

Is mahogany dysgenically selected?

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SUMMARY

One concern in the ongoing debate over the conservation status of mahogany has been the possibility that selective logging, as a form of negative phenotypic selection, might have led to deterioration in the genetic quality of populations. The incidence and degree of such 'dysgenic' effects is discussed, based on a consideration of mahogany logging practices, their expected genetic effects and empirical data on phenotypic selection in forest trees. Loggers have tended to avoid diseased, small, very large and poorly-formed individuals, and consequently logging has tended to increase the proportion of poor quality phenotypes relative to that before logging; in at least some conditions, selection differentials have been strongly negative. However, the upper limit for heritability of logger-selected traits in naturally-regenerated mahogany is probably no more than *c.* 0.1. Consequently, and assuming relatively extreme but realistic negative selection differentials of 50%, the maximum negative dysgenic response to a single logging-mediated phenotypic selection event is expected to be relatively small, i.e. $\leq 5\%$. This expectation is consistent with the empirical information from mahogany and other taxa. The implications of any dysgenic effects depend very much on the use and the future of dysgenically-selected populations. In managed populations, dysgenic effects could be reversed through positive selection. In the case of exploited but currently unmanaged natural populations, dysgenic selection is primarily of importance insofar as it affects fitness. As a threat to mahogany conservation and long-term sustainable production, it is probably insignificant in comparison with other genetic and non-genetic factors.

Keywords: dysgenic selection, genetic erosion, Meliaceae, Neotropics, selective logging, *Swietenia*

INTRODUCTION

The conservation status of mahogany (*Swietenia* spp.), particularly big-leaf, Brazilian or Honduras mahogany (*S. macrophylla* King), has recently attracted international attention (Bonner 1994; Friends of the Earth 1995; Robbins 2000; Jordan 2001; Greenpeace 2001). One concern has been that selective logging might have led to deterioration in the genetic quality of mahogany populations (CITES [Convention on International Trade in Endangered Species of Wild Fauna and Flora] 1997). However, there is disagreement about whether such effects have actually occurred. For example, Figueroa Colón (1994) remarked that 'allegations of genetic erosion in big-leaf mahogany (Styles & Khosla 1976)'... i.e. caused by selective harvesting... 'cannot be corroborated with factual information', whereas Namkoong *et al.* (2000) commented that 'dysgenic selection has been documented for *Swietenia macrophylla* King (mahogany) in Central America (Styles 1972)'. We attempt to inform this debate through a consideration of genetic and ecological factors and their probable implications. Although recent concerns have centred on *S. macrophylla*, we also consider *S. humilis* Zucc. (Pacific mahogany) and *S. mahagoni* (L.) Jacq. (small-leaf mahogany).

We define dysgenic selection as a reduction in the reproductive contribution of genetically superior individuals (i.e. relative to population members as a whole, for commercially or ecologically important traits), caused by their removal (felling) from the population. We examine the likelihood of dysgenic selection having occurred in mahogany by considering two classes of evidence: firstly, the intensity of phenotypic selection practised by loggers, and its expected genetic consequences; secondly, empirical evidence of the results of phenotypic selection in mahogany and other species. Genetic erosion due to random genetic drift is not the subject of this article, although we acknowledge that this may be of at least equal importance.

MAHOGANY LOGGING AS PHENOTYPIC SELECTION

The proposition that mahogany logging has been selective implies both that not all mahogany trees are removed, and that the probability of an individual tree being felled depends

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partly on its phenotype. Although mahogany logging has been practised by highly diverse groups, in different countries, environments and historical periods (for example from Florida to Bolivia, from modern logging companies to the slave-based operations of the colonial Caribbean), historical (see Miller 1941) and contemporary (Gullison *et al.* 1996) records, as well as the logic of commercial self-interest, leave little room for doubt that mahogany loggers have tended to leave some trees, and furthermore that they have tended to take ‘better’ trees than they leave. Below, we consider the nature of this selection, particularly the traits selected for and the intensity of selection.

Selected traits

There is evidence that diverse and sometimes correlated phenotypic characteristics have been taken into account by mahogany loggers. Here, these are considered under the three broad categories of tree healthiness, size and form.

Healthiness

Lamb (1966) reported that, historically, loggers avoided defective trees, such as those with termite infestation or heart-rot. Von Hagen (1940), reporting on contemporary logging practice on the Mosquito Coast (eastern Honduras), described a specific case: ‘care is taken to allow the termite-infested trees to stand . . . so that a method of natural reforestation is ensured’. More recently, Gullison *et al.* (1996) related that Bolivian chain-saw operators leave trees unfelled when trial chainsaw cuts reveal rot. These reports clearly imply that both modern-day and historical logging practice tends to favour healthier trees and, therefore, to increase the mean degree of heart-rot or termite infestation among trees in logged forests relative to that in unlogged forests.

Tree size

Loggers have selected both for and against large trees. In general, whether because of compliance with legal cutting limits or out of commercial self-interest, trees below a certain diameter have often been avoided. Conversely, older, larger trees have been avoided by loggers because of healthiness requirements (large old trees are more likely to be seriously diseased) and because harvesting equipment was unable to handle very large trees. Weaver and Sabido (1997) noted that, in Belize, ‘traditionally . . . trees too large to cut remained in the forest, incidentally serving as seed sources’. Because of the higher capacity of modern equipment, present day avoidance of large trees is likely to be purely because of heart-rot (Gullison *et al.* 1996). The direction and intensity of selection for tree size is further considered below.

