The large anisotropy in the transverse direction of juvenile wood may be due to a combination of factors, including the restraining effect of ray cells, deviations in microfibril angles in the cell wall, and differences in cell wall thickness and lignin

content between the radial and tangential faces of fibers (Skaar 1988; Zobel and Sprague 1998). These factors may affect the anisotropy to different degrees, depending on the species, specimens and environmental conditions (Tsoumis 1991). It is believed that the thick rays of the hardwoods contribute not only to reduce radial shrinkage but also to increase tangential shrinkage as a result of Poisson's effects (Goulet and Fortin 1975).

Judging from the coefficients of variation (CVs), radial shrinkage showed slightly more variation than tangential shrinkage, while partial shrinkage showed relatively more variation than total shrinkage (Table 4.1). A similar result for juvenile wood of *Azadirachta excelsa* was reported by Trockenbrodt et al. (1999).

4.5.2 Variation in wood shrinkage and basic density

There were significant differences in total tangential and volumetric shrinkages between the two planting zones used in the test (Table 4.2). Differences in shrinkage due to planting sites have been reported for other species (e.g. Sesbou and Nepveu 1990; Yang et al. 2002; Pliura et al. 2005). Presumably, environmental differences among sites produce differences in density, anatomical structure, extractives, chemical composition and/or mechanical stress of the wood, and these in turn affect shrinkage (Tsoumis 1991).

Table 4.2. Analysis of covariance of wood shrinkage properties and basic density for *Calycophyllum spruceanum* at 39 months. Analyses are given for all trees across zones, and separately for trees in the middle and upper zones of the watershed.^{a, b, c}

| SV | Partial shrinkage | | | | | | Total shrinkage | | | | | | Basic density | | | |
|--------|-------------------|------------------|--------|------|--------|------|-----------------|------|-------|------|-------|------|---------------|------|--------|------|
| | R | | V | | T/R | | R | | T | | V | | T/R | | P > F | VAR |
| | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR |
| Z | 0.937 | --- | 0.249 | --- | 0.269 | --- | 0.170 | --- | 0.047 | --- | 0.039 | --- | 0.965 | --- | 0.123 | --- |
| R(Z) | <0.001 | --- | 0.007 | --- | 0.001 | --- | 0.123 | --- | 0.009 | --- | 0.003 | --- | 0.008 | --- | 0.003 | --- |
| P | 0.013 | 0.0 ^b | 0.221 | 3.2 | 0.129 | 3.3 | 0.124 | 1.2 | 0.023 | 0.7 | 0.079 | 1.4 | 0.042 | 2.0 | <0.001 | 4.5 |
| F(P) | <0.001 | 15.4 | 0.002 | 14.1 | <0.001 | 16.0 | 0.041 | 6.7 | 0.006 | 13.5 | 0.011 | 12.1 | 0.013 | 9.3 | <0.001 | 17.0 |
| P*Z | 0.869 | 0.0 | 0.465 | 0.0 | 0.462 | 0.2 | 0.675 | 0.0 | 0.768 | 0.0 | 0.792 | 0.0 | 0.785 | 0.0 | 0.823 | 0.0 |
| P*R(Z) | 0.735 | 0.0 | 0.289 | 0.0 | 0.444 | 0.0 | 0.587 | 0.0 | 0.828 | 0.0 | 0.155 | 0.5 | 0.585 | 0.0 | 0.320 | 0.0 |
| F(P)*Z | 0.679 | 0.0 | 0.240 | 5.1 | 0.383 | 2.6 | 0.344 | 1.4 | 0.151 | 5.9 | 0.042 | 10.0 | 0.237 | 3.8 | 0.612 | 0.0 |
| Dim | 0.035 | --- | 0.926 | --- | 0.685 | --- | 0.017 | --- | 0.543 | --- | 0.674 | --- | 0.150 | --- | <0.001 | --- |
| EMC | <0.001 | --- | <0.001 | --- | <0.001 | --- | 0.151 | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Res | --- | 84.6 | --- | 77.6 | --- | 77.9 | --- | 90.7 | --- | 79.9 | --- | 76.0 | --- | 84.9 | --- | 78.5 |

^a SV = sources of variation: Z = zone, R(Z) = replication in zone, P = provenance, F(P) = family in provenance, interactions [P*Z, P*R(Z), F(P)*Z], Dim = dimension of wood sample, EMC = equilibrium moisture content of wood sample, Res = Residual.

^b Covariates: Dim and EMC for partial shrinkage; Dim only for total shrinkage and density.

^c P > F = significance of F ratio. VAR = percentage of the total phenotypic variance explained by the variance component.

^d Degrees of freedom: Z = 1, R(Z) = 4, P = 6, F(P) = 190, P*Z = 6, P*R(Z) = 24, F(P)*Z = 165, Dim = 1, Res = 368 (if model includes both Dim and EMC) or 369 (if model includes only Dim), Total = 766.

^e Variance component was close to zero.

B. Middle zone ^e

| SV | Partial shrinkage | | | | | | Total shrinkage | | | | | | Basic density | | | | | | | | |
|------|-------------------|------|--------|--------|--------|-------|-----------------|-------|-------|-------|-------|-------|---------------|-------|-------|-------|-------|-----|-------|-----|------|
| | R | | | V | | | T/R | | | R | | | T | | | V | | | T/R | | |
| | P > F | VAR | --- | P > F | VAR | --- | P > F | VAR | --- | P > F | VAR | --- | P > F | VAR | --- | P > F | VAR | --- | P > F | VAR | |
| R | <0.001 | --- | 0.001 | <0.001 | --- | 0.370 | --- | 0.016 | --- | 0.004 | --- | 0.003 | --- | 0.430 | --- | 0.346 | --- | --- | --- | --- | --- |
| P | 0.170 | 0.0 | 0.506 | 0.3 | 0.339 | 0.9 | 0.626 | 0.0 | 0.048 | 0.7 | 0.488 | 0.0 | 0.404 | 0.0 | 0.502 | 0.0 | 0.141 | 4.4 | --- | --- | --- |
| F(P) | 0.324 | 10.5 | 0.090 | 15.4 | 0.092 | 16.6 | 0.333 | 3.3 | 0.091 | 14.8 | 0.017 | 17.2 | 0.016 | 17.7 | 0.132 | 11.1 | 0.056 | 8.8 | --- | --- | --- |
| P*R | 0.906 | 0.0 | 0.574 | 1.1 | 0.692 | 0.1 | 0.760 | 0.0 | 0.898 | 0.0 | 0.277 | 1.9 | 0.376 | 0.3 | 0.585 | 0.9 | 0.078 | 0.2 | --- | --- | --- |
| Dim | 0.107 | --- | 0.858 | --- | 0.835 | --- | 0.054 | --- | 0.101 | --- | 0.870 | --- | 0.540 | --- | 0.040 | --- | 0.020 | --- | --- | --- | --- |
| EMC | <0.001 | --- | <0.001 | --- | <0.001 | --- | 0.162 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Res | --- | 89.5 | --- | 83.2 | --- | 82.4 | --- | 96.7 | --- | 84.5 | --- | 10.9 | --- | 82.0 | --- | 88.0 | --- | --- | --- | --- | 86.6 |

C. Upper zone ^f

| SV | Partial shrinkage | | | | | | Total shrinkage | | | | | | Basic density | | | | | | | | |
|------|-------------------|------|--------|-------|--------|------|-----------------|------|--------|-------|--------|------|---------------|------|-------|-------|--------|------|-------|-----|------|
| | R | | | V | | | T/R | | | R | | | T | | | V | | | T/R | | |
| | P > F | VAR | --- | P > F | VAR | --- | P > F | VAR | --- | P > F | VAR | --- | P > F | VAR | --- | P > F | VAR | --- | P > F | VAR | |
| R | 0.303 | --- | 0.705 | --- | 0.780 | --- | 0.079 | --- | 0.003 | --- | 0.633 | --- | 0.224 | --- | 0.002 | --- | <0.001 | --- | --- | --- | --- |
| P | 0.253 | 0.0 | 0.210 | 4.1 | 0.145 | 4.2 | 0.221 | 1.6 | 0.597 | 0.0 | 0.515 | 1.2 | 0.579 | 0.5 | 0.120 | 1.9 | 0.002 | 4.7 | --- | --- | --- |
| F(P) | 0.005 | 15.2 | <0.001 | 21.1 | <0.001 | 19.3 | 0.030 | 12.6 | <0.001 | 22.5 | <0.001 | 24.6 | <0.001 | 24.4 | 0.009 | 16.7 | <0.001 | 20.5 | --- | --- | --- |
| P*R | 0.363 | 0.0 | 0.169 | 0.0 | 0.247 | 0.0 | 0.362 | 0.0 | 0.545 | 0.0 | 0.173 | 0.5 | 0.218 | 0.0 | 0.657 | 0.0 | 0.826 | 0.0 | --- | --- | --- |
| Dim | 0.269 | --- | 0.993 | --- | 0.778 | --- | 0.231 | --- | 0.417 | --- | 0.450 | --- | 0.323 | --- | 0.858 | --- | 0.002 | --- | --- | --- | --- |
| EMC | <0.001 | --- | <0.001 | --- | <0.001 | --- | 0.609 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Res | --- | 84.8 | --- | 74.8 | --- | 76.5 | --- | 85.8 | --- | 77.5 | --- | 73.7 | --- | 75.1 | --- | 81.4 | --- | --- | --- | --- | 74.8 |

^a SV = sources of variation: R = replication, P = provenance, F(P) = family in provenance, interaction [P*R], Dim = dimension of wood sample, EMC = equilibrium moisture content of wood sample, Res = Residual.

^b Covariates: Dim and EMC for partial shrinkage; Dim only for total shrinkage and density.

^c P > F = significance of F ratio. VAR = percentage of the total phenotypic variance explained by the variance component.

^e Degrees of freedom: R = 2, P = 6, F(P) = 171, P*R = 12, Dim = 1, EMC = 1, Res = 141 (if model includes both Dim and EMC) or 142 (if model includes only Dim), Total = 334.

^f Degrees of freedom: R = 2, P = 6, F(P) = 184, P*R = 12, Dim = 1, EMC = 1, Res = 225 (if model includes both Dim and EMC) or 226 (if model includes only Dim), Total = 431.

Variation due to replications within zones was significant for nearly all shrinkage properties and basic density, especially in the zone with slower tree growth (middle zone of the watershed). The relatively large variation due to replications probably reflects the erratic weeding practices of farmers, as noted previously for tree growth and wood density (Sotelo Montes et al. 2003; Weber and Sotelo Montes 2005; Sotelo Montes et al. 2006a, chapter 2). Their weeding practices undoubtedly produced considerable spatial and temporal variation in soil moisture, temperature and fertility among and within the replications. Rainfall and soil fertility were lower in the middle than in the upper zone of the watershed, so environmental differences produced by the farmers' practices would have a relatively greater effect in the middle zone. This in turn could make it more difficult to detect significant genetic variation in the middle zone (discussed below). Significant variation in shrinkage among replications was also observed in a study of *Eucalyptus camaldulensis* evaluated in two sites with different soil characteristics (Sesbou and Nepveu 1990). Due to the occurrence of variation among replications, data should be adjusted for the block effect before selecting superior families and trees within families. In addition, when the replications are transformed into seed orchards, the mortality should be considered in the selection of the best performing families and trees.

In the analysis across zones, there was significant variation in radial shrinkage, the total coefficient of anisotropy (T/R ratio) and basic density due to provenances, and in all shrinkage properties and basic density due to families within provenances (Table 4.2). Families within provenances accounted for a larger percentage (VAR) of the total phenotypic variance than provenances. VAR due to families within provenances was generally larger for basic density than for the shrinkage properties, and for partial than for total shrinkage. Moreover, differences in shrinkage properties and basic density among provenances and families were relatively stable across zones, judging from the fact that variation due to the interactions with zones was generally not significant (except families by zones for total tangential and volumetric shrinkage). Results reported here for basic density were similar to those observed using disks sampled at breast height on the same trees (Sotelo Montes et al. 2006a, chapter 2).

Analyses within zones gave some contrasting results regarding variation due to provenances and families within provenances (Table 4.2). Total radial shrinkage was the only shrinkage property

that varied significantly among the provenances, but only in the middle zone of the watershed. Variation due to families within provenances was significant for only two shrinkage properties in the middle zone (total tangential and volumetric shrinkage), but for all shrinkage properties in the upper zone. Variation in density due to both provenances and families within provenances was significant only in the upper zone. Furthermore, the analyses suggested that genetic variation was larger (larger VAR) in the planting zone with faster tree growth (upper zone). Therefore, there is considerable potential to select families with lower wood shrinkage, especially in zones with faster tree growth, but less potential to select provenances. However, the selection of families with lower wood shrinkage poses a challenge considering the positive correlations between tree growth, wood shrinkage and density (discussed below).

Significant variation in wood shrinkage has also been observed among hybrid poplar clones (Nepveu et al. 1978; Koubaa et al. 1998; Pliura et al. 2005); families of *Betula pendula* (Nepveu and Velling 1983), *Eucalyptus dunnii* (Henson et al. 2004) and *E. urophylla* (Scanavaca and Garcia 2004); and provenances of *E. camaldulensis* (Sesbou and Nepveu 1990). Large phenotypic differences between trees were also observed in *Quercus petraea* and *Q. robur* (Zhang et al. 1994).

The dimension and/or equilibrium moisture content of the wood sample (covariates Dim and EMC, Table 4.2) had a significant effect on some shrinkage properties and basic density. Dim was significant for partial radial shrinkage, the partial T/R ratio and density in the analysis of covariance across zones; for the total T/R ratio and density in the middle zone; and for density in the upper zone. In all cases, values were slightly greater for the larger dimension. We did not expect much difference in basic density and shrinkage between the two dimensions, based on previous work (Hernández 1993a). However, our sampling procedure could have produced this slight difference in density and shrinkage between the two dimensions because basic density is positively correlated with stem diameter in this species (Sotelo Montes et al. 2006a, chapter 2), we used the larger sample for trees with larger stem diameter and, in general, density is positively correlated with shrinkage (Tsoumis 1991). EMC had a significant effect on nearly all partial shrinkage properties in the analyses across the two zones and within each zone.

4.5.3 Heritability of juvenile-wood shrinkage and basic density

In the analysis across zones, estimates of h_i^2 were highest for basic density, generally similar for tangential, radial and volumetric shrinkage, and lowest for the coefficient of anisotropy (T/R ratio) (range from 0.21 to 0.53, Table 4.3). Nepveu (1984) reported similar results for *Quercus petraea*, *Q. robur* and *Q. rubra*. Nepveu and Velling (1983) also found that volumetric shrinkage was inherited fairly strongly in *Betula pendula*. Henson et al. (2004) reported that h_i^2 of radial and tangential shrinkage was 0.56 and 0.70, respectively for *Eucalyptus dunnii*, while Scanavaca and Garcia (2004) reported that it was only 0.17 for *E. urophylla*. The estimated h_i^2 for basic density of wood samples in the present study was similar to the value obtained using disks sampled at breast height from the same trees (Sotelo Montes et al. 2006a, chapter 2).

Considering only the h_i^2 , selection would be most effective if based on wood density, somewhat less effective if based on linear and volumetric shrinkage, and least effective if based on the T/R ratio. However, the response to selection also depends on the selection intensity and magnitude of total phenotypic variance (Falconer and Mackay 1996).

In general, the h_i^2 of traits was higher in the planting zone with faster tree growth than in the zone of slower growth (upper and middle zones, respectively). In the middle zone, h_i^2 of all traits was essentially zero except for total tangential and volumetric shrinkage ($h_i^2 = 0.53$). In the upper zone, however, h_i^2 estimates ranged from 0.38 to 0.75. This suggests that selection based on juvenile-wood shrinkage would be more effective in zones with faster tree growth. Similar results were observed for h_i^2 of growth traits at 39 months in the same provenance/progeny test (Sotelo Montes et al. 2006a, chapter 2). Campbell and Sorensen (1978) hypothesized that the expression of genetic variation in growth traits would be greater in test environments with faster tree growth. If juvenile-wood traits are genetically correlated with growth traits, as they are for most traits in the present study, then one might expect the h_i^2 for both growth and wood traits to be higher in zones with faster tree growth.

