

Some Evolutionary Consequences of Being a Tree

Rémy J. Petit¹ and Arndt Hampe^{1,2}

¹Institut National de la Recherche Agronomique, UMR Biodiversity, Genes and Communities, F-33610 Cestas, France; email: petit@pierreton.inra.fr

²Consejo Superior de Investigaciones Científicas, Estación Biológica de Doñana, Integrative Ecology Group, E-41080 Sevilla, Spain; email: arndt@ebd.csic.es

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Abstract

Trees do not form a natural group but share attributes such as great size, longevity, and high reproductive output that affect their mode and tempo of evolution. In particular, trees are unique in that they maintain high levels of diversity while accumulating new mutations only slowly. They are also capable of rapid local adaptation and can evolve quickly from nontree ancestors, but most existing tree lineages typically experience low speciation and extinction rates. We discuss why the tree growth habit should lead to these seemingly paradoxical features.

“Few there are [...] who seem to clearly realize how broad a lesson on the life-history of plants is written in the trees that make the great forest regions of the world.” Clarke 1894

Substitution rate: number of nucleotide differences that accumulate in a sequence per unit of time, usually much more than one generation

1. INTRODUCTION

The importance of trees for sustaining life in general and biodiversity in particular can hardly be overstated. An estimated 27% of the terrestrial surface of Earth is (still) covered by forests (FAO World Resources 2000–2001), and trees make up around 90% of Earth’s biomass (Whittaker 1975). Not surprisingly, forests also harbor the vast majority of the world’s terrestrial biodiversity. Estimates of global tree species richness range from a low 60,000 (Grandtner 2005) to 100,000 taxa (Oldfield et al. 1998), that is, as much as 15% to 25% of the 350,000–450,000 vascular plants of the world (Scotland & Wortley 2004). Unfortunately, ongoing deforestation (estimated at 9.4 million hectares per year in the 1990s) and other human-induced changes have brought >10% of the world’s tree species close to extinction (Oldfield et al. 1998). The impact of global change will depend to a great extent on the reaction of trees and the ecosystems they sustain (e.g., Ozanne et al. 2003; Petit et al. 2004a, 2005b). Mitigating these harmful consequences requires knowledge of tree biodiversity and evolution. However, trees are not only overexploited but also understudied in many respects, because their size and life span make them difficult subjects for experimental investigations (Linhart 1999).

The tree growth habit has evolved many times. This is probably the reason why few attempts have been made over the past several decades to consider trees collectively and discuss their mode of evolution. This apparent lack of interest contrasts with a strong tradition in earlier years (e.g., Arber 1928; Clarke 1894; Grant 1963, 1975; Sinnott 1916; Stebbins 1958). The current interest in comparative biology, thanks to the development of accurate phylogenies and powerful analytical methods, should help revive this tradition. Far from representing a problem, the multiple origins of trees will actually facilitate this work, as each distinct tree lineage can be viewed as an independent evolutionary experiment. Comparative analyses should help elucidate if typical tree features such as tallness, longevity, and fecundity affect their evolutionary dynamics.

From an evolutionary standpoint, trees have several intriguing and apparently paradoxical features. In particular, they often have high levels of genetic diversity but experience low nucleotide substitution rates and low speciation rates. They also combine high local differentiation for adaptive traits with extensive gene flow. Moreover, exceptional maintenance of species integrity in the face of abundant interspecific gene flow seems to be the rule in trees.

In this review, we first compare existing definitions of the tree habit and then identify and discuss trees’ major ecological characteristics. Second, we examine why trees generally harbor such high levels of genetic diversity and can adapt rapidly to local conditions. Third, we ask why trees have such a low pace of evolution at longer timescales, both in terms of DNA sequence and character change within lineage and in terms of diversification rate. Finally, we discuss how to reconcile the observations of rapid microevolution and slow macroevolution. Much of the earlier work on the

evolutionary consequences of the tree growth habit dates from the 1950s (Stebbins 1950, 1958, 1974; Grant 1958). This type of analysis, in which life history traits and reproductive characteristics of plants were viewed as an integrated set of attributes (the so-called genetic system) contributing to adjusting levels of genetic diversity to the ecological demand, has lost popularity. However, the need for broad synthetic approaches aimed at organizing and interpreting the growing body of knowledge on these topics is greater than ever.