Form

Finally, although mahogany trees growing in natural forest tend to be relatively well-formed (for example Snook 1993, p. 130), individuals with low, heavy branches and short merchantable logs nevertheless occur. In some cases, such

low value trees may nevertheless be cut (for example when chainsaw loggers are paid ‘piece-rate’; A.G. Blundell, personal communication 2003; J.E. Grogan, personal communication 2003). However, in general, loggers, particularly before the advent of modern harvesting equipment, are less likely to go to the expense of felling and extracting trees with little commercial value. Thus, in the case of Quintana Roo, Snook (1996) commented that ‘until the 1980s, high standards for export or for local veneer production resulted in imperfect mahogany trees being left standing after logging operations’. It therefore seems reasonable to conclude that in some cases negative selection for tree form has been applied.

Intensity of selection

Selection is defined not only by its target trait(s), but also by its strength, as measured by the selection differential S :

$$S = \mu_s - \mu,$$

where μ = the phenotypic population mean before selection (logging) and μ_s = the mean of selected (i.e. remnant) trees (Falconer 1989). S may also be expressed as a multiple of the phenotypic standard deviation of the population and trait, in which case it is termed the selection intensity (i); when a normally distributed trait is subjected to truncation selection (i.e. when the best, or worst, $x\%$ are chosen as progenitors of the next generation), i for a given selected proportion can be determined from tables of the properties of the normal distribution (Falconer 1989). Both ways of quantifying the strength of selection are of use in the present context.

Several authors have published information of relevance to the estimation of historical selection differentials associated with mahogany logging. This information is summarized below. In some cases, inter-trait correlations may occur. As a result, negative selection for one characteristic may offset negative selection in another. For example, loggers have often left ‘standing rotten’ trees (implying negative selection pressure for freedom from rot), which tend to be of above-average dimensions (implying positive selection pressure for tree size). Specific examples of this are considered below. In calculating selection differentials, we make no assumptions regarding the age-structure of the stands. Rather, we consider age differences as one more factor likely to cause low heritabilities of phenotypic differences. Nevertheless, in two cases, we do consider the effect on calculated selection differentials of excluding trees in size classes <20 cm.

Logging efficiencies

Snook (1996, citing various authors) writes that mahogany logging commonly results in the removal of ‘95% or more’ of trees, leaving only damaged or non-commercial individuals. A selected proportion of 5% is equivalent to a selection intensity of 2.06σ (standard deviations), expected to be equal to approximately one-third of the range of a given trait (Sokal & Rohlf 1995). Zimmerman *et al.* (2001) reported that in

Table 1 Estimated selection differentials for diameter at breast height in actual and hypothetical logging operations in mahogany populations in Bolivia, Brazil, Mexico and Venezuela. ¹Estimates of means derived from frequency distributions, following Sokal and Rohlf (1995, p. 57). ²From figure 5 in Gullison *et al.* (1996); minimum size-class included in original data was 60–80 cm. ³From figure 13 in Gullison *et al.* (1996); minimum size-class included in original data was 50–60 cm. ⁴From figure 6-G in Snook (1993); minimum size-class included in original data was 0–10 cm, values in parentheses were calculated after excluding this and the 10–20 cm class. ⁵From figure 7 in Grogan *et al.* (2002); minimum size-class included in original data was 20–30 cm. ⁶Based on pooled frequency distributions of 5 stands; minimum size-class included in original data was 0–20 cm, values in parentheses were calculated after excluding this class.

Source	Location	Population mean dbh (cm) ¹	Remnant tree mean dbh (cm) ¹	Selection differential (cm)	Percentage selection differential
<i>Actual logging operations</i>					
Gullison <i>et al.</i> 1996 ²	Chaimanes, Bolivia (Jaimanche)	88	70	–18	–20.4
Gullison <i>et al.</i> 1996 ²	Chaimanes, Bolivia (Monte Grande)	145	176	+31	+21.4
Gullison <i>et al.</i> 1996 ²	Chaimanes, Bolivia (Fátima)	113	114	+1	+0.9
Gullison <i>et al.</i> 1996 ³	Chaimanes, Bolivia (unspecified)	112	80	–32	–28.6
Snook 1993 ⁴	Noh Bec, Quintana Roo, Mexico	41 (49)	26 (33)	–15 (–16)	–36.7 (–32.3)
<i>Hypothetical operations, assuming removal of all trees ≥ 55 cm (Grogan <i>et al.</i>), or 50 cm (Finol) diameter classes</i>					
Grogan <i>et al.</i> 2002 ⁵	South Pará, Brazil	59	35	–24	–40.0
Finol 1964 ⁶	Barinas, Venezuela	62 (70)	32 (42)	–30 (–28)	–48.4 (–40.0)

indigenous reserves in Pará State (Brazil) logging of some populations is likely to have resulted in the removal of 78–85% of reproductive individuals. This would leave a negatively selected proportion of 12% (i.e. 100–78), equivalent to 1.67 σ . However, because the remaining trees were left mainly as a consequence of accessibility rather than quality problems, the actual selection intensity would be lower.

Logging in Bolivia: Gullison *et al.*'s (1996) data

The data presented by Gullison *et al.* (1996, figs 5, 13) permit direct calculation of selection differential for diameter at breast height (Table 1). The calculations confirm that logging may lead to both positive and negative selection for tree size. The positive selection differentials result principally from non-harvesting of large 'standing rotted' trees (trees expressly left as seed trees tended, by contrast, to be smaller than the mean).