Table 4.3. Heritability of wood shrinkage properties and basic density for *Calycophyllum spruceanum* at 39 months. Heritability is given for all trees, and separately for trees in the middle and upper zones of the watershed. The standard error is given in parentheses.^{a, b}

| Trait | Across zones (N = 767) | Middle zone (N = 335) | Upper zone (N = 432) |
|-------------------|---------------------------|--------------------------|-------------------------|
| Partial shrinkage | | | |
| R | 0.46 (0.16) | NSF | 0.46 (0.25) |
| T | 0.44 (0.16) | NSF | 0.66 (0.25) |
| V | 0.50 (0.16) | NSF | 0.60 (0.25) |
| T/R | 0.21 (0.15) | NSF | 0.38 (0.25) |
| Total shrinkage | | | |
| R | 0.41 (0.16) | NSF | 0.68 (0.25) |
| T | 0.37 (0.15) | 0.53 (0.33) | 0.75 (0.24) |
| V | 0.39 (0.16) | 0.53 (0.33) | 0.74 (0.24) |
| T/R | 0.29 (0.15) | NSF | 0.51 (0.25) |
| Basic density | 0.53 (0.16) | NSF | 0.65 (0.25) |

^a Data for partial shrinkage are adjusted for dimension and equilibrium moisture content of the wood sample. Data for total shrinkage and density are adjusted for dimension only.

^b NSF = Family within provenance was not significant ($P > 0.05$) in the analysis of covariance, so heritability was not calculated.

N = Number of trees.

4.5.4 Phenotypic and genetic correlations between wood shrinkage and the tree's growth and wood density

Pearson correlations, using data of individual trees from both planting zones, indicated that wood of larger trees tended to have more tangential, radial and volumetric shrinkage, and a larger coefficient of anisotropy (T/R ratio; i.e., less dimensional stability) (Table 4.4). Correlations with basic density suggested that denser wood had more tangential, radial and volumetric shrinkage, and a larger T/R ratio. Although these correlations were statistically significant, the relationships were relatively weak and ranged from 0.08 to 0.35. Phenotypic correlations within zones gave some contrasting results compared with the correlations across zones. The positive correlations between radial shrinkage (especially total) and tree growth (height and/or Dbh) were generally more significant in the upper zone (the zone of faster tree growth) than in the middle zone. Therefore, partial volumetric shrinkage was positively correlated with Dbh only in this zone.

Most of the genetic correlations among shrinkage, basic density and growth were considered statistically significant using data of individual trees from both planting zones and in the upper zone (Table 4.5). In general, they expressed the same relationships as the phenotypic correlations, but there were some differences: for example the genetic correlation between basic density and the T/R ratio was not significant. Genetic correlations were not estimated in the middle zone because variance due to families within provenances was not significant ($P > 0.05$) for one or both variables.

Table 4.4. Pearson correlations between wood shrinkage properties and the tree's height, diameter at breast height (Dbh) and wood basic density (BD) for *Calycophyllum spruceanum* at 39 months. Correlations are given for all trees across zones, and separately for trees in the middle and upper zones of the watershed. The significance is given in parentheses.^{a, b}

| Shrinkage | Across zones (N = 765 with height, 767 with Dbh and BD) | | | Middle zone (N = 333 with height, 335 with Dbh and BD) | | | Upper zone (N = 432) | | |
|-----------|---|------------------|------------------|--|------------------|------------------|-------------------------|------------------|------------------|
| | Height | Dbh | BD | Height | Dbh | BD | Height | Dbh | BD |
| Partial | | | | | | | | | |
| R | 0.08 (0.022) | NS | 0.15 (<0.001) | NS | NS | NS | 0.10 (0.048) | NS | 0.22 (<0.001) |
| T | 0.28 (<0.001) | 0.23 (<0.001) | 0.25 (<0.001) | 0.21 (<0.001) | 0.11 (0.040) | 0.24 (<0.001) | 0.23 (<0.001) | 0.20 (<0.001) | 0.35 (<0.001) |
| V | 0.25 (<0.001) | 0.20 (<0.001) | 0.22 (<0.001) | 0.17 (0.002) | NS | 0.19 (<0.001) | 0.21 (<0.001) | 0.17 (<0.001) | 0.33 (<0.001) |
| T/R | 0.20 (<0.001) | 0.20 (<0.001) | 0.10 (0.007) | 0.18 (<0.001) | 0.16 (0.004) | 0.13 (0.022) | 0.14 (0.003) | 0.16 (0.001) | 0.13 (0.005) |
| Total | | | | | | | | | |
| R | 0.18 (<0.001) | 0.16 (<0.001) | 0.13 (<0.001) | 0.15 (0.005) | NS | 0.12 (0.023) | 0.15 (0.001) | 0.13 (0.008) | 0.18 (<0.001) |
| T | 0.35 (<0.001) | 0.31 (<0.001) | 0.28 (<0.001) | 0.33 (<0.001) | 0.23 (<0.001) | 0.29 (<0.001) | 0.27 (<0.001) | 0.26 (<0.001) | 0.37 (<0.001) |
| V | 0.33 (<0.001) | 0.29 (<0.001) | 0.23 (<0.001) | 0.30 (<0.001) | 0.21 (<0.001) | 0.24 (<0.001) | 0.26 (<0.001) | 0.24 (<0.001) | 0.33 (<0.001) |
| T/R | 0.15 (<0.001) | 0.13 (<0.001) | 0.15 (<0.001) | 0.15 (0.006) | 0.11 (0.040) | 0.16 (0.005) | 0.10 (0.032) | 0.11 (0.019) | 0.17 (<0.001) |

^a Data for partial shrinkage are adjusted for dimension and equilibrium moisture content of the wood sample. Data for total shrinkage and density are adjusted for dimension only.

^b NS = correlation not significant ($P > 0.05$).

N = Number of trees.

Table 4.5. Genetic correlations between wood shrinkage properties and the tree's height, diameter at breast height (Dbh) and wood basic density (BD) for *Calycophyllum spruceanum* at 39 months. Correlations are given for all trees across zones, and separately for trees in the upper zone of the watershed. The standard error is given in parentheses. Correlations considered statistically significant are underlined.^{a, b}

| Shrinkage | Across zones (N = 765) | | | Upper zone (N = 432) | | |
|-----------|------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| | Height | Dbh | BD | Height | Dbh | BD |
| Partial | | | | | | |
| R | 0.22 (0.24) | 0.18 (0.27) | <u>0.34</u> (0.20) | 0.02 (0.38) | 0.28 (0.38) | 0.19 (0.31) |
| T | <u>0.40</u> (0.22) | <u>0.59</u> (0.18) | <u>0.51</u> (0.18) | <u>0.38</u> (0.27) | <u>0.77</u> (0.14) | <u>0.33</u> (0.24) |
| V | <u>0.37</u> (0.21) | <u>0.46</u> (0.21) | <u>0.56</u> (0.15) | <u>0.37</u> (0.28) | <u>0.76</u> (0.15) | <u>0.37</u> (0.24) |
| T/R | 0.17 (0.36) | <u>0.46</u> (0.31) | 0.15 (0.32) | <u>0.51</u> (0.31) | <u>0.74</u> (0.20) | 0.27 (0.33) |
| Total | | | | | | |
| R | <u>0.43</u> (0.22) | <u>0.41</u> (0.24) | <u>0.30</u> (0.22) | 0.05 (0.31) | 0.15 (0.33) | 0.19 (0.25) |
| T | <u>0.54</u> (0.20) | <u>0.80</u> (0.11) | <u>0.62</u> (0.16) | <u>0.31</u> (0.26) | <u>0.64</u> (0.19) | <u>0.31</u> (0.22) |
| V | <u>0.54</u> (0.20) | <u>0.70</u> (0.15) | <u>0.69</u> (0.13) | <u>0.30</u> (0.27) | <u>0.56</u> (0.22) | <u>0.32</u> (0.23) |
| T/R | 0.03 (0.32) | 0.29 (0.31) | 0.20 (0.27) | <u>0.34</u> (0.32) | <u>0.62</u> (0.24) | 0.18 (0.30) |

^a Data for partial shrinkage are adjusted for dimension and equilibrium moisture content of the wood sample. Data for total shrinkage and density are adjusted for dimension only.

^b Correlations were not estimated in the middle zone because variance due to families within provenance was not significant ($P > 0.05$) for one or both variables.

N = Number of trees.

Both phenotypic and genetic correlations indicated that denser wood tended to have more tangential, radial and volumetric shrinkage. This is related to the fact that denser wood has a larger volume of cell walls that can contain more moisture (Tsoumis 1991). Positive correlations between density and tangential, radial and/or volumetric shrinkage have been reported for several

hardwoods, including *Betula pendula* (Nepveu and Velling 1983), *Quercus petraea* and *Q. rubra* (Nepveu 1984) and *Petersianthus macrocarpus* (Poku et al. 2001). However, there was no significant relationship between density and shrinkage in intensive sampling of one tree of *Populus deltoides*, and two trees of *Liriodendron tulipifera* and *Liquidambar styraciflua* (Shupe et al. 1995a, 1995b, 1995c).

The T/R ratio is expected to decrease with increasing density (Tsoumis 1991). In the present study, however, denser wood tended to have a slightly larger T/R ratio, based on the phenotypic but not on the genetic correlation. Hock and Mariaux (1984) reported a positive phenotypic correlation between density and the T/R ratio for *Terminalia superba* but no significant correlation for *Tectona grandis*. Nepveu (1984) also reported positive correlations (phenotypic and genetic) for *Quercus petraea*, but no significant correlations for *Q. robur* and *Q. rubra*. Therefore, this relation seems to be species dependent.

The positive correlations between tree growth and the shrinkage properties in the present study probably reflect the underlying relationship between growth and wood density in this species: larger trees tend to have denser wood in the lower stem (Weber and Sotelo Montes 2005; Sotelo Montes et al. 2006a, chapter 2). Relationships between tree growth and shrinkage have been investigated in some other species, and presumably depend on the relationship between growth and wood density for each species. For example, the correlation between tree growth and wood shrinkage was negative for *Betula pendula* (Nepveu and Velling 1983) and *Terminalia superba* (Hock and Mariaux 1984), positive for *Gilbertiodendron dewevrei* (Hock and Mariaux 1984), and not significant for *Tectona grandis* (Hock and Mariaux 1984) and *Populus deltoides* x *P. nigra* hybrid clones (Koubaa et al. 1998). Moreover, Pliura et al. (2005) found that the correlation varied considerably among sites for *P. deltoides* x *P. nigra*, *P. trichocarpa* x *P. deltoides* and *P. maximowiczii* x *P. balsamifera* hybrid clones.

The positive genetic correlations between tree growth, shrinkage and wood density pose a challenge to *C. spruceanum* breeders. In general, the statistically significant correlations suggest that selecting trees with denser wood will result in more tangential, radial and volumetric shrinkage. Similar results would be expected if faster-growing trees were selected. In light of these results, one could suggest that tree breeders evaluate a large number of families and trees in

order to find trees with acceptable growth, shrinkage and wood density. For example, in the present study approximately 0.3% of the trees had a coefficient of total anisotropy ≤ 1.5 , combined with values for wood density, height and Dbh that were slightly greater than the average. Based on this percentage, we estimate that a tree breeder would have to evaluate over 19,000 trees in order to obtain 50 different genotypes with acceptable levels of total anisotropy, wood density and growth. This would be extremely expensive, and is not practical for tree improvement programs in developing countries.

Tree breeders, therefore, should assess which traits are most important for current and future markets and design their breeding strategy accordingly. For example, if wood volume and density are priorities, then faster-growing trees with denser wood should be selected. But if wood with relatively low shrinkage and high dimensional stability are priorities, then slower-growing trees with lower wood density should be selected. Considering this trade-off, we would recommend the development of multiple breeding populations (Namkoong et al. 1988) for these extremes. Alternatively, selection indices could be developed for a single breeding population in order to minimize the increase in shrinkage that will result from selecting faster growing trees with denser wood (Baker 1986).

It must be emphasized that the relationships reported in the present study are based on juvenile wood of thinned trees. Caution should be taken in predicting shrinkage behavior of mature wood from the density of juvenile wood (Koubaa et al. 1998). Additional research is necessary, therefore, to evaluate these relationships for mature wood sampled from randomly selected trees.

4.6 Conclusions

There is genetic variation in wood shrinkage of *C. spruceanum* at an early age, and a greater proportion of this variation occurs among families within provenances than among provenances. This result, combined with the moderate heritability levels, suggest that there is potential to improve wood quality in terms of shrinkage in this species. Heritability estimates suggest that selection would be more effective for linear and volumetric shrinkage than for dimensional stability, and in zones with faster tree growth. However, genetic correlations indicate that selecting faster-growing trees and/or trees with greater wood density would produce wood with

greater tangential, radial and volumetric shrinkage. In order to simultaneously increase tree growth and wood density and reduce wood shrinkage in the same breeding population, tree breeders would have to develop selection indices that would minimize the increase in shrinkage associated with faster growing trees and denser wood. However, this would require evaluating a large number of families and trees to find enough genotypes with acceptable tree growth, wood density and shrinkage. Alternatively, the development of multiple breeding populations could be advisable to produce improved germplasm with the desired wood properties for specific markets. The results presented in this study are based on trees that were selectively thinned, so it would be important to verify in future studies whether results using randomly selected trees are similar. In addition if wood samples differ in dimension or EMC, it would be also important to verify whether data need to be adjusted. Additional research is needed to evaluate (a) genetic correlations between shrinkage properties of juvenile and mature wood, (b) heritability of shrinkage properties, as well as genetic correlations among tree growth, density and shrinkage of mature wood.

Chapitre 5 Genetic variation in wood mechanical properties, and their correlations with tree growth and wood density of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon

5.1 Résumé

Calycophyllum spruceanum (Benth.) Hook. f. ex K. Shum. est une espèce importante croissant dans le bassin amazonien péruvien. Étant donné la surexploitation des populations naturelles, les utilisateurs deviennent dépendants de jeunes arbres de qualité génétique potentiellement inférieure. Par conséquent, la variation des propriétés de bois juvénile devrait être étudiée pour déterminer si la qualité du bois peut être maintenue ou améliorée par croisements. Un essai de provenance/descendance a été effectué afin d'évaluer la variation génétique, de la croissance et des propriétés du bois de jeunes arbres, la force de leur contrôle génétique, ainsi que leurs relations au niveau génétique et phénotypique. Cet article présente les résultats obtenus pour la résistance maximale (σ_L) et le coefficient de déformation statique (s_{11}) en compression longitudinale, le s_{11} dynamique en direction longitudinale (mesuré par ultrasons) et la masse volumique séchée à l'air à l'âge de 39 mois. Nos résultats indiquent que le bois juvénile de *C. spruceanum* a des perspectives excellentes d'utilisation pour le bois de charpente. Nous avons trouvé des variations significatives dans toutes les propriétés du bois entre les familles à l'intérieur des provenances et, dans la majorité des cas, entre les provenances (sauf pour le s_{11} dynamique). En général, les familles représentaient un plus grand pourcentage de la variation phénotypique totale que les provenances. Les estimations d'héritabilité étaient plus élevées pour σ_L et pour s_{11} statique que pour s_{11} dynamique et la masse volumique. Les corrélations génétiques ont indiqué que la sélection des arbres avec un bois plus dense et/ou des arbres à croissance plus rapide aurait un effet positif sur quelques propriétés mécaniques du bois. La méthode de la vitesse de propagation des ondes ultrasonores semble appropriée pour l'évaluation non-destructive de la rigidité de bois juvénile de cette espèce.