Lignophytes: plants having an external layer of porous bark and an internal core of wood produced by the cambium

2. WHAT IS A TREE? MAJOR FEATURES AND CONSTRAINTS OF THE TREE GROWTH HABIT

2.1. What Is a Tree?

With one known exception—*Prototaxites*, a 9-m-high tree-like holobasidiomycete or lichen that dominated the land flora 350–400 Myr ago (Hueber 2001, Selosse 2002)—all organisms ever considered to be trees are vascular plants (tracheophytes). As such, they share features such as indefinite and flexible growth, modular structure, lack of clear separation between germline and soma, reversible cellular differentiation, great phenotypic plasticity and physiological tolerance, and presence of haploid and diploid multicellular generations (Bradshaw 1972). Evolution of trees cannot be understood without due consideration of these attributes.

The particular character of the tree growth form has always been recognized and, since Theophrastus (born c. 370 BC), botanists have generally distinguished between trees, shrubs, and herbs. From a functional point of view, trees share a number of features, such as large size, long life span, and a self-supporting woody perennial trunk, but not one is really exclusive. According to Van Valen (1975), a tree is, in the ecological sense, “any tall woody plant.” However, trees are generally distinguished from shrubs and vines, so most researchers prefer to be more specific. For instance, for Thomas (2000), “a tree is any plant with a self-supporting, perennial woody stem”; for Donoghue (2005) the tree growth habit is characterized by “tall plants, with a thickened single trunk, branching well above ground level”; and for Niklas (1997) a tree is “any perennial plant with a permanent, woody, self-supporting main stem or trunk, ordinarily growing to a considerable height, and usually developing branches at some distance above the ground.” The modulations introduced express the need to accommodate situations where plants generally considered to be trees adopt unusual habit or size in some environments. Finally, somewhat arbitrary definitions can be found in the forestry literature, for inventory purposes: “Trees are woody plants with one erect perennial stem, a definitely formed crown, a height of at least 4 m and a stem diameter at breast height of at least 5 cm” (Little 1979).

The presence of wood is sometimes taken as an argument to circumscribe trees to the lignophytes (see Niklas 1997). Interestingly, recent molecular genetic and genomic studies in *Populus* and *Arabidopsis* have shown that the genes responsible for cambium function and woody growth are not unique to woody plants: Genes involved in the vascular cambium of woody plants are also expressed in the regulation of the shoot apical meristem of *Arabidopsis* (Groover 2005). This might explain why

Allometry: the study of size and its consequences

woodiness can evolve so readily (as observed in many island radiations; e.g., Böhle et al. 1996, Carlquist 1974) and led Groover (2005) to conclude that forest trees “constitute a contrived group of plants that have more in common with herbaceous relatives than we foresters like to admit.”

According to Arber (1928), one needs to go beyond textbook definitions and acknowledge that the difference between trees and other plants is mostly a question of scale. Below, we provide an account of the prominent features of the tree growth habit from an ecological standpoint. In so doing, we follow Arber (1928) and stress questions of scale and allometry.

2.2. Prominent Tree Features

The woody habit involves a series of ecological benefits and constraints that have contributed to the dominance of trees across many ecosystems worldwide and to their scarcity or complete absence from others. According to Harper (1977, p. 599), the major advantage of a woody growth habit is that “it can give perenniality to height.” These two components are tightly linked, as a high stature can obviously not be attained without the corresponding life span. Tallness and longevity are also the prerequisites for another central feature of trees: their large, sometimes huge lifetime reproductive output, despite a somewhat delayed maturity.

Although it is clear that these characteristics have been molded by selection pressures (Niklas 1997), they are subject to a diversity of anatomical, physiological, or ontogenetic constraints (e.g., Mencuccini et al. 2005, Niklas 1997, Rowe & Speck 2005, Silvertown et al. 2001). Major steps to understand the primary causes of the evolution of the tree growth habit have been made by simulating adaptive walks through the morphospace of early vascular land plants (Niklas 1997). These studies indicate that growing tall is indeed an adaptive process; in particular, “tree-like morphologies bearing lateral planated branching systems or foliage leaves occupy adaptive peaks” (Niklas 1997). Altogether, the tree growth form can be viewed as an integrated ecological strategy involving many trade-offs (**Table 1**). In the following we discuss implications of the tree habit and outline the major characteristic of trees’ life cycle.