In the operations described by Gullison *et al.* (1996, fig. 5), around 7% of trees (5 of 75 live trees) were left unharvested because of standing rot. Heart-rot is relatively common in mahogany trees over 40 cm in diameter (Lamb 1966), approaching 100% in some areas (J.E. Grogan, personal communication 2003). Trees left because of heart-rot are likely to be the most severely affected individuals. If the degree of heart-rot in the population is approximately normally distributed, then selection (i.e. retention rate) of 7% would correspond to selection intensity of 1.92 σ (Falconer 1989). Assuming scoring of heart-rot infestation on a scale of, for example, 0–100, then rules-of-thumb for estimation of population parameters (i.e. mean = mid-range and standard deviation = range/6.5; Sokal & Rohlf 1995) would suggest a mean of 50 units and a standard deviation of 15.4 units

(= range/6.5), respectively, implying a negative selection differential of 1.92 \times 15.4, *c.* 30 units or 60% relative to the mean. However, Gullison *et al.* (1996) recorded that six more trees were left as seed trees or were missed by the loggers, reducing the selection differential for this trait by approximately half.

In other cases, loggers may be less selective than in the operations described by Gullison *et al.* (1996), because many trees may be felled irrespective of their degree of heart-rot, leading to proportions selected lower than 7%. In part, this is because chain-saw operators are often paid 'piece-rate'. Furthermore, with modern equipment, felling of trees is relatively cheap in comparison to searching and extraction, and may be the most efficient way of evaluating the degree of heart-rot. Even when lower sections are diseased, valuable timber, particularly that corresponding to the prized 'pyramid' figure caused by branch intersections (Lamprecht 1990; J.E. Grogan, personal communication 2003), may nevertheless be extracted from higher up the bole. In itself, reduced selectivity in felling of trees (i.e. felling of less desirable individuals, irrespective of whether they are later extracted) could lead to larger negative selection differentials. For example, if only the most severely infected 1% of trees is left standing for this reason, selection intensity would be 2.66 σ . However, this increase would be at least partially offset because the proportion of remnant trees left for other reasons (such as inaccessibility or poor form), and therefore presumably uninfected, would be correspondingly higher.

Logging in Quintana Roo, Mexico: Snook's (1993) data

Snook (1993, p. 100) presented a diameter class frequency distribution for a 4-ha sample transect in Quintana Roo,

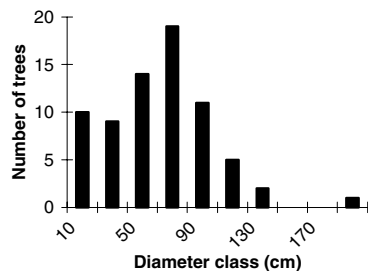


Figure 1 Diameter size class frequency distribution of mahogany trees in the Caimital forest, Baranis, Venezuela (redrawn from data in Finol 1964).

including basal diameters of trees already logged. Our calculations indicate that selection differential for diameter from the above logging was approximately -37% with respect to the mean (Table 1). The frequency class distribution includes trees in 0–10 cm and 10–20 cm diameter classes. The estimated selection differential when these classes are ignored is slightly lower (see Table 1). According to Snook (1993), all trees in the 0–60 cm range were members of the same post-hurricane cohort, whereas the harvested trees were those that survived the hurricane.

Inferences based on published frequency distributions

Grogan *et al.* (2002, p. 20) presented estimated diameter class frequency distributions for unlogged populations in Pará, Brazil. Assuming harvesting of all trees in diameter classes of ≥ 55 cm, selection differentials for these populations would be -40% (Table 1). Retention of some larger trees as seed trees would not much affect this scenario; our calculations (not shown) indicate that retention of 10% of the trees in each of the larger diameter classes would change the negative selection differential from -40% to -31% .

Finol (1964, p. 37) presented a diameter class frequency distribution for mahogany in a forest that had been logged of the ‘finest’ individuals 10–20 years previously. As might be expected, the data resemble a truncated normal distribution, i.e. the right half appears to have been depleted in the first cut (Fig. 1). A hypothetical second cut, eliminating individuals in the 50 cm and higher classes would have selection differential of -30cm , i.e. -48.4% with respect to the mean before the second cut (Table 1). Omitting individuals in the 0–20 cm size class lowers the selection differential slightly (Table 1). Had both logging operations been carried out at the time of the second (hypothetical) cut, then, assuming an unlogged population mean corresponding to the mid-range diameter class (90 cm), the overall selection differential would have been $c. (32-90) = -58$ cm (Table 1), i.e. -64% with respect to the population mean.