5.2 Abstract

Calycophyllum spruceanum (Benth.) Hook. f. ex Shum. is an important timber-species in the Peruvian Amazon Basin. Due to overexploitation in natural populations, users are becoming dependent on young trees of potentially lower genetic quality. Therefore, variation in juvenile-wood properties should be investigated to determine whether wood quality can be maintained or, if necessary, improved by breeding. A provenance/progeny test was established to evaluate genetic variation in growth and wood properties of young trees, the strength of their genetic control as well as their interrelationships both at the genetic and the phenotypic level. This paper presents results obtained for ultimate crushing strength (σ_L), the static compliance coefficient (s_{11}) in longitudinal compression, the dynamic s_{11} in the longitudinal direction (determined by ultrasound) and air-dry density at 39 months. Results indicate that the mechanical properties of juvenile wood of this species are adequate for structural uses. There was significant variation in all wood properties due to families within provenances, and in all but dynamic s_{11} due to provenances. Families accounted for a larger percentage of the total phenotypic variance than provenances. Heritability estimates were higher for σ_L and static s_{11} than for dynamic s_{11} and density. Genetic correlations indicate that selecting trees with denser wood and/or faster growing trees would have a positive effect on some mechanical properties. A non-destructive ultrasonic method appeared suitable for estimating juvenile-wood strength and stiffness of this species.

5.3 Introduction

Plantation forestry is an attractive management option in the tropics given the high growth rates normally observed. However, trees grown under these conditions usually have a higher portion of juvenile wood compared with trees in natural stands, and this can affect wood properties (Zobel and Sprague 1998; Bowyer et al. 2003; Saranpää 2003). Understanding this variation and the factors involved is essential in order to maintain or, if required, improve wood properties for specific uses (Tsoumis 1991). There has been relatively little research on genetic variation in wood properties of juvenile wood, their heritability, their correlation with tree growth and their impact on end-use products (Zobel and Sprague 1998). This research is essential to design tree-improvement programs that provide high quality seed for plantation forestry in the tropics (Simons et al. 1994).

Strength and stiffness are important mechanical properties that determine the wood's suitability for structural uses (Jozsa and Middleton 1994). Wood density is usually a good predictor of strength and stiffness (Panshin and De Zeeuw 1980), but these properties can be influenced by other factors, including the variability among trees within species and environmental conditions that affect tree growth (Tsoumis 1991). Destructive methods are usually used to evaluate mechanical properties. However, a large number of living trees needs to be evaluated using non-destructive methods in order to create breeding or production populations with trees possessing the best attributes. Non-destructive acoustical methods have been developed to evaluate wood properties (Herzig 1991; Bucur 2005), and several researchers have used these methods successfully (Kyokong and Bello 1977; Hernández et al. 1998; Oliveira et al. 2002; Ilic 2003).

Calycophyllum spruceanum (Bentham) Hooker f. ex Shumann (Rubiaceae family), known as capirona in Peru, is an important hardwood species for farming communities in the Peruvian Amazon (Sotelo Montes and Weber 1997). Its dense, diffuse-porous wood (Keenan and Tejada 1984) is mainly used for construction poles, charcoal and firewood, but there is also demand in national and international markets for furniture, wall paneling and parquet floors (Toledo and Rincón 1996). Capirona is a pioneer species that colonizes the floodplain and disturbed forests in the Amazon of Peru, Brazil, Ecuador and Colombia (Linares et al. 1992). Trees can attain heights of 35 m and stem diameters of 1.8 m at breast height (Sears 2003). In Peru, farmers and industry have been harvesting the best canopy-level trees in accessible natural populations, without considering management plans to ensure that the genetic quality was maintained for subsequent generations. As a result, users are becoming dependent on young trees, which may have lower genetic quality for timber. In response to this problem, efforts have been made in order to set up seed orchards to produce high-quality seed for the establishment of small-scale forestry/agroforestry plantations in farming communities (Weber et al. 2001).

A provenance/progeny test of *C. spruceanum* was established in the Peruvian Amazon Basin and evaluated at 39 months. Results indicated that there was significant variation in tree growth and wood density due to provenances and families within provenances. Wood density had a higher heritability than growth, and these variables were positively correlated at the genetic and phenotypic levels (Sotelo Montes et al. 2006a, chapter 2). This paper presents additional results from the same provenance/progeny test. The main objectives were to (a) determine the relative

magnitude of variation in juvenile-wood mechanical properties (ultimate crushing strength – σ_L , static and dynamic parallel compliance coefficients – s_{11}) due to provenances and families within provenances, (b) evaluate the heritability of the mechanical properties, (c) evaluate the phenotypic and genetic correlations among tree growth traits, wood density and the mechanical properties and (d) evaluate the usefulness of non-destructive methods for predicting crushing strength and static stiffness. Results are compared with those of other species, and some practical implications are discussed.

5.4 Materials and methods

5.4.1 Sample region, study area, experimental design and management of the provenance/progeny test

The sample region and provenance/progeny test are located in the Aguaytía watershed of the western Peruvian Amazon (Figure 2.1). Open-pollinated seeds were collected from 200 selected mother trees (families) of *Calycophyllum spruceanum* growing in natural stands located in seven geographic locations (provenances) distributed in the lower, middle and upper parts of the watershed. The test was established on sites with upland, non-alluvial soils. In general, soil fertility and mean annual rainfall increase from the lower to the upper parts of the watershed. Details about the distribution of *C. spruceanum* in the sample region, sampling procedures, tree selection criteria, and the climate and soils in the sample region and study area are given elsewhere (Sotelo Montes et al. 2006a, chapter 2).

The experimental design was a randomized complete block with 15 replications: five replications were established on different farms in each of the lower, middle and upper parts of the watershed (hereafter called planting zones). In each replication, the 200 families were randomly assigned to 200 experimental plots, with two trees per plot. Spacing was 2.5 by 2.5 m within and between rows. Two rows of border trees surrounded the experimental design on each site. Dead trees were replaced during the first dry season, but data collected on replants were not included in the analyses. Although each replication was established on a relatively homogenous site, the size of the replication with border rows was relatively large (~ 0.3 ha), and this could have resulted in fairly large micro-environmental differences within replications. Management practices included

a cover crop, fertilizer application, branch pruning and manual weeding (Sotelo Montes et al. 2006a, chapter 2). One tree in each experimental plot was selectively thinned 39 months after planting, based on tree form (primarily stem bifurcations in the canopy) and growth.

5.4.2 Traits measured in the provenance/progeny test

Measurements of mechanical properties were made on the thinned trees of only six of the 15 replications: three each in the middle and upper zones of the watershed. The other nine replications (two each in the middle and upper zones, and the five in the lower zone) were excluded because mean diameter of the trees was too small to provide enough samples of sufficient size for mechanical tests. Prior to thinning, tree height was measured to the nearest cm using a meter stick or a telescopic measuring pole. After thinning, stem diameter at breast height (Dbh, 1.3 m above ground level, without bark) was measured to the nearest 0.1 cm using callipers for small trees and diameter tape for larger trees.

Although the thinned trees were not randomly selected from the two trees in each experimental plot, it is unlikely that this would affect the results about the relative magnitude of variation in wood properties due to provenances and families within provenances, as well as the correlations between tree growth and wood properties. The following reasons can be advanced to support this assumption. (1) Wood properties were not used as selection criteria in the thinning. (2) Mean height of the thinned trees was essentially the same as the mean height of all trees in the six replications (8.6 m and 8.4 m, respectively). Dbh was only measured on the thinned trees, but as it was highly correlated with height (Sotelo Montes et al. 2006a, chapter 2), we expect the same results. (3) Wood samples were obtained from the lower stem, well below the stem bifurcations in the canopy. This sampling procedure was used for all plots so it should not have any significant bias on mean height, Dbh or wood properties of any particular family.

Air-dry density, ultimate crushing strength in the longitudinal direction (σ_L), static and dynamic parallel compliance coefficients (static and dynamic s_{11} , respectively) were determined from one wood sample per tree. The static and dynamic s_{11} are the reciprocals of the static (E_s) and dynamic (E_d) modulus of elasticity, respectively.

Sampling involved two steps for air-dry density, σ_L and the static s_{11} . First, a 45-cm long stick was prepared: this was located close to the bark, in the south-facing quadrant of the stem, between 75 and 120 cm above ground level. Cross-sections of the sticks were 2.5 x 2.5 cm for larger trees (group A, greater than approximately 7.0 cm in Dbh), and 2.0 x 2.0 cm for smaller trees (group B, less than approximately 7.0 cm in Dbh). Sticks were stored under controlled conditions (60% relative humidity – RH, 20°C) for approximately 6 months to attain equilibrium moisture content (EMC mean = 12.2%) before processing. One defect-free sample was then prepared from each stick. Two sizes were used for measurements: 8 x 2 x 2 cm for the larger trees, and 6 x 1.5 x 1.5 cm for the smaller trees. This was done in order to sample the maximum number of trees in each planting zone, and to have the last two growing seasons represented in the samples. As a result, data would have to be adjusted to eliminate any difference in air-dry density and mechanical properties due to the sample dimension.

Measurements of σ_L , static s_{11} and air-dry density were based on standard procedures (ASTM 1994), except for the sample dimensions. Air-dry volume of each sample was calculated from its length and cross-sectional area, and air-dry weight was measured to the nearest 0.001g. The ratio of air-dry weight to volume was used to estimate air-dry density (kg/m^3). Parallel-to-grain compression tests were then carried out on a MTS ALLIANCE RT/50 machine. Strain in the longitudinal direction was measured over a span of 50 mm (group A) or 40 mm (group B) in the central part of the sample, using a two-side clip gauge provided with a Sangamo DG1.0 linear displacement sensor. Cross-head speed was set to 0.67 mm/min for group A and 0.50 mm/min for group B in order to obtain a similar elastic strain rate of approximately 0.3%. The σ_L was obtained from the maximum load at failure and cross-sectional area of the sample. Test results were also used to calculate the compliance coefficients in the longitudinal direction (static s_{11}). Finally, the samples were oven-dried at 103°C for 48 hours and then cooled down to room temperature over phosphorous pentoxide. Oven-dry weight was then measured to the nearest 0.001g and EMC was calculated.

The dynamic s_{11} was determined for 101 of the 200 families studied. Families for the dynamic s_{11} measurements were selected using a stratified random sampling procedure. The number of families per stratum (provenance) was proportional to the total number of families in the stratum. The dynamic s_{11} was determined for 441 trees, of which 323 were also used for the determination

of σ_L , static s_{11} and air-dry density of the specimen. An increment core of 10 mm diameter was extracted at breast height from each tree after the thinning. The core extended from bark to bark through the pith following the north-south orientation. The longitudinal direction of each core was marked immediately after extraction. Subsequently, the cores were conditioned at 20°C and 60% RH for about 6 months to attain an EMC of 11.7%. A segment of the core (20 mm long) from the south side of the tree, close to the bark, was then prepared for the test.

The dynamic s_{11} was measured using an ultrasonic method described in detail by Herzig (1991) and Yang and Fortin (2001). Each segment was placed between two ultrasonic transducers (transmitter and receiver), and a 1 MHz frequency wave was propagated in the longitudinal direction through the segment. The time taken by the wave to pass through the segment was read to the nearest 10^{-6} of second. Three replicated measurements were made on each segment, and time readings were only accepted when a maximum amplitude and well-defined transmitted wave onset could be seen on the oscilloscope display. The distance of wave propagation was equal to the diameter of the segment: this was measured to the nearest 0.001 mm. A correction factor was applied to the calculation of wave velocity through the core in order to compensate for the error caused by the presence of the coupling medium (neoprene membrane) and the transport of electric waves within the measuring circuit (Herzig 1991; Yang and Fortin 2001). A plexiglas core, with the same dimension as the wood core, was used as a reference to determine the correction factor. The dynamic s_{11} was calculated using the following equation: $s_{11} = (\rho v^2)^{-1}$ (MPa)⁻¹, where ρ = air-dry density (kg/m³) at time of testing, and v = velocity (m/s) of wave propagation. The air-dry density used in this formula was determined using X-ray densitometry for a 20-mm long section of wood sampled at breast height and carefully matched to the 20-mm long segment (hereafter called either density of the slice or ρ_{20}). It should be noted that the values were not corrected to take into account the effect of Poisson's ratio on the wood segments. Therefore, the dynamic s_{11} should be considered as apparent as proposed by Bucur (1981). Finally, the EMC of the segments was determined after the test following the procedure previously described.

5.4.3 Statistical analyses

The SAS[®] statistical package, version 9.1 (SAS Institute Inc., 2002-2003), was used for all statistical analyses. Data transformations were not required to satisfy the assumptions of analysis of variance and other analyses. Analyses of tree height and stem diameter were reported elsewhere (Sotelo Montes et al. 2006a, chapter 2).

Analyses of variance of dynamic s_{11} and covariance of the other wood properties were carried out across and by planting zones (GLM procedure, partial sums of squares estimation method). Variance of dynamic s_{11} was analyzed according to a mixed linear model with the following sources of variation: zone, replication within zone [Rep(Zone)], provenance (Prov), family within provenance [Fam(Prov)], and the interactions [Prov*Zone, Prov*Rep(Zone), Fam(Prov)*Zone]. For density, σ_L and static s_{11} , the model also included dimension (Dim) and equilibrium moisture content (EMC) of the wood sample as covariates because σ_L and static s_{11} were significantly affected by EMC in the middle zone of the watershed ($P = 0.012$ and 0.026 with 283 and 393 trees, respectively). Zone was treated as a fixed factor and the others as random factors. Some F-ratios involved more than one mean square in the denominator (“quasi” F-ratios), and were tested with approximate degrees of freedom. Analyses were also carried out within each zone if there was a significant difference in the wood property due to zones and/or a significant interaction between zones and provenances/families.

Data for density of the compression specimen, σ_L and static s_{11} were adjusted across zones for Dim and EMC (based on covariate relationships) but not for dynamic s_{11} and density of the slice (ρ_{20}). Variance components were estimated using the VARCOMP procedure with the restricted maximum likelihood method. Phenotypic correlations (Pearson r) were calculated at the tree level (CORR procedure). Simple and multiple linear regressions (REG procedure) using the same sample size (323 trees) were used to develop models for predicting σ_L and static s_{11} from ρ_{20} and dynamic s_{11} . Individual tree heritability (h_i^2), genetic correlations, and their standard errors were estimated using formulas described elsewhere (Becker 1984; Falconer and Mackay 1996). Trait values were standardized (Steel et al. 1997) for calculation of genetic correlations. Individual tree heritability (h_i^2) was estimated assuming partial inbreeding (Sotelo Montes et al. 2006a, chapter 2): in this case, additive genetic variance was estimated as $3\sigma_f^2$. This assumption and estimation

method have been used for some other tropical hardwood species (Hodge et al. 2002; Hodge and Dvorak 2004) in order to provide a conservative estimate of h_i^2 .

5.5 Results and discussion

5.5.1 Means and coefficients of variation of wood mechanical properties and density

Mean air-dry density of *Calycophyllum spruceanum* wood [slice (ρ_{20}) and compression specimen = 761 and 717 kg/m³, respectively for 323 trees, data not tabled] was significantly greater (paired t-test, $P < 0.001$) for the ρ_{20} than for the compression specimen. It is likely that the mean density of ρ_{20} was greater because (a) density increases from the pith to the bark (Sotelo Montes et al. unpublished data), (b) the 20 mm slices and the compression specimens were obtained close to the bark, but the compression specimens varied more in the radial position given the machining requirements (orientation of samples, jointing, and planing), (c) the slices were obtained at 1.3 m above ground whereas the compression specimens were obtained between 0.75 and 1.2 m above ground, and (d) density was estimated by two different procedures and with a different number of trees and families.