2.2.1. Tallness. Trees grow tall where resources are abundant, stresses are minor, and competition for light takes place (e.g., Falster & Westoby 2003, King 1990, Loehle 2000). Large size enables them to create a physical and chemical environment that influences their own performance and that of interacting organisms (e.g., Boege & Marquis 2005, Herwitz et al. 2000, Ricklefs & Latham 1992). High stature helps mitigate the effects of disturbances that take place primarily at ground level, such as grazing and trampling by large herbivores or fires (Ordóñez et al. 2005), but it makes trees highly susceptible to other disturbances such as wind (Gutschick & BassiriRad 2003, Loehle 1988, Rowe & Speck 2005). Growing tall requires the development of resistant supporting and protective tissues. This generates high costs of maintenance, reduces growth rates, and limits the existence of trees to areas that provide a minimum long-term input of energy, water, and nutrients (Ward et al. 2005a, Wardle et al. 2004).

Table 1 Some advantages and drawbacks of the tree growth form

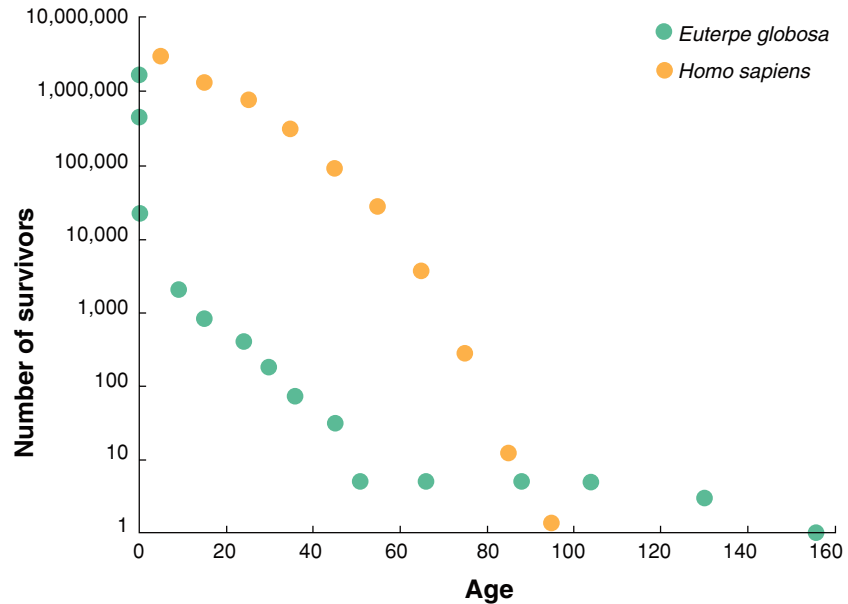
Advantage	Drawback
Great potential of biomass gain	High maintenance costs
High competition after successful establishment	Extremely high recruit mortality
Endurance to short-term resource depletion	Increased probability of suffering catastrophic events
Escape from disturbances at ground level (e.g., grazing, fire)	Exposure to physical disturbances above ground (in particular wind)
Life-long increase in storage capacity and fecundity	High investment in supporting tissues and defense mechanisms reduces overall allocation to reproduction
Great lifetime fecundity	Delayed maturity
Little dependence on particular reproductive events	Trade-off between present reproductive output and future growth, survival, and reproduction
Attraction of mutualists (e.g., pollinators, seed dispersers, herbivore predators)	Attraction of antagonists (e.g., herbivores, pathogens)
Satiation of enemies (e.g., mast-fruiting)	Satiation of mutualists (e.g., geitonogamy, disperser satiation)
Large pollen and seed production and release height facilitate gene dispersal	Low plant density complicates mating and increases pollen limitation
Relatively little seed limitation of recruitment	Strong limitation of suitable sites and time windows for recruitment
Effective population size close to adult population size	Large differences in life spans exacerbate inequality in individual lifetime fecundity
Local adaptation favored by strong selection during early life stages	Local adaptation hindered by high gene flow
Reduced accumulation of mutations per unit of time	Increased mutation rate per generation
Strong inbreeding depression increases outcrossing rate and maintains genetic diversity	Lifelong accumulation of somatic mutations results in susceptibility to inbreeding depression
Long life span reduces extinction risk	Long generation time reduces speciation rate
Extensive intra- and interspecific gene flow reduces extinction risk	Extensive intra- and interspecific gene flow reduces speciation rate
Slower evolution than mutualists results in greater share of resources for host trees (Red King effect)	Slower evolution than antagonists results in host trees lagging behind in arms races (Red Queen effect)