Selection intensities: conclusions

Conclusions regarding probable values of selection differential vary somewhat with respect to the three trait groups

mentioned. For tree size, differentials are likely to be highest when remnant trees (whether after one or more than one cut) consist of submerchantable or otherwise small trees, with few or no ‘standing rotted’ individuals. If there is a relatively large number of ‘standing rotted’ large trees, then selection differentials may even be positive. In general, strongly negative selection differentials for tree size may be a relatively recent phenomenon, caused by the logging of increasingly smaller trees (Veríssimo *et al.* 1995; Weaver and Sabido 1997), the capacity of modern equipment to handle even the largest trees and an increasing tendency to fell rotten trees. Logging practice with regard to diseased trees may effectively determine selection differentials for tree size in some populations, as, indeed, is evident in the Gullison *et al.* (1996) data. By contrast, historical logging may have resulted in lower differentials for size. The historical practice of 30–40 year cutting cycles described by Weaver and Sabido (1997) would lead to removal of the great majority of harvestable trees of a given cohort, the small number of small remnant trees then being balanced by the unharvestable large trees. In present-day logging operations, only trees with critical form or heart-rot problems are likely to be left. In itself, this implies strongly negative selection intensities for these traits. However, as it also implies low numbers of remaining trees, these negative intensities could be offset by low numbers of trees left for other reasons, i.e. trees missed by loggers, or trees left because of critical accessibility problems. In addition, assuming that trees with heart-rot do not tend to have below average form, negative phenotypic values of trees left because of heart-rot problems would be offset by those of trees left because of form problems. It is possible that historical logging was associated with more strongly negative differentials for disease and form, not because the mean values of trees left for these reasons were worse, but because, as more trees were left because of form and heart-rot, their negative deviation from the population mean would be less mitigated by trees left for other reasons.

It is evident from the above that logging in mahogany populations has been characterized by a range of selection differentials, varying according to the traits under consideration, demographic data and logging practice. Although, in some cases, differentials have undoubtedly been zero or even positive, we suggest that, in general, and particularly in more recent logging, the effect of logging a given cohort, whether in one or successive cuts, has been to increase the proportion of poor quality phenotypes relative to that before logging. In considering the genetic implications of such selection, we assume relatively extreme negative selection differentials (i.e. 50% with respect to the mean), because this permits us to set upper limits on the effects of dysgenic selection.

Expected genetic consequences of phenotypic selection as practised by loggers

Intense phenotypic selection does not in itself guarantee genetic change in succeeding generations. Its effects depend on the degree of additive genetic control of the phenotypic

variation. In traits influenced both by many genes and diverse environmental factors, such as growth and form of forest trees, there is no simple 'one-to-one' relationship between genotype and phenotype; two trees with exactly the same genotypes can have very different phenotypes. Rather, there is a statistical relationship, measured by the heritability, which is most easily considered as a regression coefficient:

$$\hat{G} = bP,$$

where \hat{G} is the expected additive genotypic value of an individual and P its phenotypic (observed) value, both expressed as deviations from the population mean (the additive genotypic and phenotypic means are the same, because the environmental and genetic dominance deviations from the phenotypic mean sum to zero) (Falconer 1989). The value of b (heritability) ranges from zero to one. In the unlikely event of phenotype being determined solely by the additive genotype, $\hat{G} = P$ and therefore $b = 1$. When there is no genetic effect on the phenotype, there are, by definition, no additive genetic deviations from the phenotypic mean, in which case genotypic values (i.e. the additive genetic deviations from the population mean) are constant at zero, and $b = 0$.

The heritability expresses the degree to which phenotypic differences are inherited. In a study based mostly on temperate species, particularly Pinaceae, Cornelius (1994a) found that heritabilities in a range of growth and form traits tended most frequently to lie in the range 0.1–0.3. Some estimates of heritability for mahogany populations are listed in Table 2, which also includes some of the few published estimates of heritability for other tropical broad-leaved species. Taking into account that at least two of the heritability estimates for mahogany are artificially inflated owing to confounded provenance effects (i.e. between-population or between-region genetic differences), these are consistent with the general trends noted for other taxa.

However, these estimates cannot be unreservedly applied in the present context. This is because they are derived from field experiments, and estimate the degree of genetic control in such experiments. Heritability in natural forest is likely to be appreciably lower, partly because, in experiments, phenotypic values can be adjusted for measured environmental effects (e.g. block effects; Cotterill 1987), leading to higher correlation between genotype and phenotype. Moreover, there are at least four other reasons to expect non-genetic effects on tree phenotype to be much stronger in natural forests. First, phenotypic variation in tree size may be due partly or, in some cases, principally, to age rather than genetic differences. This applies especially to stands with less uniform age-class distribution, such as those described by Grogan *et al.* (2002), but also to populations in which post-catastrophe regeneration is typical, as exemplified by Snook's (1993) data (see section on selection intensities), where the harvested and remnant trees belonged to different cohorts. As persistence after catastrophic disturbance is characteristic of mahogany, and indeed fundamental to the evolutionary-reproductive strategy proposed by

Table 2 Published heritability estimates in mahogany and other tropical broadleaved species. ¹Estimate inflated by confounded provenance effect. ²Based on exotic provenance of unknown origin (i.e. place from which seed of a non-native species was originally introduced (Burley & Wood 1976)) and may be inflated by confounded origin effect.