Mean values for σ_L and density of juvenile wood in the present study (Table 5.1) were lower than those reported by Keenan and Tejada (1984) for mature wood of *C. spruceanum*. This was expected based on differences in density and other properties between juvenile and mature wood (Tsoumis 1991). However, the specific strength (ratio of σ_L to density of the compression specimen) of *C. spruceanum* juvenile wood (70) was similar to that of mature wood (72, Keenan and Tejada 1984). This means that when adjusted for differences in density both juvenile and mature wood of *C. spruceanum* have a similar strength in parallel compression, even though they might differ in several characteristics, including microfibril angles, proportion of rays, fiber length, cell wall thickness, as well as the content of lignin, extractives and other chemical constituents (Skaar 1988; Tsoumis 1991; Lei et al. 1997; Zobel and Sprague 1998; Evans et al. 2000; Bowyer et al. 2003). The specific strength of wood varies among species. For example, compared with other tropical hardwoods, the specific strength in parallel compression of juvenile wood of *C. spruceanum* was lower than that of *Tectona grandis* wood evaluated at 8 years in

Table 5.1. Descriptive statistics of density, ultimate crushing strength (σ_L), static and dynamic parallel compliance coefficients (s_{11}) for *Calycophyllum spruceanum* wood at 39 months.^a

| Trait | Mean | CV ^b | Range | N ^c |
|--|------|-----------------|-------|----------------|
| Air-dry density (kg/m ³) | 718 | 5.9 | 250.0 | 676 |
| Ultimate crushing strength, σ_L (MPa) | 50.1 | 10.1 | 28.2 | 676 |
| Static s_{11} (TPa ⁻¹) | 75.3 | 18.2 | 77.2 | 676 |
| Dynamic s_{11} (TPa ⁻¹) | 77.3 | 15.7 | 72.2 | 441 |

^a Data for density, σ_L and static s_{11} are adjusted for dimension and equilibrium moisture content of the wood sample.

^b CV= Coefficient of variation (%).

^c Number of trees.

plantation (78, air-dry density = 580 kg/m³; Rivero 2004); and similar to mature wood of *Cariniana domestica*, *Copaifera officinalis* and *Terminalia guianensis* grown in natural stands (71, 70, 72, respectively, with air-dry density = 720, 730 and 740 kg/m³, respectively; Keenan and Tejada 1984).

Juvenile wood of *C. spruceanum* is relatively stiff, which is also important for structural uses. Its specific stiffness in parallel compression (ratio of static modulus of elasticity [E_s] to density of the compression sample = 18494) was higher than the specific stiffness in static bending of juvenile wood of *T. grandis* (17812; Rivero 2004). It was also higher than the specific stiffness in static bending of *C. officinalis* mature wood, but lower than that of *C. domestica* and *T. guianensis* mature wood (16529, 22345 and 18957, respectively; Keenan and Tejada 1984).

The dynamic s_{11} is usually lower than the static s_{11} , as observed in mature wood of conifers (Bodig and Jayne 1982) and hardwoods (Bucur 1983; Oliveira et al. 2002). The difference between the dynamic and static s_{11} tends to be smaller in parallel compression tests than in bending tests (Herzig 1991). This is because the ultrasonic method, which is used to determine the dynamic s_{11} , deals mostly with elastic effects (Bucur 1983), whereas the static bending test deals with shear effects (Ilic 2001). Moreover, the difference between the dynamic and static s_{11} in static bending tests is smaller for increment cores than for standard specimens (Bucur 1983).

The mean values for dynamic s_{11} and static s_{11} (75.3 and 75.4 TPa⁻¹, respectively; data not tabled) were not significantly different (paired t-test, P = 0.80) when compared using the same sample size (323 trees). However, when the mean dynamic and static s_{11} were expressed as specific

values (i.e. divided by their density) and compared for the same number of trees, the specific dynamic s_{11} was about 6% lower than the specific static s_{11} and this difference was statistically significant (paired t-test, $P < 0.001$). This result is consistent with previous values reported for other hardwood species (Bodig and Jayne 1982; Bucur 1983; Hernández and Restrepo 1995; Hernández et al. 1998; Oliveira et al. 2002; Bucur 2006).

The CVs for static and dynamic s_{11} of *C. spruceanum* wood (Table 5.1) were similar to those reported for other species (Hernández and Restrepo 1995; Bucur 2005). Judging from the CVs, there was relatively more variation in the static and dynamic s_{11} than in σ_L .

5.5.2 Variation in wood mechanical properties and density

Environmental conditions affect tree growth and can indirectly produce variation in mechanical properties (Tsoumis 1991). For example, significant differences between sites were observed in Dbh and E_d of juvenile wood of selected clones of *Cryptomeria japonica* (Nakada et al. 2003). However, in the present study there were no significant differences in density and mechanical properties between the two planting zones (Table 5.2). Similar results were observed for basic density of cross-sectional disks (Sotelo Montes et al. 2006a, chapter 2) and density of wood slices (Sotelo Montes et al. unpublished data) sampled at breast height in trees from the same two zones. The environmental difference between the two planting zones was probably not large enough to produce significant differences in these wood properties, even though there were significant differences in tree growth between zones (Sotelo Montes et al. 2006a, chapter 2).

There was statistically significant variation in all wood properties due to families within provenances, although variation in air-density of the compression specimen was barely significant (Table 5.2). In addition, variation due to provenances was significant for all properties except dynamic s_{11} . Families within provenances accounted for a larger percentage of the total phenotypic variance (VAR) than provenances, especially for σ_L and static s_{11} . In addition, the percentage of variance explained by families within provenances was larger for static than for dynamic s_{11} .

Table 5.2. Analysis of covariance of air-dry density, ultimate crushing strength (σ_L) and the static parallel compliance coefficient (static s_{11}), and analysis of variance of the dynamic parallel compliance coefficient (dynamic s_{11}) for *Calycophyllum spruceanum* wood at 39 months.^{a, b}

| Source of variation | Density | | | σ_L | | | Static s_{11} | | | Dynamic s_{11} | | |
|---------------------|---------|--------|-------|------------|-------|--------|-----------------|-------|-------|------------------|-------|-----|
| | DF | P > F | VAR | P > F | VAR | P > F | VAR | P > F | VAR | DF | P > F | VAR |
| Zone | 1 | 0.065 | --- | 0.140 | --- | 0.143 | --- | 1 | 0.237 | --- | --- | |
| Rep(Zone) | 4 | 0.368 | --- | 0.110 | --- | 0.461 | --- | 4 | 0.293 | --- | --- | |
| Prov | 6 | <0.001 | 3.8 | 0.001 | 4.6 | 0.005 | 2.6 | 6 | 0.098 | 4.7 | 4.7 | |
| Fam(Prov) | 189 | 0.054 | 7.7 | <0.001 | 18.2 | <0.001 | 15.2 | 94 | 0.014 | 6.9 | 6.9 | |
| Prov*Zone | 6 | 0.999 | 0.0 | 0.909 | 0.1 | 0.995 | 0.0 | 6 | 0.339 | 0.0 | 0.0 | |
| Prov*Rep(Zone) | 23 | 0.161 | 0.0 | 0.126 | 0.0 | 0.230 | 0.0 | 24 | 0.170 | 1.3 | 1.3 | |
| Fam(Prov)*Zone | 154 | 0.088 | 8.2 | 0.154 | 1.9 | 0.713 | 0.0 | 89 | 0.726 | 0.0 | 0.0 | |
| Dim | 1 | 0.198 | --- | 0.599 | --- | 0.922 | --- | --- | --- | --- | --- | |
| EMC | 1 | 0.916 | --- | 0.339 | --- | 0.307 | --- | --- | --- | --- | --- | |
| Residual | 289 | --- | 80.3 | --- | 75.2 | --- | 82.2 | 216 | --- | 87.1 | 87.1 | |
| Total | 674 | --- | 100.0 | --- | 100.0 | --- | 100.0 | 440 | --- | 100.0 | 100.0 | |

^a Dimension (Dim) and equilibrium moisture content (EMC) of the wood sample are covariates for density, σ_L and static s_{11} .

^b DF = degrees of freedom. P > F = significance of F ratio. VAR = percentage of the total phenotypic variance explained by the variance component.

Moreover, differences in mechanical properties and density among provenances and families were relatively stable across zones, judging by the fact that variation due to the interactions (provenance by zone, family within provenance by zone) was not statistically significant.

These results suggest that greater gains in wood mechanical properties could be achieved by selecting the best families within provenances after having selected the best provenances. However, the most appropriate strategy depends on several factors, including the amount of phenotypic variance in the trait, its heritability and its genetic correlations with other traits (discussed below), as well as economic considerations (Namkoong et al. 1988).

Genetic variation in mechanical properties has also been observed in other hardwood species. For example, significant variation has been reported for juvenile wood of hybrid poplar clones (Hernández et al. 1998) and families of *Eucalyptus grandis* (Santos et al. 2003), and for mature wood of clones of *C. japonica* (Fujisawa et al. 1994) and provenances of *T. grandis* (Bhat and Priya, 2004).

The dimension of specimens (covariate Dim in Table 5.2) did not have a significant effect on density, σ_L and static s_{11} in the analysis of covariance across zones. This is consistent with previous research investigating the effect of sample dimension on wood properties (Hernández 1993b; Ilic 2003), and is likely related to the fact that the samples had the same length:width ratio (4:1).

5.5.3 Heritability of juvenile-wood mechanical properties and density

Estimates of h_i^2 were moderately high for σ_L (0.51) and static s_{11} (0.47), and relatively low for air-dry density of the compression specimen (0.24) and dynamic s_{11} (0.22) (Table 5.3). Therefore, considering only the h_i^2 , selection would be most effective if based on σ_L , slightly less effective if based on static s_{11} , and least effective if based on air-dry density and dynamic s_{11} .

Other researchers have also reported moderate to high heritability values for strength and stiffness in parallel to the grain compression of juvenile wood. For example, h_i^2 was 0.57 for σ_L of *Eucalyptus grandis* (Santos et al. 2003). Broad-sense heritability, which is higher than narrow

Table 5.3. Heritability of density, ultimate crushing strength (σ_L), static and dynamic parallel compliance coefficients (s_{11}) for *Calycophyllum spruceanum* wood at 39 months.^a

| Trait | Heritability | Standard error | Number of trees |
|---------------------------------------|--------------|----------------|-----------------|
| Density (kg/m ³) | 0.24 | 0.17 | 676 |
| σ_L (MPa) | 0.51 | 0.18 | 676 |
| Static s_{11} (TPa ⁻¹) | 0.47 | 0.18 | 676 |
| Dynamic s_{11} (TPa ⁻¹) | 0.22 | 0.19 | 441 |

^aData for density, σ_L and static s_{11} are adjusted for dimension and equilibrium moisture content of the wood sample.

sense heritability (h_i^2) because it is estimated from clones (Falconer and Mackay 1996), was 0.47 for σ_L , 0.34 for static s_{11} (both determined using small, clear standard samples) and 0.66 for dynamic s_{11} (determined using increment cores) of juvenile wood from hybrid poplar clones (Hernández et al. 1998), and ranged from 0.60 to 0.86 for E_d (determined by a non-destructive method) of mature wood from *C. japonica* clones (Fujisawa et al. 1992).

5.5.4 Phenotypic and genetic correlations between the tree's growth and wood mechanical properties and density

Phenotypic correlations (Pearson r , Table 5.4) indicated that denser wood tended to have greater strength and stiffness (i.e. lower value of static and dynamic s_{11}), as reported for mature wood in a number of other hardwood species (Bodig and Jayne 1982; Tsoumis 1991; Hernández et al. 1998; Bowyer et al. 2003; Hernández 2006c). In diffuse-porous hardwoods, generally there is little or no relationship between tree growth and the wood's density or mechanical properties (Saranpää 2003). For example, no significant correlation was observed between tree growth and (a) the mechanical properties of several diffuse porous hardwoods (Zhang 1995), (b) density and dynamic s_{11} for mature wood of *Alnus acuminata* H.B.K. (Hernández and Restrepo 1995), and (c) bending properties, E_s and σ_L for juvenile wood of *Alnus rubra* Bong (Lei et al. 1997). Hernández et al. (1998) noted a weak negative correlation between growth rate and juvenile-wood density of hybrid poplar clones, but the correlation between growth rate and mechanical properties was either weak and negative or not significant. However, due to the positive correlation between

Table 5.4. Pearson and genetic correlations between ultimate crushing strength (σ_L), static and dynamic parallel compliance coefficients (s_{11}) and the tree's height, stem diameter at breast height (Dbh) and density for *Calycophyllum spruceanum* wood at 39 months. The significance (for Pearson r) or standard error (for genetic correlation) is given in parentheses, followed by the number of trees involved in the calculation.^a

| Trait | Pearson correlations | | | Genetic correlations ^b | | |
|------------------|---------------------------|---------------------------|---------------------------|-----------------------------------|---------------------------------|---------------------------------|
| | Height | Dbh | Density | Height | Dbh | Density |
| σ_L | 0.210 (0.009) 674 | 0.094 (0.014) 676 | 0.697 (<0.001) 676 | 0.085 (0.338) 674 | 0.143 (0.255) 674 | <u>0.749</u> (0.146) 674 |
| Static s_{11} | -0.156 (<0.001) 674 | -0.067 (0.080) 676 | -0.443 (<0.001) 676 | -0.238 (0.358) 674 | -0.204 (0.278) 674 | <u>-0.360</u> (0.322) 674 |
| Dynamic s_{11} | -0.282 (<0.001) 438 | -0.266 (<0.001) 441 | -0.445 (<0.001) 323 | <u>-0.507</u> (0.247) 438 | <u>-0.753</u> (0.162) 438 | UND ^c |

^a Data for density, σ_L and static s_{11} are adjusted for dimension and equilibrium moisture content of the wood sample.

^b Genetic correlations that are larger than their standard error are underlined.

^c UND: Estimate of variance component for dynamic s_{11} was zero (using 323 trees), so correlation is undefined and standard error cannot be calculated.

growth and density in *C. spruceanum* (Weber and Sotelo Montes 2005; Sotelo Montes et al. 2006a, chapter 2), larger trees also tended to have wood with greater strength and stiffness.

Genetic correlations indicated the same general relationships as those shown by the phenotypic correlations (Table 5.4). However, with the exception of the dynamic s_{11} , all genetic correlations with tree height and Dbh had large standard errors and cannot be considered statistically significant. These results suggest that any gain in growth following selection and breeding could also bring about some gain, although small, in wood stiffness.

5.5.5 Predictive ability of non-destructive methods

The phenotypic correlations between wood strength and stiffness were strong (not tabled). These results are in agreement with previous work (Bodig and Jayne 1982; Tsoumis 1991; Bowyer et al. 2003). As expected, the correlation between σ_L and static s_{11} ($r = -0.812$, $n = 676$, $P < 0.001$)

was stronger than that between σ_L and dynamic s_{11} ($r = -0.567$, $n = 323$, $P < 0.001$). This is because the σ_L and static s_{11} were measured from the same specimen, whereas the dynamic s_{11} was measured from an increment core (even though it was extracted close to the static specimen).

The non-destructive ultrasonic method appears to be useful for estimating the static strength and stiffness of juvenile wood of *C. spruceanum* (Table 5.5). Dynamic s_{11} explained approximately 30% of the variation in σ_L and static s_{11} ($R^2 = 0.322$ and 0.303 , respectively). Stronger relationships in these properties were, however, reported for other hardwood species at older ages (Bucur 1983; Hernández et al. 1998; Oliveira et al. 2002).

Wood density might also be a useful criterion for the indirect selection of *C. spruceanum* trees with desirable wood mechanical properties (Table 5.5). Indeed, density (ρ_{20}) of the wood slice explained on one hand approximately 30% of the variation in σ_L ($R^2 = 0.304$) but on the other hand was not very effective for predicting static s_{11} ($R^2 = 0.124$).