Tall stature also tends to increase gene flow. For instance, the height of release is often (yet not necessarily) related to the median transport distance of wind-dispersed pollen and seeds (Nathan et al. 2002, Okubo & Levin 1989, Portnoy & Willson 1993). Tall, conspicuous plants with large flower or fruit displays also tend to attract disproportionately many animal pollinators and seed dispersers (Ghazoul 2005). The latter holds likewise for antagonists such as herbivores or pathogens, however.

Height is probably the plant trait that has most often been included in comparative studies. Westoby et al. (2002) consider it a leading dimension of plant ecological strategies, as it conveys knowledge on many other aspects of species' ecology. The upper limit to plant height has been the object of many studies and debate that will not be reviewed in detail here. Two major hypotheses coexist, the respiration hypothesis and the hydraulic-limitation hypothesis (e.g., Mencuccini et al. 2005). However,

Figure 1

Survivorship curves for a large plant (the palm *Euterpe globosa*) and a large animal (*Homo sapiens*). Note the concave versus convex relationship first noticed by Szabó (1931). Data for the tree is from Van Valen (1975).



Generation time: the time from seed to seed

evolution should not lead to a single limiting factor, according to the principle of equalization of marginal returns on alternative expenditures (Westoby et al. 2002). Hence, species are not expected to grow as tall as physically possible because of various trade-offs, for example with reproduction, wood density (and hence longevity), or leaf mass (e.g., Loehle 1988).

2.2.2. Extended life cycle. Although great advances have been made in our understanding of initial recruitment processes in forests and in the modeling of vegetation dynamics (e.g., Clark et al. 1999, Loehle 2000), extremely few studies have considered the entire tree life cycle. A notable exception is the work of Van Valen (1975), who presented the first complete life table for a tree, the tropical palm *Euterpe globosa*. According to his computations, only one seed in one million produces a shoot that reaches the canopy in this species. The resulting demographic curve, when expressed in logarithmic terms, is highly convex, contrary to that of many large animals, as first pointed out by Szabó (1931) (**Figure 1**). In this palm species, generation time was estimated to be 101 years, a value intermediate between age at maturity (50 years) and maximum observed life span (156 years). These values underline the need to distinguish between age at maturity, generation time, and life span, which are often inappropriately used interchangeably in the literature.

2.2.3. Seed production. Estimates of lifetime reproductive output for trees are rare (Moles et al. 2004), but it is clear that many trees produce prodigious numbers of seeds. Reproduction is costly and trade-offs with vegetative growth are well-known (e.g., Obeso 2002). Niklas & Enquist (2003) proposed an allometric model for reproduction

in seed plants that shows that the annual reproductive biomass scales with the two-thirds power of the standing shoot biomass; in other words, allocation to reproduction decreases with size. Hence, larger plants would produce comparatively fewer seeds if seed size scaled isometrically with plant size. Aarssen (2005) tested this latter relation for 600 North American species and found that seed length increases only at about half the rate of plant height, indicating that the prevalent evolutionary trend (i.e., the deviation from allometric scaling) is toward comparatively smaller seeds, thus maintaining fecundity at the expense of seed provisioning. Moreover, the variability in seed length grows disproportionately with plant height. Similar results were obtained by Moles et al. (2004) for plant and seed mass. Aarssen (2005) argued that the observed patterns might be a simple consequence of the fact that the spectrum of possible seed sizes broadens with plant size.

Contrary to animals, plant fecundity usually increases more or less continually through an individual's life (Franco & Silvertown 1996). Hence, the lifetime seed production of trees is typically orders-of-magnitude greater than that of herbs, even though decreasing allocation results in a lower annual output of seeds per unit of canopy (Moles et al. 2004). Unfortunately, as for many other relationships, it remains unclear if individual variation in lifetime fecundity is greater in trees than in herbs or if it scales isometrically.