<i>Species & trait</i>	<i>Estimates</i>	<i>Source</i>
<i>Alnus acuminata</i>		
Height	0.29	Cornelius <i>et al.</i> (1996b)
Stem straightness	0.12	Cornelius <i>et al.</i> (1996b)
<i>Cordia alliodora</i>		
Stem form	0.03, 0.06	Boshier & Henson (1997)
Height	0.07, 0.29	Boshier & Henson (1997)
Diameter	0.13, 0.14	Boshier & Henson (1997)
<i>Eucalyptus deglupta</i>		
Height	0.15–0.27	Cornelius <i>et al.</i> (1995)
<i>Eucalyptus urophylla</i>		
Growth traits	0.11–0.49	Wei & Borralho (1998)
<i>Gmelina arborea</i>		
Height	0.07–0.17	Lokmal (1994)
Diameter	0.12	Lokmal (1994)
Diameter	0.19–0.31	Cornelius & Hernández (1995)
Straightness	0.21	Lokmal <i>et al.</i> (1991)
Straightness	0.08–0.29	Cornelius & Hernández (1995)
<i>Vochysia guatemalensis</i>		
Height	0.03	Cornelius & Mesén (1997)
Diameter	0.05	Cornelius & Mesén (1997)
Stem straightness	0.08	Cornelius & Mesén (1997)
Mahogany <i>Swietenia macrophylla</i>		
Number of forking points	0.56 ¹ , 0.42 ²	Newton <i>et al.</i> (1996)
Height	0.38 ¹ , 0.11 ²	Newton <i>et al.</i> (1996)

Snook (1993, 1996), it is clear that a given stand may contain trees originating from different successive disturbance events. Also, in some cases, advance regeneration may exist. For example, Dickinson and Whigham (1999) reported a density of 16 mahogany seedlings ha⁻¹ in closed canopy forest in Quintana Roo (the size criterion for classification as 'seedlings' was not given, but mean height was 21 cm and range was 16–30 cm). Gullison *et al.* (1996) reported a similar density (17 seedlings ha⁻¹) in one area of the Chaimanes forest, Bolivia, and 174 seedlings (i.e. ≤2.5 cm diameter at breast height [dbh]) ha⁻¹ in three other areas. After suitable disturbance, development of members of such seedling banks should be more rapid than that of post-catastrophe regeneration.

Second, competition (particularly inter-specific) for light, water and nutrients in natural forest is likely to be very much more variable and less controlled than in plantations. Third, microsite differences, unaffected by the homogenizing effect of site preparation, are likely to be greater in natural forests. Finally, the natural clumping of related trees (because

of limited seed dispersal) implies reduced genetic variation within such neighbourhoods (Ledig 1974). The final three factors all decrease heritability by increasing the relative importance of environmental effects on the phenotype. We would therefore suggest that Namkoong's (1970) comment that 'the heritability for growth traits in trees might reasonably be expected to lie around 0.05 if measured under the highly variable environments of natural forests' can be very reasonably applied to mahogany populations.

Form is generally considered to have higher heritabilities than growth. However, this tendency, which in any case appears to be poorly supported by empirical data (Cornelius 1994a), again reflects plantation conditions. It is by no means clear that the tendency of a given genotype (typically, in the literature, of *Pinus*) to produce crooked stems in a rather uniform competitive environment (i.e. an even-aged, evenly-spaced plantation) is a trait comparable to a tendency to poor form of a mahogany genotype in a highly heterogeneous competitive environment, where both competing vegetation (especially lianas) and shoot-borer (*Hypsipyla grandella* Zeller [Lepidoptera: Pyralidae]) attack are common causes of form defects. We suggest that Namkoong's (1970) comments on probable values of heritabilities of growth are equally applicable to tree form in natural forest, and that 0.1 is probably an upper limit for heritability of logger-selected traits in naturally-regenerated mahogany.

Manion (1991) describes four models of infection and invasion by heart-rot fungi, all of which ultimately depend on invasion through wounds. *Hypsipyla* attack exposes the pith of saplings and constitutes one wounding mechanism, as has been documented for white pine weevil (*Pissodes strobi* Peck [Coleoptera: Curculionidae]) attack on eastern white pine (*Pinus strobus* L.) (Manion 1991). Because the incidence of *Hypsipyla* attack tends to be positively related to vigour (Dickinson & Whigham 1999), which in turn is likely to have non-zero heritability, the incidence of wounding could be partially genetically controlled. It is also possible that fast-growing trees are more able to heal wounds. However, neither trait seems likely to have higher heritability than growth rate itself, particularly in the case of incidence, when the effects of tree age and the occurrence of random wounding (caused, for example, by tree falls or generalist browsing) are considered. The same is likely to apply to butt-rot caused by root-disease fungi such as brown root-rot (*Phellinus noxius* [Corner] G. Cunn) (Singh *et al.* 1980). We therefore suggest that incidence and severity of tree defects owing to pests and diseases are also likely to exhibit low heritabilities, i.e. similar to those projected for size or form traits.

Expected response to phenotypic selection (\hat{R}), whether positive (genetic improvement) or negative (dysgenic), is predicted by the following equation:

$$\hat{R} = Sh^2,$$

where S is the selection differential and h^2 = heritability (Falconer 1989). Selection differentials of -50% with respect

to the mean and heritabilities of 0.1 imply predicted negative response to selection of up to -5% . Although it is conceivable that higher selection intensities could occur in extreme situations, such as retention of small numbers of very poorly formed trees (and no others), it seems likely that heritabilities would frequently be lower than 0.1. We therefore consider that -5% represents an approximate maximum negative dysgenic response to a single logging-mediated phenotypic selection event. By the latter, we mean the logging, in one operation or over several decades, of the trees already present on a given site. Recurrent selection in subsequent generations is briefly considered below.

The above maximum represents the predicted (negative) response to selection in an individual population, or perhaps more usefully, the expected mean response to selection in a set of such populations (for example over a whole logged region of many square kilometres, which would contain a series of overlapping breeding groups or neighbourhoods). Within such a set of populations, there will be variation in the size of the response, as the predicted response expresses a statistical rather than an exact relationship. Low heritabilities describe a situation in which genotype is poorly correlated with phenotype. In the same way as any weak statistical relationship requires a large sample size for detection, so, if in a tract of forest containing 1000 mahogany trees all except the two 'worst' were removed, there is a high probability that the predicted response would not occur. Indeed, random positive effects could even occur.