The inclusion of both ρ_{20} and dynamic s_{11} as independent variables in a multiple regression model did improve the ability of these non-destructive methods to predict σ_L (Table 5.5). Although the two independent variables together explained approximately 42% of the variation in σ_L , most of this variation was explained by dynamic s_{11} (32%). For predicting static s_{11} , when dynamic s_{11} was in the equation, the additional variation explained by ρ_{20} was not significant ($P = 0.07$). Therefore, dynamic s_{11} was better than ρ_{20} for predicting both σ_L and static s_{11} .

In conclusion, the dynamic s_{11} was the best predictor of static s_{11} , and the σ_L was better predicted when considering both dynamic s_{11} and ρ_{20} as independent variables. However, these results are based on juvenile wood and cannot be extrapolated to mature wood.

Table 5.5. Simple and multiple linear regressions for predicting ultimate crushing strength (σ_L) and static parallel compliance coefficient (static s_{11}) of *Calycophyllum spruceanum* wood at 39 months. Independent variables include air-dry density of the slice (ρ_{20}) and dynamic s_{11} , which were measured using non-destructive methods.

| Dependent variable | Regression equation ^a | R ² ^b | CV ^c |
|--------------------|--|-----------------------------|-----------------|
| σ_L | 4.2 + 0.060 (ρ_{20}) | 0.304 | 8.3 |
| σ_L | 69.8 – 0.26 (dynamic s_{11}) | 0.322 | 8.2 |
| Static s_{11} | 153.8 – 0.103 (ρ_{20}) | 0.124 | 16.7 |
| Static s_{11} | 23.4 + 0.69 (dynamic s_{11}) | 0.303 | 14.9 |
| σ_L | 33.9 + 0.039(ρ_{20}) – 0.18 (dynamic s_{11}) | 0.417 | 7.7 |

^a Pr >[t] <0.001 for regression coefficients in all models with 323 trees. Means for dependent and independent variables: σ_L = 49.9 MPa, static s_{11} = 75.4 TPa⁻¹, dynamic s_{11} = 75.3 TPa⁻¹, ρ_{20} = 761 kg/m³.

^b R² = Coefficient of determination of model.

^c CV = Coefficient of variation of model (%).

5.6 Conclusions

Results indicate that (a) juvenile wood of *C. spruceanum* is relatively strong and stiff, (b) there is genetic variation in juvenile-wood mechanical properties, and (c) a greater proportion of this variation occurs among families within provenances rather than among provenances. Heritability estimates suggest that selection would be more effective for ultimate crushing strength and the static parallel compliance coefficient than for air-dry density of the specimen and the dynamic parallel compliance coefficient. Genetic correlations indicate that selecting trees with denser wood and/or faster growing trees would increase strength and/or stiffness of the wood. These results, combined with results from another study of genetic variation in tree growth, suggest that there is potential to simultaneously improve tree growth, density and some mechanical properties of juvenile wood of this species. In addition, the non-destructive ultrasonic method appears suitable for estimating mechanical properties of juvenile wood of this species. Additional research is needed to evaluate (a) genetic correlations between mechanical properties of juvenile and mature wood; (b) heritability of mechanical properties of mature wood; (c) genetic correlations among tree growth, density and mechanical properties of mature wood; and (d) the ability of the non-destructive ultrasonic method to predict mechanical properties of mature wood of this species.

Chapitre 6 Radial variation in wood density and correlations with growth of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon

6.1 Résumé

La variation radiale dans la masse volumique a été étudiée pour 1225 arbres âgés de 39 mois à l'aide d'un essai de provenance/descendance de *Calycophyllum spruceanum* (Benth.) Hook. f. ex Shum. L'étude a été établie dans trois zones de plantation localisées dans le bassin de l'Amazonie péruvienne. La masse volumique séchée à l'air a été déterminée avec l'aide d'un densitomètre à rayons X de la moelle à l'écorce sur les spécimens découpés en tranches prélevés du côté sud de la tige. La masse volumique augmentait significativement de la moelle à l'écorce dans toutes les zones de plantation. La différence de la masse volumique entre la moelle et l'écorce était plus grande dans les zones où les arbres croissaient plus rapidement et pour les arbres à croissance plus rapide. Les corrélations phénotypiques ont également suggéré que la sélection des arbres à croissance plus rapide pourrait conduire à la production du bois avec une masse volumique moins homogène. Cela pourrait mener à des variations radiales pour d'autres propriétés qui soient corrélées avec la masse volumique. Nous comparons les résultats obtenus pour cette espèce avec d'autres espèces de feuillus tropicaux, et quelques implications pratiques sont discutées.

6.2 Abstract

Radial variation in wood density was investigated for 1225 trees at 39 months in a provenance/progeny test of *Calycophyllum spruceanum* (Benth.) Hook. f. ex Shum. The test was established in three planting zones located in one watershed in the Peruvian Amazon. Air-dry density was measured by x-ray densitometry from pith to bark on slices of wood sampled from the south-facing direction of the stem. Density increased significantly from pith to bark in all planting zones. The difference in density between the pith and bark was larger in the zones where trees grew more rapidly, and for trees with faster growth. Phenotypic correlations also suggested that selecting faster growing trees would result in less homogeneous wood density. This could lead to radial gradients in other properties that are correlated with density. Results are compared with other tropical hardwoods, and some practical implications are discussed.

6.3 Introduction

Fast growing and high-yielding tree plantations are becoming an important source of wood in tropical countries. *Calycophyllum spruceanum* (Bentham) Hooker f. ex Shumann (Rubiaceae family), known as capirona in Peru, is a valuable tree species that is being used in agroforestry plantations in the Peruvian Amazon (Sotelo Montes and Weber 1997). Its wood is appreciated in national and international markets for furniture, wall paneling and parquet floors (Toledo and Rincón 1996). It is a fast-growing pioneer species that colonizes the floodplain and disturbed forests in the Amazon of Peru, Brazil, Ecuador and Colombia (Linares et al. 1992). Trees in natural forests can reach 35 m in height and 1.8 m in diameter at breast height (Sears 2003). The wood is diffuse-porous and quite dense in natural stands (Keenan and Tejada 1984) and at a young age in plantations (Sotelo Montes et al. 2006a, chapter 2). Stems can be harvested for construction poles after 2 to 3 years, or for sawn timber after 15 to 20 years, and then coppiced for successive harvests. Farmers and industry commonly use wood from young trees, and they will use it even more in the future with the promotion of agroforestry and small-scale plantation forestry. Consequently, the properties of juvenile wood should be investigated more extensively (Zobel and Sprague 1998).

Radial variation in wood density within the tree stem has practical implications because it can directly affect shrinkage, strength and stiffness (Tsoumis 1991). When measured outward from the pith, properties of juvenile wood make a gradual transition toward those of mature wood (Bowyer et al. 2003). The effect of juvenile wood on wood properties has been investigated in several hardwood species in natural stands, but there has been limited research in hardwoods grown in plantations. Radial variation has been reported for several tropical hardwoods, including mature wood in natural stands (Wiemann and Williamson 1988, 1989a, 1989b; Butterfield et al. 1993; Hernández and Restrepo 1995; McDonald et al. 1995; Woodcock 2000; Parolin 2002), as well as juvenile (Butterfield et al. 1993) and mature wood in plantations (de Castro et al. 1993). In general, fast-growing pioneer species exhibit a radial increase in density from pith to bark, whereas slower-growing, late-successional species exhibit the reverse pattern (Woodcock and Shier 2002). The diffuse-porous hardwoods also exhibit a general increase in density from pith to bark (Panshin and de Zeeuw 1980).

A provenance/progeny test of *C. spruceanum* was established in one watershed in the Peruvian Amazon Basin (Sotelo Montes et al. 2006a, 2006b, 2006c, 2006d; chapters 2, 3, 4 and 5, respectively). The test demonstrated that there is significant genetic variation in wood density and tree growth, that density is under stronger genetic control than growth, and that there is a positive genetic correlation between growth and density at 39 months of age (Sotelo Montes et al. 2006a, chapter 2). This indicates that both wood volume and density of this species could be simultaneously improved in a tree breeding program by selecting faster growing trees. However, producing faster growing trees might produce larger radial (Woodcock and Shier 2002) and vertical gradients in wood density (Weber and Sotelo Montes 2005). Since density is positively correlated with wood shrinkage, strength and stiffness in *C. spruceanum* (Sotelo Montes et al. 2006c, 2006d; chapters 4 and 5, respectively), this could result in wood with less uniform properties and lower economic value. This paper presents additional results from the same provenance/progeny test at 39 months. The major objectives are to determine (a) if there is significant radial variation in wood density, and (b) if the difference in density between the bark and pith is positively correlated with tree growth. The major results are compared with other tropical hardwoods, and some practical implications are discussed.

6.4 Materials and methods

6.4.1 Sample region, study area, experimental design and management of the provenance/progeny test

The sample region and provenance/progeny test are located in the Aguaytía watershed of the western Peruvian Amazon (Figure 2.1). Open-pollinated seeds were collected from 200 selected mother trees (families) of *C. spruceanum* growing in natural stands in seven geographic locations (provenances) in the lower, middle and upper parts of the watershed. The number of selected trees was proportional to the total number in the provenance (~20% of trees selected). The test was established in the lower, middle and upper parts of the watershed. In general, soil fertility and mean annual rainfall increase from the lower to the upper part of the watershed. Details about the distribution of *C. spruceanum* in the sample region, sampling procedures, tree selection criteria, and the climate and soils in the sample region and study area are given elsewhere (Sotelo Montes et al. 2006a, chapter 2).

The experimental design was a randomized complete block (RCB) with 15 replications in total: five were established on different farms in each of the lower, middle and upper parts of the watershed (hereafter called planting zones). In each replication, the 200 families were randomly assigned to 200 experimental plots, with two trees per plot. Spacing was 2.5 by 2.5 m within and between rows. Two rows of border trees surrounded the experimental design on each site. Dead trees were replaced during the first dry season, but data collected on replants were not included in the analyses. Management practices included a cover crop, fertilizer application, branch pruning and manual weeding (see Sotelo Montes et al. 2006a for details, chapter 2). One tree in each experimental plot was thinned 39 months after planting. Thinning was mainly based on tree form (primarily stem bifurcations in the canopy) and growth.

6.4.2 Traits measured in the provenance/progeny test

Measurements were made on the thinned trees in nine of the 15 replications: three each in the lower, middle and upper zones of the watershed at 39 months. The other six replications (two in each planting zone) were excluded because mean diameter of trees was too small to provide adequate samples for determination of wood density. Although the thinned trees were not randomly selected from the two trees in each experimental plot, it is unlikely that this would affect the general conclusions. There are at least three reasons to support this assumption. (1) Wood density was not used as a selection criterion in the thinning. (2) Means for height and diameter (at 10 cm above ground) of the thinned trees (6.95 m and 9.24 cm, respectively) were essentially the same as the means for all trees in the nine replications (6.83 m and 9.16 cm, respectively). Therefore, we would expect that the mean density of the thinned trees would be similar to that of all trees in the nine replications. (3) Analysis of variance of height and diameter of the thinned trees produced essentially the same results as the analysis of variance of all trees in the nine replications, and all trees in the test. This indicates that the thinned trees were a representative sample, in terms of height and diameter, of all trees in the test.

Tree height was measured to the nearest cm using a meter stick or a telescopic measuring pole. Stem diameter at breast height (Dbh, 1.3 m above ground level) was measured to the nearest 0.1 cm using callipers for small trees and diameter tape for larger trees.

Wood samples for determination of density were obtained following a three-step process: (1) a cross-section disk (10 cm thick) was cut at breast height from each tree and stored at 4°C for 4 months; (2) a round slice (1.8 mm thick, without defects) was cut from the disk; (3) a strip (25 mm wide) was then ripped from bark to bark, passing through the pith and following the south to north direction. After cutting, the strips were conditioned at 20°C and 60% RH for 120 days to attain equilibrium moisture content (EMC) of approximately 12%, considered as the air-dry condition.

Air-dry density (air-dry mass to air-dry volume, kg/m^3) was measured with an X-ray densitometer (QTRS-01X tree ring analyzer; QMS 1999) in the southernmost radial direction of the strips. Density was measured every 0.04 mm for strips less than 20 mm in length, and every 0.24 mm for strips longer than 20 mm. For each tree, density data (excluding the pith and bark) were divided in three sample sections of equal length, hereafter called the inner, middle and outer sections. Mean air-dry density was calculated for each sample section, using at least 30 data points (sections with less than 30 data points were eliminated).

6.4.3 Statistical analyses

The SAS[®] statistical package, version 9.1 (SAS Institute Inc. 2002-2003), was used for all statistical analyses. Data transformations were not required to satisfy the assumptions of analysis of variance and other analyses. Analysis of variance of density was carried out across and within planting zones using the MIXED procedure with repeated measurements (i.e. the three sections) and the restricted maximum likelihood method. A full model was analyzed first, and was then reduced by eliminating the non-significant ($P > 0.30$, Milliken and Johnson 1992) sources of variation. The reduced model included the following sources of variation for the analysis across zones: sample section (S), zone (Z), replication nested in zone [R(Z)], provenance (P), family nested in provenance [F(P)], and the interactions [sample section by zone (S*Z), sample section by replication in zone (S*R(Z)), provenance by replication in zone (P*R(Z)) and family in provenance by zone (F(P)*Z)]. Sample section, zone and their interaction were fixed effects, and the other sources of variation were random effects. The model for the analyses within zones was similar to that used across zones, except that there was no source of variation due to zone and, therefore, no interactions with zones. Some F-ratios for testing fixed effects involved more than

one mean square in the denominator, and were tested with approximate degrees of freedom (Satterthwaite approximation). Least squares means (LSMEANS) were calculated for density in each sample section, and differences between each pair of LSMEANS were tested using t-tests. For each random effect, the Z-test was used to test if the variance component was significantly different from zero. Pearson correlations were calculated (CORR procedure) between growth traits and the mean air-dry density of each sample section as well as the difference in density between the outer and inner sections. Correlations were calculated for individual trees across zones and separately within each zone.

6.5 Results and discussion

Descriptive statistics of wood density of *Calycophyllum spruceanum* at 39 months are presented in Table 6.1. The mean air-dry density (720 kg/m^3) was very similar to the value observed in a parallel study carried out in the same provenance/progeny test (718 kg/m^3 ; Sotelo Montes et al. 2006d, chapter 5). The coefficient of variation (CV) was very low and almost identical (6%) with the other study (Sotelo Montes et al. 2006d, chapter 5). Low CVs have also been reported for juvenile wood of other tropical hardwoods in plantation (MacDonald et al. 1997; Wei and Borralho 1997; Bauch and Dünisch 2000; Miranda et al. 2001b; Raymond and Muneri 2001).

It was previously reported that trees grew more rapidly in the middle and upper zones than in the lower zone of the watershed. For example, mean tree height and diameter (10 cm above ground) at 39 months were 3.3 m and 4.8 cm, 6.7 m and 9.0 cm and 8.6 m and 11.4 cm, respectively in the lower, middle and upper zones (Sotelo Montes et al. 2006a, chapter 2).