Finally, much attention has been paid to the phenomenon of mast seeding in trees (i.e., the synchronous intermittent production of large seed crops). Overall, it appears that fruit crop size scales positively with its among-year variability (Kerkhoff & Ballantyne 2003). But it remains unclear whether this phenomenon results mostly from weather conditions or represents an evolved plant reproductive strategy to improve pollination efficiency and outcrossing levels (in wind-pollinated species), and/or to increase offspring survival through predator satiation. Recent meta-analyses of extensive data sets indicate that both components may be involved to varying extents (Kelly & Sork 2002).

2.2.4. Establishment. As trees tend to live in comparatively stable habitats and generation turnover is slow, only an extremely small fraction of the seeds produced during an individual's lifetime will eventually survive to maturity. This has important consequences for trees' evolution. First, the considerable selection potential during early life stages should favor local adaptation of recruits, particularly for traits that enhance competitive ability (such as early growth and delayed maturity). By contrast, selective culling during trees' establishment appears to have little influence on population demography (Franco & Silvertown 1996). Second, because much of the density-dependent mortality takes place before maturity in trees, their effective population size should be closer to the actual adult census size compared to herbs, contributing to preserve genetic diversity (Dodd & Silvertown 2000).

2.2.5. Age at maturity. One classical trade-off in population dynamics is that between early growth and age at maturity. Precocity of reproduction has a great influence on the potential growth rate of a population (Harper 1977). Only very stringent competition for resources (e.g., light) during the early life of trees can select for

delayed maturity. Among trees, there is a great variation in age at maturity. Woody angiosperms tend to reproduce sooner than gymnosperms [modal class is 1–5 years compared to 6–20 years (Verdú 2002)]. Age at maturity has received some attention by molecular biologists. Genetic manipulations demonstrate that juvenile trees can be induced to flower by modifying the expression of a single gene, e.g., *LFY* in transgenic poplars (reviewed in Martín-Trillo & Martínez-Zapater 2002). Hence, as for secondary growth, the evolution of shortened maturity does not require profound genetic changes at the molecular level. (The converse is not necessarily true, however; the evolution of delayed maturity might be more complex.)

2.2.6. Longevity. A long life span is favored in stable habitats as long as it remains advantageous to allocate resources to future reproduction. Great longevity provides several obvious advantages. First, once successfully established, plants can endure periods of environmental stress while taking advantage of relatively short pulses of less harsh conditions. In particular, long-lived species can endure periodic reproductive failures without direct negative demographic consequences (Ashman et al. 2004, Calvo & Horvitz 1990). This flexibility might explain why woody plants generally display stronger pollen limitation than herbs (Knight et al. 2000). Second, spreading reproduction over many years boosts lifetime reproductive output. However, a long life span also means that individuals have to cope with variable environmental conditions including catastrophic events (Gutschick & BassiriRad 2003). Hence, allocations to growth, reproduction, and survival need to be adjusted throughout lifetime. Such plasticity would in turn contribute to enlarge trees' potential habitats (e.g., Hampe & Bairlein 2000, Jónsson 2002), resulting in considerable buffering against extinction (Hampe & Petit 2005).

2.2.7. Senescence. The extreme longevity observed in woody plants makes them useful models for senescence research and trees have actually started to attract the interest of gerontologists (e.g., Flanary & Kletetschka 2005, Lanner 2002, Larson 2001). As pointed out by Williams (1957), the degree of senescence is a function of the lifetime distribution of reproductive effort, so senescence should be far lower in organisms that increase reproduction with age, like trees.

Extreme conditions (e.g., low temperatures, drought or wind) are associated with the occurrence of particularly old and slow-growing trees (e.g., Laberge et al. 2000, Lanner 2002, Larson et al. 1999), suggesting that low metabolism contributes to their delayed senescence. Until recently, it was generally assumed that whole-organism metabolic rate scales with the three-fourths power of body mass in all organisms (Gillooly et al. 2001). Hence, trees would inherently experience reduced metabolic rates simply owing to their size. However, Reich et al. (2006) have shown that the metabolic rate of plants (including herbs, woody plant seedlings and young saplings) instead scales approximately isometrically with plant size, thereby discarding allometry as a possible source of reduced metabolic rate in trees. Nevertheless, the remarkable amount of resources that woody plants need to invest in supporting structures and defenses (such as a thick bark or defensive chemicals) is generally related to a reduction of growth rate and, hence, of metabolism (Loehle 1988).