There are three additional notable factors that might mitigate dysgenic selection effects. First, pollen flow from neighbouring unlogged forest, if present, will mitigate adverse changes in allelic frequencies (in the same way as pollen flow into seed orchards may reduce genetic gain). Second, increased post-logging nearest-neighbour distance between trees might lead to a higher average distance of pollen flow. If, as in *S. humilis* (White & Boshier 2000), spatial genetic structure occurs (i.e. neighbouring trees tend to be more closely related than spatially separated trees), this would lead to less mating between relatives and possibly to reduced neighbourhood inbreeding depression. This would be expected to increase tree fitness and, possibly, growth rate, but would probably not affect form traits, unless these were related to fitness. Although the opposite effect of reduced outcrossing from increased spacing has been observed in *Shorea megistophylla* (Dipterocarpaceae) (Murawski *et al.* 1994), this resulted from higher rates of selfing and would not be expected in *S. macrophylla*, which appears to be self-incompatible (Loveless & Gullison 2003). Third, logged trees may already have contributed gametes to the next generation, either as progenitors of seedling bank individuals, or through pre-logging pollination of maturing fruits of remnant trees. Where logging does lead to conditions suitable for successful regeneration, such 'beyond the grave' effects could offset the negative contribution of remnant trees. Typically, however, selective logging is not followed by successful regeneration (Snook 1993, 1996; Verissimo *et al.* 1995; Gullison *et al.* 1996;

Dickinson & Whigham 1999). Rather, when it occurs at all, it is most likely to be as a result of larger-scale disturbance at some time in the future. In this case, remnant trees will predominate as progenitors of future generations in logged forests, and the removal of the better trees will reduce or even nullify their lifetime reproductive output. In general, therefore, 'beyond the grave' effects thus seem unlikely to be important in mitigating dysgenic selection, although this does not preclude the possibility that harvested trees might contribute through long-distance pollination to gene pools of neighbouring populations where conditions might have favoured regeneration. One exception, the case of overlapping generations, is discussed below.

Recurrent selection

Selection has also a temporal dimension, as genetic improvement and its reverse can be applied in successive generations, producing cumulative response. With constant heritabilities and selection differentials, the cumulative response to selection relative to the initial population mean is a simple multiple of the formula for response to selection:

$$\hat{R} = tSh^2,$$

where t = number of generations (Charlesworth 1994).

In the case of *S. macrophylla*, the longest relatively continuous logging activity appears to have been imposed on populations in Belize, where logging began around 1750. Assuming a relatively short generation time of 70 years, it is conceivable that a cumulative negative response over the 3–4 generations might have reached 15–20%. However, we stress that this is based on our projected maxima for both selection differential and heritability. Furthermore, it requires assumptions on regeneration ecology that may be unrealistic. As mentioned above, mahogany regeneration appears to require greater disturbance than that normally associated with species-selective logging. Many remnant trees will reproduce successfully only after later disturbance, and they may do so either locally (as seed trees) or remotely, as pollen donors. Consequently, it may be many years before progeny of remnant trees (the next generation) become established, and it may or may not be concentrated in the logging area. In addition, although logging in Belize has continued over a considerable period, this does not necessarily imply that operations have been carried out on successive generations within the same stands.

Grogan *et al.* (2002) suggested that different regeneration scenarios may apply in some forests of south-eastern Pará, Brazil, where size class distributions and other parameters suggested 'recruitment... at shorter time intervals and smaller spatial scales'. In such conditions, there will be a more marked overlap of generations than under the catastrophic disturbance model. As more advanced generations (more recent generations) will tend to be more highly dysgenically selected (because of accumulation of selection response

from previous generations), age-class will be correlated with mean genotypic value. Under such conditions, cumulative response cannot be predicted based on the above equation (Ducrocq & Quaas 1988). Although prediction equations become complex for selection with overlapping generations (see Charlesworth 1994), general consequences of overlapping generations become clear when this scenario is compared with the discrete generations model. Under the latter, a given cohort arises purely from reproduction of remnant trees of the previous generation, whereas with overlapping generations, progenitors of a given generation will also include those from previous less dysgenic generations. It follows that, in forests with this sort of age structure the rate of genetic degradation will be slower, i.e. cumulative negative response at a given time is expected to be lower. Although there is no evidence that the forests described by Grogan *et al.* (2002) have been subjected to long-term harvesting pressure, it is worth noting that in practice, even populations with regeneration patterns following the catastrophic model are likely to exhibit some degree of generational overlap, for the reasons indicated above (see discussion of heritability values).

EFFECT OF PHENOTYPIC SELECTION IN MAHOGANY AND NATURAL POPULATIONS OF FOREST TREES IN GENERAL: EMPIRICAL STUDIES

As outlined above, a priori we would expect any dysgenic selection effects to be of relatively small magnitude, i.e. no greater than 5%. We now consider whether this expectation is supported by empirical information. There appear to be no data sets of performance of mahogany progeny collected from stands before and after selective logging. For this reason, we consider other, indirect, sources of evidence as to the likely incidence of dysgenic selection. First, we consider experimental data on the effect of phenotypic selection in natural stands of mahogany. Second, we consider the much larger body of similar information available for other species.