Table 6.1. Descriptive statistics of mean air-dry wood density for *Calycophyllum spruceanum* at 39 months. Mean density was calculated for three equally-spaced sections between the pith and bark at breast height (inner, middle, outer). The difference in density between the outer and inner sections is also presented. Statistics are given for all trees across zones, and separately for trees in the lower, middle and upper zones of the watershed.^a

| Mean air-dry density (kg/m ³) | Mean | St. dev. | CV | Minimum | Maximum |
|---|------|----------|------|---------|---------|
| <u>Across zones (N = 1225)</u> | | | | | |
| Overall mean | 720 | 45 | 6.3 | 549 | 853 |
| Inner section | 672 | 47 | 7.0 | 470 | 848 |
| Middle section | 719 | 55 | 7.6 | 501 | 891 |
| Outer section | 769 | 55 | 7.2 | 565 | 905 |
| Difference: outer – inner section | 97 | 54 | 55.5 | -168 | 237 |
| <u>Lower zone (N = 314)</u> | | | | | |
| Overall mean | 699 | 42 | 6.0 | 549 | 807 |
| Inner section | 668 | 50 | 7.5 | 470 | 848 |
| Middle section | 689 | 50 | 7.2 | 501 | 817 |
| Outer section | 739 | 50 | 6.8 | 595 | 870 |
| Difference: outer – inner section | 71 | 51 | 73.0 | -150 | 197 |
| <u>Middle zone (N = 426)</u> | | | | | |
| Overall mean | 726 | 44 | 6.0 | 593 | 853 |
| Inner section | 672 | 48 | 7.1 | 545 | 816 |
| Middle section | 726 | 52 | 7.2 | 586 | 860 |
| Outer section | 780 | 53 | 6.7 | 594 | 899 |
| Difference: outer – inner section | 108 | 55 | 50.7 | -168 | 236 |
| <u>Upper zone (N = 485)</u> | | | | | |
| Overall mean | 728 | 44 | 6.1 | 569 | 835 |
| Inner section | 674 | 45 | 6.8 | 531 | 835 |
| Middle section | 731 | 53 | 7.3 | 539 | 891 |
| Outer section | 780 | 53 | 6.8 | 565 | 905 |
| Difference: outer – inner section | 106 | 49 | 46.5 | -81 | 237 |

^a CV = coefficient of variation (%).

Mean density increased from the inner to the outer section of the stem (Table 6.1), exhibiting the type 1 pattern according to Panshin and de Zeeuw (1980). This is in agreement with the general pattern that Woodcock and Shier (2002) observed for fast-growing pioneer species. In contrast, slower-growing late-successional species generally exhibit a radial decrease from pith to bark. Woodcock and Shier (2002) hypothesized that the radial increase in pioneer species reflects a shift in resources from height growth to structural reinforcement of the trunk as the trees reach the canopy. As Wiemann and Williamson (1989a, 1989b) explained, rapid height growth is essential for young trees of pioneer species in the humid tropics because there is intense

competition for light. But as the tree increases in height, it must also increase its structural stability, and this can be achieved by producing successively denser wood each year. In addition, the trunk of tall trees in the canopy may be subject to greater stress due to wind loading, and this can be reduced by producing denser wood near the base of the tree (Mosbrugger 1990; Niklas 1997b). Based on this reasoning, Parolin (2002) suggested that the radial increase in density from pith to bark might explain why a pioneer species with low wood density (like *Cecropia latiloba*) is relatively long lived in the Amazonian floodplains.

In the present study, mean density of all trees exhibited a 15% increase from pith to bark (Table 6.1). The radial variation in wood density was, however, higher for trees with higher growth rates (mean of 11% for trees in the lower zone compared with 16% in the middle and upper zones). This result is consistent with the hypotheses of Wiemann and Williamson (1989a, 1989b), Mosbrugger (1990) and Niklas (1997b) mentioned above. However, the increase of wood density from pith to bark is relatively low, even though it is within the range of other hardwood species from the Amazon (Woodcock 2000; Parolin 2002). The relatively low radial variation might be due to the young age of the trees in this study (Wiemann and Williamson (1989a), and/or because the wood density of *C. spruceanum* is greater than most of the pioneer tree species growing in the Amazon floodplain (Parolin 2002). It is known that the radial variation in density is less for denser woods than for lighter woods (Parolin 2002; Woodcock and Shier 2002). In addition, the relatively wide spacing among trees in this test could have produced little competition for light among trees, especially in the lower zone. This would lead to lower radial variation in wood density, especially in the lower zone. The radial increase in density reflects radial changes in anatomical characteristics (Dadswell 1958; Zobel and Sprague 1998). For diffuse-porous hardwoods, the density can increase if there is an increase in the proportion of fibers, the length of fibers, the thickness of fiber walls and/or in the diameter of vessels; and/or if there is a decrease in the number of vessels per surface area. For example, the radial increase in density was due primarily to the proportion of fibers in *Heliocarpus appendiculatus* (McDonald et al 1995), but to the fiber length in *Hyeronima alchorneoides* and *Vochisia guatemalensis* (Butterfield et al. 1993).

Although 95% of the trees exhibited a radial increase in density from pith to bark, there was considerable variation in the density gradient among trees. The difference in mean density between the outer and inner section ranged from -168 to 237 kg/m³ among all trees across zones, and the CV for this difference was very high (Table 6.1). The difference was negative for 5% of the trees, 0-50 kg/m³ for 13%, 50-100 kg/m³ for 31%, 100-150 kg/m³ for 36% and greater than 150 kg/m³ for 15% of the trees. Moreover, many trees exhibited non-linear patterns of radial variation in density. Hernández and Restrepo (1995) also found different gradients for radial variation in wood density among trees of *Alnus acuminata* H.B.K. sampled in different geographical regions.

Woodcock and Shier (2002) noted that the “general pattern” for radial variation often hides the fact that there may be many patterns among trees of the same species within the same stand. According to these authors, differences in radial variation among trees reflect the micro-environmental variability within the stand, which is relatively greater for young saplings than for older trees in the canopy. They argued that saplings may produce low- or high-density wood depending on their local micro-environment, whereas older trees in the canopy tend to converge towards an “optimal” density for the species and stand. Therefore, they hypothesized that the range in density among older trees in the canopy would be largest near the pith (i.e. the wood produced at the sapling stage) and smallest near the bark.

Although *C. spruceanum* trees were measured at 39 months in the present study, results in the lower planting zone were consistent with the hypothesis proposed by Woodcock and Shier (2002). First of all, there was no consistent pattern of variation in the range of wood density from the inner to the outer sections of the stem among the three zones. For example, the range decreased from pith to bark in the lower planting zone but tended to increase from pith to bark in the middle and upper zones: the range in density in the inner and outer sections, respectively, was 378 and 275 kg/m³ in the lower zone, 271 and 305 kg/m³ in the middle zone, and 304 and 340 kg/m³ in the upper zone (Table 6.1). As indicated previously, trees grew more slowly in the lower zone, compared with the middle and upper zones. Moreover, results suggested that there was relatively more micro-environmental variability in the replications located in the lower zone (Sotelo Montes et al. 2006a, chapter 2). The differences in micro-environmental variability were

probably related to the lower rainfall and less fertile soils in the lower zone, combined with farmers' erratic weeding habits. Therefore, results in the lower zone of the present study were consistent with the "micro-environmental variability" hypothesis proposed by Woodcock and Shier (2002). Results in the other two zones may reflect the fact that genetic control of wood density of *C. spruceanum* at 39 months is stronger in planting zones where trees grow more rapidly (Sotelo Montes et al. 2006a, chapter 2). Different patterns of radial variation in density at an early age in this species might be due to "micro-environmental variability" in zones where trees grow slowly, but primarily to genetic differences among trees in zones where trees grow rapidly. Genetic studies of radial variation at older ages in different planting zones are required in order to test this hypothesis.

The analysis of variance confirmed that the increase in mean density from pith to bark was statistically significant (Table 6.2). T-tests of LSMEANS (not shown) indicated that the three pair-wise differences in density between sample sections (outer–middle, outer–inner, middle–inner) were significant in the analysis of all trees across zones ($P < 0.001$) and in all three planting zones with one exception in the lower zone (middle–inner, $P > 0.05$). As expected from the discussion above, there was a significant interaction between sample section and planting zone, confirming that radial variation was not the same in all three planting zones. The radial gradient in wood density of *Vochysia guatemalensis* also differed among four sites in Costa Rica (Gonzalez and Fisher 1998).

The gradient in wood density was larger and almost linear in the middle and upper zones, but smaller and not linear in the lower zone (Figure 6.1). Therefore, results suggest that the radial gradient in density will be greater in zones where trees grow more rapidly. This is consistent with a study of vertical variation in wood density of this species at an early age (Weber and Sotelo Montes 2005): density was higher near the base of the stem and lower in the upper stem below the live crown; and this difference was greater in zones where trees grew faster.

Table 6.2. Analysis of variance of radial differences in mean air-dry wood density for *Calycophyllum spruceanum* at 39 months. Analyses are given for all trees across zones, and separately for trees in the lower, middle and upper zones of the watershed.^{a, b, c, d}

| Source of Variation | Across zones | | Source of Variation | Lower zone | | Middle zone | | Upper zone | |
|------------------------|--------------|------|------------------------|------------|------|-------------|------|------------|------|
| | P | VAR | | P | VAR | P | VAR | P | VAR |
| <u>Fixed effects:</u> | | | <u>Fixed effects:</u> | | | | | | |
| S | <0.001 | --- | S | 0.005 | --- | 0.002 | --- | <0.001 | --- |
| Z | 0.054 | --- | --- | --- | --- | --- | --- | --- | --- |
| S*Z | 0.026 | --- | --- | --- | --- | --- | --- | --- | --- |
| <u>Random effects:</u> | | | <u>Random effects:</u> | | | | | | |
| R(Z) | 0.131 | 3.4 | R | 0.264 | 3.0 | 0.292 | 3.7 | 0.197 | 4.5 |
| S*R(Z) | 0.015 | 4.1 | S*R | 0.112 | 4.1 | 0.090 | 7.2 | 0.155 | 1.0 |
| P | 0.121 | 2.3 | P | 0.231 | 2.3 | 0.219 | 2.0 | 0.220 | 1.6 |
| F(P) | <0.001 | 12.0 | F(P) | <0.001 | 34.8 | <0.001 | 28.6 | <0.001 | 28.2 |
| P*R(Z) | 0.024 | 1.1 | P*R | * | 0.0 | 0.086 | 1.9 | 0.086 | 1.9 |
| F(P)*Z | <0.001 | 18.0 | --- | --- | --- | --- | --- | --- | --- |
| Residual | <0.001 | 59.1 | Residual | <0.001 | 55.8 | <0.001 | 56.6 | <0.001 | 62.8 |

^a Sources of variation: S = sample section (inner, middle, outer), Z = zone, R = replication, R(Z) = replication in zone, P = provenance, F(P) = family in provenance, interactions [S*Z, S*R, S*R(Z), P*R, P*R(Z), F(P)*Z].

^b P = significance of F ratio for fixed effects and Z test for random effects. (* = variance component equals 0)

^c Degrees of freedom for numerator and denominator of F ratios for fixed effects: 2 and 6.76 for zone, 2 and 11.9 for sample section, 4 and 11.9 for sample section*zone in analysis across zones; 2 and 3.91 for sample in the lower, and 2 and 4 for sample in the middle and upper zones of watershed.

^d VAR = percentage of the total phenotypic variance explained by the variance component.

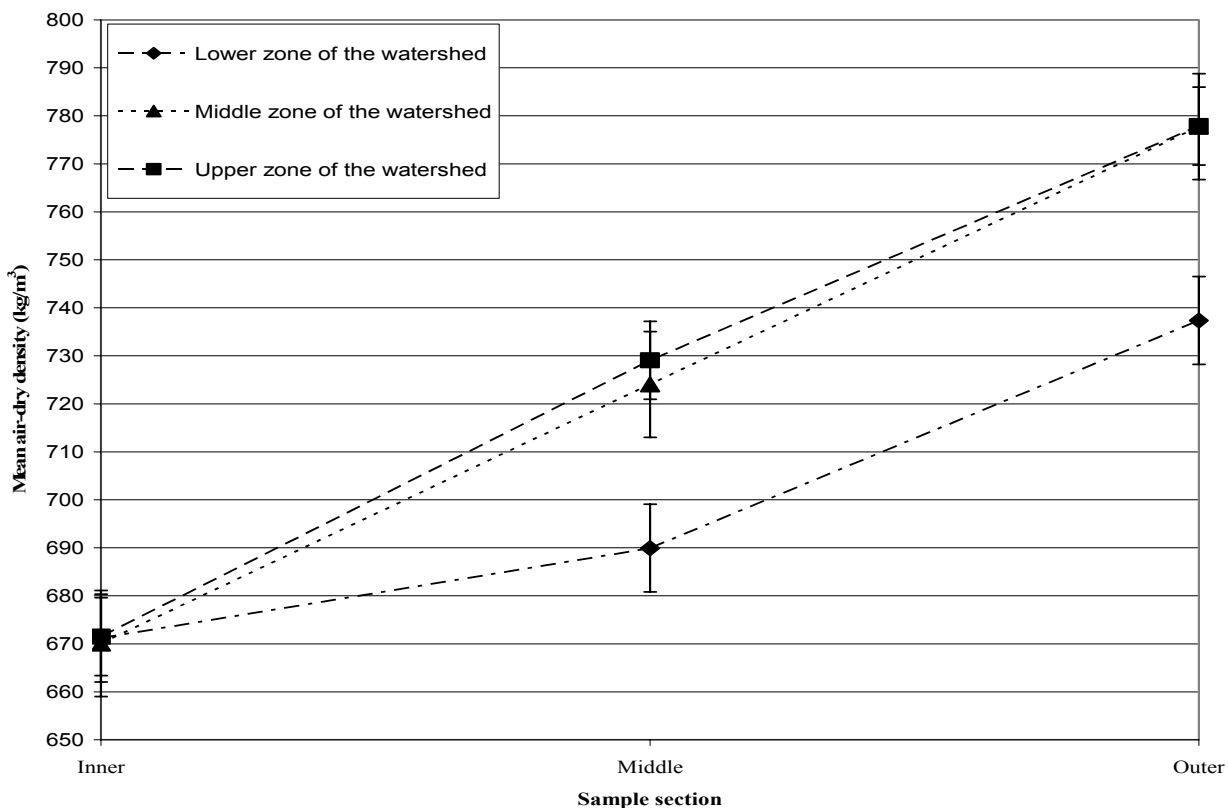


Figure 6.1. Mean air-dry density of wood of *Calycophyllum spruceanum* at 39 months. Least squares means are plotted for three equally-spaced sample sections in the stem at breast height (inner, middle, outer) in three planting zones. Vertical bars indicate ± 1 standard error.

Although mean wood density was lowest in the lower planting zone (Table 6.1), the difference in mean density among the three planting zones was not highly significant (Table 6.2). A similar result was observed for basic density of the same trees (Sotelo Montes et al. 2006a, chapter 2) and in another test of this species conducted in the same three planting zones (Weber and Sotelo Montes 2005). The environmental difference among the planting zones in this watershed was probably not large enough to produce more significant differences in wood density, even though there were significant differences in tree growth among the zones (Weber and Sotelo Montes 2005; Sotelo Montes et al. 2006a, chapter 2).

There was significant variation in wood density due to families within provenances (Table 6.2). However, the significant interaction between zones and families shows that differences among families were not stable across all three zones. In other words, some families had relatively high density in some zone(s) but relatively low density in other zone(s). Significant variation in basic wood density due to families was also observed in a parallel study (Sotelo Montes et al. 2006a, chapter 2), but differences among families were stable across all three zones in that study. In addition, there was significant variation in density due to provenances in the parallel study mentioned above, but not in the present study. The difference in results between the two studies is likely due to the different methods used to determine wood density.

Pearson correlations indicated that larger trees (i.e., taller and/or with greater Dbh) tended to have denser wood in the outer and middle stem sections (Table 6.3). These correlations are consistent with those reported for basic density measured at the same height (Sotelo Montes et al. 2006a, chapter 2), and may be interpreted in terms of the mechanical design of trees (Mosbrugger 1990). In contrast, most correlations between growth and density of the inner stem section were not significant or were too weak to be of practical interest, suggesting that tree growth has relatively little effect on density in this position.