Trees dispose of a suite of active and passive mechanisms to repair, isolate, or replace deteriorated tissues (Loehle 1988). These can greatly increase life span thanks to the modular structure of plant growth and to the fact that at least some cell lines inside meristems retain the juvenile ability to contribute to new growth (Lanner 2002). Low extrinsic mortality and efficient repair mechanisms would promote resource allocation to repair (especially early in life), resulting in delayed growth rate and maturity, large size, and a dramatic increase in survival and maximum life span (Cichón 1997). Empirical support for this notion comes from a demographic analysis of herbaceous and woody plants (Silvertown et al. 2001) that detected increasing age-specific mortality near the maximum life span (that is, signs of senescence) only in the longest-lived species. So far, however, little evidence exists for whole-tree senescence in terms of changes in gene expression that might indicate genetically controlled aging mechanisms (Diego et al. 2004), although there are preliminary data indicating that both telomere length and telomerase activity could be involved in tree longevity (Flanary & Kletetschka 2005).

Inbreeding depression: the reduction in performance of progeny derived from selfing

Self-incompatibility systems: methods preventing self-fertilization in hermaphrodites through recognition and rejection of pollen expressing the same allelic specificity as that expressed in the pistils

3. TREES HAVE HIGH LEVELS OF GENETIC DIVERSITY AND EXPERIENCE RAPID MICROEVOLUTION

Comparative surveys based on molecular markers have consistently indicated that trees have more genetic diversity within their populations than herbaceous plants and shrubs (e.g., Hamrick et al. 1979; Hamrick & Godt 1989, 1996; Nybom 2004). However, genome-wide estimates of nucleotide diversity in plants are still too few to see if this trend also holds at the sequence level (Neale & Savolainen 2004). Tree populations are also less genetically structured than herbaceous plants (Hamrick & Godt 1989, 1996; Nybom 2004). Finally, trees appear to be capable of rapid adaptation to new conditions (e.g., Petit et al. 2004a). Below, we discuss possible causes that might account for these observations.

3.1. Mating System

3.1.1. Trees are predominantly outcrossed. Although many trees can self, not one is predominantly selfing (Hamrick & Godt 1996). Clarifying the causes of this marked association between life form and mating system is of utmost importance because mating system has major evolutionary consequences; in particular, it has been repeatedly shown to be one of the best predictors of the genetic structure of populations, both at presumably neutral markers (e.g., Hamrick & Godt 1989, 1996; Schoen & Brown 1991) and at quantitative traits (Charlesworth & Charlesworth 1995).

3.1.2. Proximate causes. Trees are primarily outcrossing as a consequence of mechanisms that enforce allogamy, like inbreeding depression, self-incompatibility, or dioecy. First, strong early acting inbreeding depression is particularly frequent in trees (e.g., Husband & Schemske 1996, Sorensen 1999). It ensures that all adult plants eventually result from outcrossing. Given the formidable life-long reproductive capacity

of trees resulting in high juvenile mortality and hence in “convex” demographic curves (**Figure 1**), early acting inbreeding depression might represent a demographically acceptable strategy. Although some tree populations have been identified that are largely purged of their inbreeding depression (e.g., Sorensen 2001), they are very rare and appear to have experienced a bottleneck. Second, self-incompatible species are on average markedly more long-lived than self-compatible ones, even among perennials (Ehrlén & Lehtilä 2002). RNase-based self-incompatibility is currently considered the ancestral state in the majority of eudicots (Igic & Kohn 2001), so any difference between trees and herbs would imply a more rapid loss of self-incompatibility in herbs. Third, dioecy is consistently more frequent in woody plants than in herbs (Vamosi & Vamosi 2004). Dioecy has frequently evolved following colonization of oceanic islands, along with increased size and woodiness (e.g., Böhle et al. 1996). In small colonist populations, the accumulation of deleterious mutations could cause male sterility and precipitate the evolution of gynodioecy and ultimately dioecy.