Phenotypic selection in mahogany

In 1999, two mahogany provenance–progeny common-garden field experiments were planted in northern Costa Rica (see Navarro & Hernández 2004 for details). Using field sketches and/or phenotypic scoring (scale of 1–4 for form) made during seed collection, we identified phenotypically divergent maternal phenotypes within each provenance included in the trials. We then compared the quality in the field tests of the progeny of the divergent mother-trees within each provenance, assigning to each progeny tree a rank (1–9) according to its overall quality (based on growth, stem straightness, branching and survival, i.e. missing trees were classed as inferior to surviving trees) in comparison with its eight immediate neighbours. Evaluations were 'blind', i.e. the

Table 3 Mean quality scores (see text) of progeny of mother trees of differing phenotypic quality in two provenance/progeny trials of *Smietenia macrophylla* located in Guanacaste and Alajuela provinces, Costa Rica. ¹Mother tree form was assessed on a scale of 1–4; ²progeny form was scored on a scale of 1–9.

<i>Trial and provenance</i>	<i>Mean form score of 'good' mother tree(s) (number of trees)¹</i>	<i>Mean form score of progeny of 'good' mother tree(s)²</i>	<i>Mean form score of 'poor' mother tree(s) (number of trees)¹</i>	<i>Mean form score of progeny of 'poor' mother tree(s)²</i>	<i>Difference between progeny means ('good'–'poor')</i>
<i>MACORI trial</i>					
Escárgeca	2.33 (3)	4.24	4.00 (1)	3.62	+0.62
Pocosol	3.00 (2)	4.20	4.00 (4)	3.86	+0.34
Nuevo Becal	2.00 (1)	2.77	3.00 (3)	4.51	–1.74
San Felipe	1.00 (2)	3.92	2.50 (2)	5.26	–1.34
Chapernal	3.00 (2)	3.60	4.00 (1)	2.80	+0.80
<i>Los Chiles trial</i>					
Tikal	2.00 (2)	1.31	3.00 (1)	1.57	–0.26
Lancetilla	1.86 (7)	1.32	3.25 (4)	1.57	–0.25
Mukuwas	1.00 (6)	1.34	2.00 (9)	1.33	+0.01
Tonosi	2.00 (3)	1.55	4.00 (1)	1.25	+0.30
San Emilio	2.00 (2)	1.39	3.00 (1)	1.17	+0.22
Madrazo	1.00 (2)	1.43	3.00 (1)	1.74	–0.31

Table 4 Mean diameters (mm) of progeny of mother trees of differing phenotypic form quality in two provenance/progeny trial of *Smietenia macrophylla* located in Guanacaste and Alajuela provinces, Costa Rica. ¹Mother tree form was assessed on a scale of 1–4.

<i>Provenance and trial</i>	<i>Mean form score of 'good' mother tree(s) (number of trees)¹</i>	<i>Mean dbh of progeny 'good' mother trees</i>	<i>Mean form score of 'poor' mother trees (n)¹</i>	<i>Mean dbh of progeny 'poor' mother trees</i>	<i>Difference between progeny means ('good'–'poor')</i>
<i>MACORI trial</i>					
Escárgeca	2.33 (3)	48.4	4.00 (1)	57.8	–9.40
Pocosol	3.00 (2)	62.4	4.00 (4)	46.8	15.60
Nuevo Becal	2.00 (1)	50.2	3.00 (3)	43.9	6.30
San Felipe	1.00 (2)	58.7	2.50 (2)	44.8	13.90
Chapernal	3.00 (1)	50.8	4.00 (1)	52.5	–1.70
<i>Los Chiles trial</i>					
Tikal	2.00 (2)	77.3	3.00 (1)	76.0	1.30
Lancetilla	1.86 (7)	74.6	3.25 (4)	71.9	2.70
Mukuwas	1.00 (6)	71.2	2.00 (9)	68.8	2.40
Tonosi	2.00 (3)	62.8	4.00 (1)	66.2	–3.40
San Emilio	2.00 (2)	68.4	3.00 (1)	73.2	–4.00
Madrazo	1.00 (2)	77.4	3.00 (1)	81.4	–4.00

evaluator did not know whether the progeny being scored in each case was of relatively good or relatively poor maternal phenotype. The mean rank of the progeny of phenotypically relatively good and phenotypically relatively poor mother trees within each provenance was then calculated (Table 3). We also carried out a similar comparison of progeny diameter for the same mother trees, based on paired means rather than ranks (Table 4). The resulting two sets of paired observations were then analysed using the sign test (Sokal & Rohlf 1995); if maternal phenotype were strongly related to the quality of the offspring, the sign (positive or negative) of the difference between progeny of 'good' and 'poor' phenotypes would be expected to be consistent. We found no significant or consistent difference between means of progeny from 'good' phenotypes and progeny from 'poor' phenotypes. Of the

11 paired observations, progeny of poor phenotypes were inferior in six cases and superior in five (Tables 3 and 4). The results do not suggest that poor form in mother-trees is associated with poor performance, whether in overall quality or growth rate, of progeny.