Pearson correlations also indicated that larger trees tended to have a larger difference in density between the outer and inner stem, which is consistent with other studies. For example, Woodcock and Shier (2002) reported a significant correlation between tree height and the radial gradient in density in *Acer rubrum*. Hernández and Restrepo (1995) reported that the radial gradient in *Alnus acuminata* was larger for trees with lower density. In that study, tree height and density were negatively correlated, indicating that the faster-growing trees also tended to have a larger radial gradient in density.

Table 6.3. Pearson correlations between tree growth (height, Dbh) and mean air-dry wood density for *Calycophyllum spruceanum* at 39 months. Correlations are calculated with mean density of each sample section in the stem (inner, middle, outer) and the difference between the outer and inner section; and are given for all trees across zones, and separately for trees in the lower, middle and upper zones of the watershed. The significance is given in parentheses.^{a, b}

| | Across zones | | Lower zone | | Middle zone | | Upper zone | |
|--------------------------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| Density | Height | Dbh | Height | Dbh | Height | Dbh | Height | Dbh |
| Inner section | NS | NS | NS | -0.134 (0.018) | NS | NS | 0.103 (0.023) | 0.098 (0.030) |
| Middle section | 0.453 (<0.001) | 0.452 (<0.001) | 0.212 (<0.001) | 0.174 (0.002) | 0.403 (<0.001) | 0.412 (<0.001) | 0.353 (<0.001) | 0.368 (<0.001) |
| Outer section | 0.499 (<0.001) | 0.476 (<0.001) | 0.310 (<0.001) | 0.247 (<0.001) | 0.526 (<0.001) | 0.515 (<0.001) | 0.330 (<0.001) | 0.331 (<0.001) |
| Difference: outer – inner section | 0.466 (<0.001) | 0.462 (<0.001) | 0.400 (<0.001) | 0.370 (<0.001) | 0.560 (<0.001) | 0.553 (<0.001) | 0.261 (<0.001) | 0.268 (<0.001) |

^a Sample sizes for correlations with height and Dbh, respectively: 1216 and 1225 for all trees, 312 and 314 in lower zone of watershed, 422 and 426 in middle zone of watershed, 482 and 486 in upper zone of watershed.

^b NS = not significant ($P > 0.05$).

Genetic correlations, estimated in the same test, indicate that selecting faster-growing trees of *C. spruceanum* at a young age will result in denser wood (Sotelo Montes et al. 2006a, chapter 2). The present study suggests that this selection could also result in a larger difference in density between the outer and inner stem. Since wood density is positively correlated at the genetic level with wood shrinkage, strength and stiffness (Sotelo Montes et al. 2006c, 2006d; chapters 4 and 5, respectively), this selection could produce significant radial variation in these properties which, in turn, could lower the value of the wood. Therefore, tree breeders should select trees with minimal radial variation in density for their breeding population (or populations), while also ensuring that the other physical and mechanical properties of the wood are adequate for the desired uses. This study demonstrates that there is considerable variation among trees, so selecting trees with minimal radial variation in density should not be difficult. Considering the genetic correlations among wood properties, it is possible to simultaneously increase wood volume, density, strength and stiffness at a young age in this species in a single breeding population (Sotelo Montes et al. 2006a, 2006d; chapters 2 and 5, respectively). However, a

separate breeding population would be recommended if tree breeders want to produce wood with very low shrinkage (Sotelo Montes et al. 2006c, chapter 4).

6.6 Conclusions and recommendations

This study demonstrates that there is significant radial variation in wood density of *C. spruceanum* at a young age in the Peruvian Amazon. Air-dry density increased from pith to bark in 95% of the trees sampled, but there was considerable variation among trees in the gradient from pith to bark, and the gradient was non-linear for many trees. Results suggest that the radial gradient in density will be larger for faster-growing trees and in planting zones where trees grew faster. Since tree growth, wood density, shrinkage, strength and stiffness are positively correlated at the genetic level, selection of faster-growing trees and/or trees with denser wood might produce greater radial variability not only in density but also in wood shrinkage, strength and stiffness. Tree breeders, therefore, should attempt to select trees with minimal radial gradients in wood density. Additional research on older trees of *C. spruceanum* is needed in order to evaluate (a) radial variation in wood physical and mechanical properties at different ages, (b) genetic control of these wood properties at each age, (c) genetic correlations among these properties and with tree growth at each age, and (d) age-age correlations for these wood properties and growth. This research should consider the rotation ages for its two principal wood products (construction poles, 2-3 years rotation; sawn timber, 15-20 years).

Conclusions générales

Le présent projet de recherche a été réalisé à partir d'un essai de provenance/descendance (7 provenances, 200 familles) de jeunes arbres de *Calycophyllum spruceanum* [Benth.] Hook. f. ex Shum. L'essai a été établi par le Centre Mondial pour l'Agroforesterie (ICRAF) dans trois zones de plantation localisées dans le bassin de l'Aguaytía en amazonie péruvienne. Les semences de 200 arbres-mères ont été récoltées dans le même bassin. L'objectif principal de cette recherche était d'évaluer la variation génétique de la croissance et des propriétés du bois de jeunes arbres, la force de leur contrôle génétique, ainsi que leurs corrélations au niveau génétique et phénotypique dans différentes zones de plantation.

La hauteur de l'arbre et le diamètre près du niveau du sol des arbres ont été mesurés à l'âge de 16, 28 et 39 mois. Le diamètre de la tige à la hauteur de la poitrine (1,3 m) et les propriétés du bois (masse volumique, couleur, retrait, résistance maximale [σ_L], et coefficients de déformation statique et dynamique [s_{11}]) ont été évalués à l'âge de 39 mois. La masse volumique basale a été mesurée sur rondelles de 20 mm d'épaisseur obtenues à 1,3 m de hauteur. La couleur a été évaluée par le système CIELAB sur des baguettes de 25 x 25 x 450 mm échantillonnées entre 0,75 et 1,2 m de hauteur. Le retrait et la compression longitudinale ont été mesurés sur des éprouvettes de deux dimensions (15 x 15 x 60 mm et 20 x 20 x 80 mm) obtenues entre 0,30 et 0,75 m de hauteur pour le retrait et entre 0,75 et 1,20 m de hauteur pour la compression. Le coefficient de déformation dynamique (s_{11}) a été mesuré par ultrasons sur carottes de sondages de 10 mm de diamètre extraites à 1,3 m de hauteur. La variation radiale de la masse volumique a été mesurée de la moelle à l'écorce par densitométrie à rayons X sur des lamelles de 18 x 250 mm échantillonnées à 1,3 m de hauteur.

Les conclusions de chaque volet de cette recherche ainsi qu'une conclusion générale et des recommandations sont présentées ci-dessous.

Variation de la croissance des arbres et de la masse volumique du bois

Dans une étude portant sur la croissance et la masse volumique du bois, nous avons démontré que l'on pouvait augmenter potentiellement la production des plantations forestières par la sélection

des provenances à croissance rapide et par la sélection de familles supérieures à l'intérieur de ces provenances. Puisqu'un plus grand pourcentage de la variance phénotypique totale (VAR) était dû à l'origine familiale comparativement aux provenances, un gain potentiel de rendement plus élevé peut être obtenu par la sélection des familles qui croissent plus rapidement. Par contre, les différences de rendement moyen entre les zones de plantation étaient plus importantes que les variations de rendement observées entre les familles et les provenances. Par conséquent, les plus grands gains de rendement sont susceptibles d'être obtenus si l'on sélectionne d'abord la meilleure zone de plantation et, par la suite les familles qui sont mieux adaptées à ces zones et qui croissent le plus rapidement.

Nous avons aussi démontré que la masse volumique du bois pouvait être augmentée par la sélection de meilleures familles, mais que de tels gains n'étaient pas possibles par la sélection des meilleures provenances. Même si l'effet des zones de plantation n'a pas été trouvé significatif, il n'en demeure pas moins que les conditions environnementales des zones de plantation devaient être prises en considération parce qu'elles ont un grand effet sur la croissance des arbres.

Selon nos résultats, il appert que la sélection des arbres basée sur leur croissance peut être faite à un très jeune âge. Les estimations d'héritabilité individuelle (h_i^2) pour la hauteur de l'arbre et le diamètre de la tige suggèrent que la sélection des arbres pourrait être aussi effective dès l'âge de 16 mois. En outre, la sélection peut être plus efficace dans les zones où les arbres croissent plus rapidement. Cela est dû au fait que l'héritabilité estimée au sens strict h_i^2 pour les caractères de croissance était plus élevée dans la zone où les arbres croissaient plus rapidement.

Les corrélations génétiques entre la croissance de l'arbre et la masse volumique du bois furent aussi positives et très élevées. Ceci indique que l'améliorateur peut à la fois augmenter le volume et la masse volumique du bois en sélectionnant les arbres qui croissent plus rapidement.

Variation dans la couleur du bois

Le second volet de l'étude sur la couleur de bois nous a montré que capirona présentait une couleur jaune à l'âge de 39 mois. La variation dans la clarté du bois était beaucoup plus

perceptible que la variation dans les tons rougeâtre et jaunâtre, ce qui a déjà été rapporté pour le bois d'autres feuillus tropicaux.

Nos résultats indiquent également que les zones de plantation ont produit des différences significatives dans le ton rougeâtre de la couleur du bois. Comme le marché préfère actuellement un bois plus claire et jaunâtre, nos résultats suggèrent que les zones où les arbres croissent plus rapidement seraient meilleures pour la production du ton de couleur désiré.

L'étude a fait aussi ressortir que la clarté du bois variait significativement entre les familles dans l'analyse de l'ensemble des zones. Cela indique que les familles dont le bois est de couleur plus claire (préférée par les marchés actuellement) peuvent être identifiées à un jeune âge par les programmes d'amélioration et que, si les préférences de marché changent dans le futur, on pourrait identifier les familles avec une couleur de bois plus foncée. Cette conclusion n'est toutefois valide que pour les produits de bois juvénile puisque les corrélations entre le bois mature et le bois juvénile ne sont pas connues pour cette espèce.

Nous avons aussi constaté que la couleur du bois était relativement uniforme à l'intérieur des échantillons. Cela s'avère important parce que le marché préfère des produits de couleur uniforme. Par contre, les échantillons de bois étaient relativement courts et ont été obtenus dans la partie basse de la tige.

Nos estimations de h_i^2 suggèrent que la sélection basée sur la couleur du bois serait plus effective dans les zones de plantation où les arbres croissent plus rapidement. Des résultats similaires ont été observés pour la croissance de l'arbre, la masse volumique du bois et le retrait du bois (décrite ci-dessous). Par contre, la sélection basée sur la couleur produirait des gains génétiques relativement moins considérables parce qu'on n'a retrouvé peu de variation phénotypique dans les variables de couleur et une h_i^2 modérément élevée pour les tons rougeâtre et jaunâtre.

Si on considère la force des corrélations génétiques et les erreurs standard, la sélection des arbres qui croissent plus rapidement et qui ont du bois plus dense aurait probablement peu d'effet sur la couleur du bois juvénile. Ceci est important parce qu'il en découle qu'en général, les améliorateurs pourraient se concentrer sur l'augmentation du volume et de la masse volumique du bois sans que cela ait un effet négatif sur la couleur du bois.

Variation dans le retrait du bois

Dans une troisième étude, nous nous sommes intéressés à la variation dans le retrait du bois. Il en ressort que le bois a présenté un faible retrait à l'âge de 39 mois si on considère sa masse volumique. Par contre, le coefficient d'anisotropie était de 2,2 pour le retrait total. Ce niveau élevé d'anisotropie peut être dû à une combinaison de facteurs liés au bois juvénile.

On a trouvé un effet significatif des zones de plantation sur le retrait du bois. Le retrait était plus grand dans les zones où les arbres croissaient plus rapidement et avaient une plus grande masse volumique moyenne. Par conséquent, la différence de retrait entre les deux zones est probablement due à la différence dans la masse volumique du bois.

Notre étude a aussi permis de montrer l'existence d'une variation significative de propriétés de retrait du bois entre les familles à l'intérieur d'une provenance et pour quelques propriétés de retrait entre les provenances. Les familles à l'intérieur d'une provenance expliquaient un plus grand pourcentage de la variation phénotypique totale que les provenances. Ainsi, les améliorateurs peuvent espérer des gains plus élevés de la sélection familiale que de celles des provenances. Ce résultat est important en ce sens qu'il indique que les améliorateurs peuvent sélectionner des familles présentant un retrait du bois moins élevé. Par contre, cette sélection peut résulter en l'obtention d'un bois moins dense (voir ci-dessous).

Les estimations de l'héritabilité au sens strict indiquent que le contrôle génétique était modérément fort pour le retrait linéaire et volumétrique mais qu'il était moins élevé pour le coefficient d'anisotropie. La masse volumique basale du bois avait une plus grande h_i^2 que les paramètres de retrait, ce qui indique que la sélection serait plus effective si elle était basée sur la masse volumique, quelque peu moins effective si elle était basée sur le retrait linéaire et volumétrique et encore moins effective si elle était basée sur le coefficient d'anisotropie. Comme pour la croissance, la masse volumique basale et la couleur du bois, les valeurs de h_i^2 suggèrent que la sélection basée sur le retrait du bois serait plus effective dans les zones de plantation où les arbres croissent plus rapidement.

Les estimations des corrélations génétiques obtenues dans cette étude indiquent que le bois plus dense avait une tendance à avoir un plus grand retrait linéaire et volumétrique. En outre, les plus

gros arbres avaient tendance à avoir un bois produisant des retraits linéaire et volumétrique plus grands. Cela reflète probablement les relations sous-jacentes entre la croissance de l'arbre et la masse volumique ainsi que la relation entre la masse volumique et le retrait plutôt qu'une relation directe entre la croissance de l'arbre et le retrait.

Ces corrélations génétiques posent un défi aux améliorateurs que veulent à la fois augmenter le volume et la masse volumique et réduire le retrait du bois. Nous suggérons ainsi d'identifier les caractères plus importants pour les marchés actuels et futurs et de développer une stratégie d'amélioration à l'avenant. Le développement de populations multiples d'amélioration pourrait être une stratégie plus réaliste permettant de viser le développement de variétés spécifiques pour des besoins divers et divergents.

Variation dans la résistance et la rigidité du bois

Nous nous sommes ensuite intéressés à la variation des propriétés mécaniques du bois de capirona. Il appert que le bois juvénile de *C. spruceanum* est relativement résistant et rigide si on considère sa masse volumique. Ces caractéristiques sont essentielles à des fins de construction. La résistance et la rigidité du bois n'ont pas varié beaucoup selon les zones de plantation, ce qui suggère que les différences environnementales ont peu d'effets sur ces propriétés du bois. Par contre, seules deux des trois zones de plantation ont été incluses pour cette étude.

Dans ce volet, nous avons montré que le volume, la masse volumique, la résistance et la rigidité pouvaient être haussés concurremment par la sélection génétique. Ceci s'explique par le fait qu'on a trouvé des variations génétiques significatives dans la résistance et la rigidité du bois dues aux provenances. De même des différences significatives sont ressorties dans la variation génétique due aux familles à l'intérieure d'une provenance. En fait, les estimations de h_i^2 étaient modérément élevées pour la résistance et la rigidité (légèrement plus élevée pour la résistance) et les corrélations génétiques étaient telles que la sélection des arbres qui croissent plus rapidement et/ou qui ont un bois plus dense pourrait résulter dans l'obtention d'un bois plus résistant et plus rigide.

La rigidité a été estimée dans cette étude en utilisant des méthodes destructives et non destructives (respectivement s_{11} statique et dynamique). On a trouvé des variations génétiques significatives pour les deux propriétés, mais l'ampleur de la variation génétique était légèrement plus grande pour la rigidité statique que pour celle dynamique (s_{11}). En conséquence, l'héritabilité estimée était plus élevée pour la rigidité statique que pour la rigidité dynamique. En contrepartie, la corrélation phénotypique entre ces paramètres était modérément élevée, ce qui indique que la méthode non destructive est très utile pour l'estimation de la rigidité du bois de même que de sa résistance.