3.1.3. Ultimate causes. One possible explanation for the relation between life span and mating system is that the reproductive assurance granted by selfing would be of less significance in long-lived perennials, because failures to reproduce one year do not compromise their life-long fitness (Ashman et al. 2004, Calvo & Horvitz 1990). In support of this, seed augmentation experiments indicate that seed limitation is most prevalent in early successional habitats (Turnbull et al. 2000), where selfing species are most common.

Morgan et al. (1997) have suggested that temporally fluctuating inbreeding depression could instead represent the major cause of the allogamous mating system of long-lived plants. Inbreeding depression is spread over many years in trees because of their greater longevity; this should exacerbate selection against inbred individuals because of the multiplicative effects of inbreeding depression. They also note that iteroparous perennial plants, if self-pollinated via modes of selfing that provide reproductive assurance, would potentially suffer from an additional fitness cost: that of between-season seed discounting, i.e., the loss of opportunities to produce outcrossed seed in a year with great availability of pollinators. In theory, this factor (as well as inbreeding depression over many seasons) could act as a further selective force preventing the evolution of selfing in trees.

Alternatively, the outcrossed mating system of trees could directly result from their large body size rather than from their longevity. Trees' stature necessarily leads to an elevated number of mitotic cell divisions per generation, which results in a higher incidence of deleterious recessive mutations in the gametes. Using models that allow inbreeding depression of populations to evolve and assuming that deleterious mutations accumulate on a per-generation basis, Morgan (2001) showed that perenniality should result in a reduction of inbreeding depression (by making selfing-induced purging more efficient), and in inbreeding depression being caused by increasingly recessive, rather than partially dominant, mutations. Although the latter prediction holds true [deleterious mutations are typically recessive in trees (cf. Williams & Savolainen 1996)], the first prediction is not met: Perennials experience higher not lower inbreeding depression compared to annuals. By comparing empirical data on selfing rate and

inbreeding depression, Scofield & Schultz (2006) showed that for the same selfing rate, high-stature plants tend to have lower inbreeding coefficients. This implies that they have much higher inbreeding depression than low-stature plants, suggesting high deleterious mutation rates per generation, in line with experimental evidence (see Section 4.1). Scofield & Schultz (2006) further predicted that high-stature plants should have progeny with essentially zero fitness when selfed, which is well supported by experimental evidence (e.g., Sorensen 1999).

Mutation rate: the probability of genetic change per generation

3.2. Gene Flow

3.2.1. Intraspecific gene flow. Trees seem to experience remarkably high levels of gene flow. A growing body of research indicates that pollen flow over 5 or 10 km is not uncommon, both in the tropics and in temperate settings, and for both wind- and animal-pollinated trees (Table 2). These large field estimates are backed by modeling studies and by investigations of pollen viability (Katul et al. 2006, Schueler et al. 2005). Similarly, regular long-distance seed dispersal events spanning several

Table 2 Examples of long distance pollen dispersal in trees inferred with genetic markers

Species	Pollination system	Genetic marker	Location	Distance	Ref.
<i>Fraxinus excelsior</i> (Oleaceae)	Wind	Microsatellites	Relic woodlands in Scotland	53% of successful pollination by immigrant pollen in a catchment at > 10 km from other populations	1
<i>Dinizia excelsa</i> (Fabaceae)	Bees	Microsatellites	Manaus, Brazil	Mean pollen dispersal distance of 1.5 km; pollen transport up to 3.2 km.	2
<i>Populus trichocarpa</i> (Salicaceae)	Wind	Microsatellites	Pacific Northwest, USA	27% of matings from individuals located beyond 2.7 km and up to 9.8 km	3
<i>Cecropia obtusifolia</i> (Moraceae)	Wind	Allozymes	Southern Mexico	A population at 6 km accounted for 27% of the offspring and another at 14 km accounted for 9%	4
<i>Ficus</i> spp. (Moraceae)	Wasps	Allozymes	Central Panama	Pollen dispersal estimated to occur routinely over 5.8–14.2 km between widely spaced trees	5
<i>Pinus sylvestris</i> (Pineaceae)	Wind	Microsatellites	Central Spain	4.3% of matings with pollen from >30 km	6
<i>Ceiba pentandra</i> (Malvaceae)	Bats	Microsatellites	Central Amazonia	Several matings > 5 km; up to 18.6 km	7
<i>Swietenia humilis</i> (Meliaceae)	Small butterflies, bees etc.	Microsatellites	Coastal plain, Honduras	Direct distance of pollen flow >4.5 km	8

1. Bacles et al. (2005), 2. Dick et al. (2003b), 3. DiFazio et al. (2004), 4. Kaufman et al. (1998), 5. Nason et al. (1998), 6. Robledo-Arnuncio & Gil (2005), 7. Gribel, cited in Ward et al. (2005b), 8. White et al. (2002).

kilometers have been reported (Bacles et al. 2006, Gaiotto et al. 2003, Godoy & Jordano 2001), even if the bulk of gene flow is usually mediated by pollen (Petit et al. 2005a).