Other taxa

There appear to be no published data on the genetic effects of negative phenotypic selection in trees. However, there is a fairly large body of information on the effects of positive phenotypic selection, i.e. plus-tree selection, the effectiveness of which was reviewed by Cornelius (1994b). Although, overall, the evidence suggests that plus-tree selection does tend to lead to genetic gain, he cautioned that there was a

'tendency for plus-tree selection to be less effective in natural stands than in plantations'; in the six papers concerned with selection in natural stands, genetic gain in height or diameter ranged from 0.4% to 10.9%, and, in the three cases where statistical tests were presented, means of plus-tree progeny were not significantly different from the control lots included. Our subsequent experience is consistent with this tendency: plus-tree selection was effective in plantations of *Gmelina arborea* (Cornelius 1994c) and *Cupressus lusitanica* (Cornelius et al. 1996a), but ineffective in natural stands of *Alnus acuminata* (Cornelius et al. 1996b) and *Vochysia guatemalensis* (Cornelius & Mesén 1997).

The empirical results of phenotypic selection on forest trees, including mahogany, are consistent with our expectations. They provide independent support for our suggestion that any genetic deterioration owing to dysgenic selection is likely to be relatively slight.

DISCUSSION

We argue above that, in some populations, selective logging has exerted substantial negative selection pressure on *S. macrophylla* populations, that the phenotypic variation on which this pressure acts is likely to have a small heritable component, and that there is no reason why this should not, in accordance with theoretical expectations, lead to progeny of remnant trees being on average genetically inferior. However, we suggest that this effect is likely to be slight (i.e. a maximum of 5% response per dysgenically selected generation with respect to current phenotypic and genotypic means) and consider that it might often be substantially less, or absent altogether. Although dependent on a number of assumptions, these expectations are consistent with the observed results of positive phenotypic (i.e. plus-tree) selection, which show only moderate response to deliberately applied, often highly intensive selection. Although based on consideration of *S. macrophylla*, there appear to be no obvious reasons to believe that either heritabilities or selection intensities have been higher in *S. humilis* and *S. mahagoni*. We suggest, therefore, that our conclusions also apply broadly to these species.

Our argument that dysgenic effects are likely to have been slight might seem inconsistent with field observations of phenotypes of current mahogany populations, particularly those of *S. humilis* and *S. mahagoni* (L.) Jacq. As noted above, such observations have been cited as evidence of dysgenic selection in mahogany. Certainly, the almost uniformly poor form of *Swietenia humilis* trees in the Pacific watershed of Central America is striking: most trees show multiple branching between 1.5 m and 3.0 m (Fig. 2). However, we consider that there is little justification to invoke a relatively complex phenomenon such as dysgenic selection to explain this phenomenon. In Central America, there are two factors that regularly cause low branching of young mahogany trees through destruction of the leading shoot: leaf-cutting ants (*Atta* spp.) and the attack of *H. grandella*. When such factors are controlled or absent, young Pacific mahogany trees tend



Figure 2 Dysgenic selection or insect attack? Typical form of young *Swietenia humilis* tree. Alubarén, Honduras (J.P. Cornelius).

to be unbranched (J.P. Cornelius, personal observations in two-year-old provenance trials in Comayagua, Honduras, 2002). Similarly, we have observed that *Hypsipyla*-attacked individuals of *S. macrophylla*, particularly when open-grown, will exhibit the same many-branched form, whereas unattacked *S. macrophylla*, even if derived from heavily-logged populations, will grow straight and without competing codominant branches for at least 5–6 m. We would therefore suggest that *Hypsipyla* attack is the main cause of the poor form of remnant trees of *S. humilis* in Central America. Although it could be argued that *Hypsipyla* attack itself, or its effects, have themselves been exacerbated by a correlated response to dysgenic selection (i.e. that poor form of remnant trees is owing to increased susceptibility to *Hypsipyla* attack; Newton et al. 1996), our conclusions on the probable magnitude of the genetic parameters involved also apply to this argument. Without totally discounting some such effect, it does not seem reasonable to argue that it is a primary causal factor in the poor form of remnant *S. humilis*.

The implications of dysgenic selection, when it does occur, depend very much on the use and the future of dysgenically selected populations. Where mahogany populations are being actively managed, whether *in situ* or *ex situ* (i.e. as future domesticates), there is in general no technical reason why any dysgenic effects could not be reversed through positive selection; any cost of so doing would represent an externality associated with logging. In the case of exploited but currently unmanaged (commercially exhausted) natural populations, dysgenic selection is primarily of importance insofar as it affects fitness, in other words capacity to survive and reproduce. Logger selection on tree size may reduce average fitness of populations. Such effects might be partially offset by selection against good form, as heavily branched trees may have higher numbers of flower-bearing shoots and may therefore produce more seed and pollen.

The relative benignancy of the probable impact of dysgenic selection in mahogany should not be taken to suggest that

mahogany is not frequently under risk of genetic erosion and population extinction. Rather, we would suggest that, as a threat to mahogany conservation and long-term sustainable production, dysgenic selection is insignificant in comparison with other genetic and non-genetic factors. Chief among the former is the loss of alleles and allelic complexes due to complete destruction of populations; both genetically and generally, the least-selective within-species logging practices are the most damaging and, as Ledig (1992) pointed out, high-grading, the harvesting of only the very best individuals, is far less damaging than the harvesting of all but the very worst. The reductions in population size implicit in unselective logging should also be a key concern, as they expose populations to the genetic and non-genetic stochastic risk factors associated with small population size; indeed, reduced molecular genetic variation in logged stands of mahogany has already been reported by Gillies *et al.* (1999). There are many reasons to conserve mahogany and a number of reasons to believe that existing conservation and management measures are inadequate. Clearer definition of those aspects that are of key concern can only help to inform and strengthen such measures.

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