Variation radiale de la masse volumique du bois

Le dernier volet a comporté l'étude de la variation radiale de la masse volumique du bois. Nous avons obtenu une augmentation radiale significative de la masse volumique de la moelle vers l'écorce des arbres de *C. spruceanum*. Ce résultat suit le modèle général observé pour les espèces pionnières à croissance rapide. Cependant, l'augmentation radiale moyenne de la masse volumique était de seulement 15% de la moelle vers l'écorce. Cette faible différence est probablement due au jeune âge des arbres ainsi qu'au fait que la masse volumique était très élevée pour cette espèce par rapport à d'autres espèces pionnières tropicales.

Le gradient radial de la masse volumique était plus grand pour les arbres à croissance rapide et pour les zones de plantation à plus grande croissance. Ces résultats, combinés avec le fait que la croissance et la masse volumique du bois sont positivement corrélées au niveau génétique, suggèrent que la sélection des arbres à croissance rapide devrait augmenter non seulement la masse volumique du bois mais aussi son gradient de la moelle vers l'écorce. Puisque la masse volumique est positivement corrélée au niveau génétique au retrait, à la résistance et à la rigidité du bois, cette sélection pourrait avoir comme conséquence de conduire à une hausse de la variation radiale de ces autres propriétés du bois. Les marchés préfèrent des billes dont les propriétés du bois sont uniformes, ainsi la variation radiale des propriétés physiques et mécaniques pourrait réduire la valeur marchande du bois.

Cette étude a fait ressortir une variation considérable du gradient radial entre les arbres. Plusieurs de ces arbres ont donc montré une augmentation radiale relativement faible de la masse

volumique. Par exemple, l'augmentation radiale était d'au plus 50 kg/m^3 pour 13% des arbres. Cette situation offre la possibilité de sélectionner des arbres avec un gradient radial de la masse volumique faible et de réduire par ce fait les gradients radiaux potentiels pour les autres propriétés du bois.

Remarques générales

Les résultats de cette étude indiquent que par la sélection, on peut à la fois augmenter le volume, la masse volumique, la résistance et la rigidité du bois juvénile de *C. spruceanum*, avec relativement peu d'effets sur la couleur du bois. Le retrait du bois de cette espèce est relativement peu élevé, mais si les améliorateurs veulent le réduire davantage, ils feront face à un défi puisque on a trouvé des corrélations génétiques positives entre le retrait du bois, la masse volumique du bois et la croissance de l'arbre.

Il existe très peu d'études sur la variation génétique des propriétés du bois des espèces de feuillus tropicaux. Par conséquent, beaucoup de questions générées par cette étude n'ont pas encore de réponse. Nous espérons que des recherches futures puissent venir y répondre dans un avenir rapproché.

Recommandations

À la suite des résultats des études menées dans le cadre de ce projet de doctorat, nous souhaitons terminer ce chapitre de conclusions en faisant deux recommandations:

Nous supposons que pour cette espèce, les priorités des améliorateurs sont d'augmenter le volume, la masse volumique, la résistance et la rigidité du bois. Par conséquent, nous recommandons qu'ils utilisent comme critères de sélection à la fois la croissance de l'arbre, la masse volumique, la résistance et la rigidité du bois. Par exemple, les améliorateurs pourraient d'abord sélectionner les provenances à croissance rapide en se basant sur le Dbh et, par la suite, les familles à l'intérieur des provenances qui ont un bois plus dense, résistant et rigide. Des méthodes non destructives devraient être utilisées pour déterminer la masse volumique du bois, la résistance et la rigidité. En outre, des essais de provenances/descendances ainsi que des

plantations pourraient être établies dans les zones de plantation où les arbres croissent plus rapidement.

Par contre, si la priorité va à la production d'un bois avec relativement peu de retrait et une stabilité dimensionnelle élevée, nous suggérons aux améliorateurs de sélectionner les arbres qui croissent moins rapidement avec une masse volumique moins élevée. Si on considère les corrélations génétiques existant entre le retrait du bois et d'autres caractères importants, il ne semble pas réaliste d'essayer à la fois d'augmenter le volume, la masse volumique, la résistance et la rigidité du bois et de réduire le retrait dans une même population d'amélioration. Par conséquent, des populations multiples d'amélioration devraient être développées dans ce cas extrême.

Pour répondre aux questions soulevées dans les diverses études contenues dans cette thèse, nous recommandons que des recherches soient menées sur les thèmes suivants:

- Des études sur les corrélations entre la croissance de l'arbre et les propriétés du bois ainsi que l'héritabilité de ces caractères dans des arbres plus matures, par exemple, dont l'âge est plus proche de l'âge de rotation;
- Des études sur les corrélations entre âges pour la croissance et les propriétés du bois en se basant sur l'âge de rotation pour la construction des poteaux légers (minimum de 2 à 3 ans) et du bois de sciage (de 15 à 20 ans) ainsi que des études sur l'évaluation de l'efficacité de la sélection à un très jeune âge pour cette espèce;
- Des études sur la variation des propriétés du bois en relation avec la position verticale et radiale de la tige: ces études doivent être faites (a) sur les arbres à un très jeune âge et aussi aux âges différents jusqu'à l'âge de rotation, et (b) dans une plus large amplitude de conditions environnementales;
- Des études sur la variation de la couleur avec la maturation du bois, les propriétés anatomiques et structurelles du bois et la composition chimique des constituants de la paroi cellulaire;
- Des études sur la variation génétique des propriétés du bois juvénile et mature qui déterminent la valeur acoustique pour les instruments musicaux.

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Annexes

Annexe A: Paramètres génétiques et statistiques

Formule générale d'héritabilité au sens strict:

$$h_i^2 = \frac{\sigma_A^2}{\sigma_P^2}, \quad (1)$$

où: σ_A^2 = variance génétique additive,
 σ_P^2 = variance phénotypique.

Estimation de h_i^2 pour l'ensemble des zones de plantation (de l'ANOVA pour l'ensemble de zones):

$$h_i^2 \text{ pour 2 arbres/parcelle} = \frac{3\sigma_{f(p)}^2}{(\sigma_{f(p)}^2 + \sigma_{f(p)*z}^2 + \sigma_{f(p)*r(z)}^2 + \sigma_e^2)}, \quad (2)$$

où: $\sigma_{f(p)}^2$ = composante de la variance d'un caractère due aux familles dans les provenances,
 $3 \sigma_{f(p)}^2$ = estimation de σ_A^2 ,
 $\sigma_{f(p)*z}^2$ = composante de la variance d'un caractère due à l'interaction entre les familles dans les provenances et les zones de plantation,
 $\sigma_{f(p)*r(z)}^2$ = composante de la variance due à l'interaction entre les familles dans les provenances et les répétitions dans les zones de plantation,
 σ_e^2 = composante de la variance due à l'erreur (variance entre les 2 arbres/parcelle).

$$h_i^2 \text{ pour 1 arbre/parcelle} = \frac{3\sigma_{f(p)}^2}{(\sigma_{f(p)}^2 + \sigma_{f(p)*r}^2 + \sigma_e^2)}, \quad (3)$$

où: σ_e^2 = composante de la variance due à l'erreur ($\sigma_{f(p)*r}^2$).

Estimation de h_i^2 à l'intérieur d'une zone de plantation (de l'ANOVA dans chaque zone):

$$h_i^2 \text{ pour 2 arbres/parcelle} = \frac{3\sigma_{f(p)}^2}{(\sigma_{f(p)}^2 + \sigma_{f(p)*r}^2 + \sigma_e^2)}, \quad (4)$$

où: $\sigma_{f(p)}^2$ = composante de la variance d'un caractère due aux familles dans les provenances,

$3 \sigma_{f(p)}^2$ = estimation de σ_A^2 ,

$\sigma_{f(p)*r}^2$ = composante de la variance due à l'interaction entre les familles dans les provenances et les répétitions,

σ_e^2 = composante de la variance due à l'erreur (variance entre les 2 arbres/parcelle).

$$\underline{h_i^2} \text{ pour 1 arbre/parcelle} = \frac{3\sigma_{f(p)}^2}{(\sigma_{f(p)}^2 + \sigma_e^2)}, \quad (5)$$

où: σ_e^2 = composante de la variance due à l'erreur ($\sigma_{f(p)*r}^2$).

Estimation de l'erreur-type de h_i^2 (Becker 1984):

$$\text{se}(h_i^2) = 4 \sqrt{\frac{2(1-t)^2 [1+(k-1)t]^2}{k(k-1)(s-1)}}, \quad (6)$$

où: $t = h_i^2/3$,

k = coefficient de $\sigma_{f(p)}^2$, soit du carré moyen espéré pour les familles dans les provenances (~ nombre d'arbres/famille),

s = nombre de familles.

Estimation de la corrélation génétique entre les caractères «x» et «y»:

$$r_g = \frac{\sigma_{f(p)xy}^2}{\sqrt{\sigma_{f(p)x}^2 \sigma_{f(p)y}^2}}, \quad (7)$$

où: $\sigma_{f(p)x}^2$ = composante de la variance du caractère «x» due aux familles dans les provenances,

$\sigma_{f(p)y}^2$ = composante de la variance du caractère «y» due aux familles dans les provenances,

$\sigma_{f(p)xy}^2$ = composante de la covariance entre les caractères «x» et «y» due aux familles dans les provenances, estimée par $\sigma_{f(p)xy}^2 = (\sigma_{f(p)[x+y]}^2 - \sigma_{f(p)x}^2 - \sigma_{f(p)y}^2) /$

2, où $\sigma_{f(p)[x+y]}^2$ = composante de la variance de la somme de «x» et «y» due aux familles dans les provenances.

Estimation de l'erreur type de la corrélation génétique (Falconer et Mackay 1996):

$$se(r_g) = \frac{(1-r_g^2)}{\sqrt{2}} \sqrt{\frac{[se(h_i^2 x)][se(h_i^2 y)]}{(h_i^2 x)(h_i^2 y)}}, \quad (8)$$

où: r_g = corrélation génétique entre les caractères «x» et «y»,
 $h_i^2 x$ = héritabilité du caractère «x»,
 $h_i^2 y$ = héritabilité du caractère «y»,
 $se(h_i^2 x)$ = erreur type de l'héritabilité du caractère «x»,
 $se(h_i^2 y)$ = erreur type de l'héritabilité du caractère «y».

Statistiques utilisées en ANOVA

| | |
|------------|--|
| CV | Coefficient de variation, qui est égal à la racine carrée du terme de l'erreur (l'écart type) divisée par la moyenne. |
| DF | Degrés de liberté. |
| SS | Somme des carrés. |
| MS | Moyenne des carrés, qui est égale à la somme des carrés divisée par les degrés de liberté selon les traitements ou les erreurs. |
| Rapport F | Valeur calculée de F, qui est égale à la moyenne des carrés du traitement divisée par la moyenne des carrés de l'erreur pour le traitement. Le rapport F est utilisé pour tester si chaque source de variation dans le modèle soit significative (hypothèse nulle: l'effet de la source de variation = 0 pour les facteurs fixés, ou la variance dû à la source = 0 pour les facteurs aléatoires). |
| «Quasi F» | Rapport F en lequel le dénominateur a deux ou plus moyennes carrés. |
| DF appaux. | Degrés approximatifs de liberté pour le dénominateur de «quasi F». |
| Pr > F | Signifie la probabilité d'observer une valeur de F aussi grande dû au hasard (avec les degrés de liberté donnés pour le numérateur et dénominateur). |

| | |
|------------|---|
| R^2 | Coefficient de détermination, qui est égal à la somme des carrés du modèle divisée par la somme des carrés totale. |
| z | Valeur calculée de z , pour tester si la composant de variance soit significative (par exemple, hypothèse nulle: $\sigma^2_{f(p)x}$ (composante de variance du caractère «x» dû aux familles dans les provenances) = 0): $z = (\sigma^2_{f(p)x} - 0) / [\text{écarte type } (\sigma^2_{f(p)x})]$. |
| $Pr > z$ | Signifie la probabilité d'observer une valeur de z aussi grande dû au hasard. |
| LSMEANS | Moindres Carrés Moyens. La méthode des moindres carrés est une méthode d'estimation des paramètres dans un modèle, par la minimisation de la somme des carrés des différences entre les valeurs observées et les valeurs théoriques d'une variable. |
| t | Valeur calculée de t , pour tester si la différence entre deux moyennes (estimés par LSMEANS) soit significative (hypothèse nulle: $(\bar{y}_1 - \bar{y}_2) = 0$): $t = (\bar{y}_1 - \bar{y}_2) / [\text{écarte type } (\bar{y}_1 - \bar{y}_2)]$. |
| $Pr > t $ | Signifie la probabilité d'observer une valeur de t aussi grande dû au hasard. |

Statistiques utilisées en corrélation linéaire

| | |
|-----|---|
| r | Coefficient de corrélation linéaire de Pearson: $r = \frac{\text{cov}(x,y)}{\sqrt{\text{var}(x)\text{var}(y)}}$, (9) |
| | où $\text{cov}(x,y)$ = covariance entre les caractères «x» et «y» des individus, $\text{var}(x)$ = variance en caractère «x» entre des individus, $\text{var}(y)$ = variance en caractère «y» entre des individus. |
| t | Valeur calculée de t , pour tester si le coefficient de corrélation linéaire soit significative (hypothèse nulle: $r = 0$): $t = \frac{(r - 0)}{\sqrt{(1 - r^2)/(n - 2)}}$. (10) |

$Pr > t$ Signifie la probabilité d'observer une valeur de t aussi grande dû au hasard ($n - 2$ degrés de liberté où $n =$ le nombre d'individus).

Statistiques utilisées en régression linéaire simple

y_t Valeur de y_t prédit pour la équation: $y_t = \beta_0 + \beta_1(x_t) + \varepsilon_t$, (11)

où

$t =$ échantillon de T paires des observations $[(x_1, y_1), (x_2, y_2) \dots (x_T, y_T)]$,

$y =$ variable dépendent,

$x =$ variable indépendant,

$\beta_0 =$ ordonnée à la origine de la droite,

$\beta_1 =$ pente de la droite,

$\varepsilon_t =$ erreur aléatoire (écarte entre y_t et la droite en x_t).

R^2 Coefficient de détermination, qui est égal à la somme des carrés du modèle de régression divisée par la somme des carrés totale, c'est-à-dire, la proportion de la variation totale dû au modèle.

$1 - R^2$ Proportion de la variation totale qui n'est pas dû au modèle (c'est-à-dire la proportion dû à l'erreur de la régression).

CV Coefficient de variation, qui est égal à la racine carrée du terme de l'erreur divisée par la moyenne de variable dépendent.

t Valeur calculée de t , pour tester si le coefficient de régression est significatif (hypothèse nulle: $\beta_1 = 0$):

$t = (\beta_1 - 0) / [\text{écarte type } (\beta_1)]$.

$Pr > |t|$ Signifie la probabilité d'observer une valeur de t aussi grande dû au hasard ($n - 2$ degrés de liberté où $n =$ le nombre d'individus).

Annexe B: Propriétés acoustiques

La vitesse de propagation d'une onde longitudinale

$$v = \sqrt{\frac{E}{\rho}} \cdot 10^6, = \frac{d}{t} \text{ (m/s)} \quad (12)$$

où: v = vitesse de propagation des ultrasons,

d = distance parcourue par l'onde (m),

t = temps de parcours (s),

E = module d'Young (Mpa),

ρ = masse volumique du bois à 12% de teneur en humidité (kg/m³)

Le rayonnement acoustique

$$r = \frac{v}{\rho} = \sqrt{\frac{E}{\rho^3}}, \quad (13)$$

où: r = rayonnement acoustique (m⁴/kg s).