These observations suggest that trees could experience comparatively more gene flow than herbs with the same mating system. Their high stature makes the world smaller for them. Large individuals necessarily grow at lower density, which implies a greater absolute distance between potential mates and increases pollen dispersal distances (Ward et al. 2005b). Frequent long-distance pollen movements should buffer tree populations against diversity loss resulting from fragmentation (Hamrick et al. 1991, White et al. 2002).

3.2.2. Interspecific gene flow. According to many botanists (e.g., Grant 1958, 1963; Stebbins 1950, 1958), long-lived woody perennials engage more readily in interspecific matings than other plants. Such comparisons are difficult, however, and few studies have attempted to quantify this trend. An exception is the review of Ellstrand et al. (1996), which shows that hybrids are more frequently detected in outcrossing perennials. But further work on this topic is clearly needed, as few tree-rich floras have been examined for the frequency of hybrids. In principle, this apparent propensity of trees to hybridize could at least partly account for the high levels of genetic diversity observed. It might also represent a means to colonize new habitats (Petit et al. 2004b).

3.2.3. Large effective population size. Contrary to large animals, trees can have huge global census sizes. For instance, European beech forests cover some 17 million ha, which should represent 1.5–2 billion mature individuals, assuming that there are around 100 adult trees per hectare (disregarding seedlings and saplings, most of which will not make it to the reproductive stage). Even those tree species found typically at low density (as is typical in the tropics) can have, in fact, fairly large global population sizes, because they belong to “predictable oligarchies that dominate several thousand square kilometers of forest” (Pitman et al. 2001). A few narrow endemic tree species do exist, but these are found either on oceanic islands or represent relicts that were historically more widespread, as in the case of some Mediterranean trees (Petit et al. 2005b). Large effective population size implies that polymorphisms can persist during extended periods of time. The recent finding of trans-species shared polymorphisms in allopatric tree species that have diverged over 13 Myr ago has been interpreted in this light (Bouillé & Bousquet 2005). More studies are needed to determine if such ancient polymorphisms are frequent in trees.

3.3. Asexual Reproduction

Whereas no selfing tree species has been described so far, trees with predominantly asexual reproduction exist, although they seem to be rare (Thomas 1997). Contrary to selfing, asexual reproduction does not expose recessive deleterious mutations to selection. At low population size, asexual reproduction might better preserve heterozygosity than outcrossing, at least in the short term. For instance, the sole case of

paternal apomixis ever described in plants is for a relict cypress species in the Tassili desert, which consists of fewer than 200 adult trees (Pichot et al. 2001). Further studies are needed to test whether asexual reproduction is actually less frequent in trees than in herbs.

3.4. Chromosome Number

A high basic number of chromosomes should promote diversity through its effect on recombination (Grant 1958, 1975, p. 448). Levin & Wilson (1976) have estimated that tree genera have a mean basic chromosome number of 13.1 compared to only 9.3 for herbaceous plants. The growing number of studies that estimate linkage disequilibrium from within-species sequence data should eventually allow for the testing of possible differences between trees and other plants in the recombination parameter. The first studies point to particularly rapid decay of linkage disequilibrium in trees, with polymorphic nucleotide sites a few hundred base pairs apart often being uncorrelated (Neale & Savolainen 2004).

In principle, polyploidy should also help preserve genetic diversity by increasing the number of copies of each gene. However, no study seems to have compared its prevalence in trees and in herbs, although other correlates of polyploidy have been identified (Ramsey & Schemske 1998).

3.5. Diversifying Selection

Trees are exposed to highly heterogeneous biotic and abiotic conditions within their individual lifetimes and across their ranges. Linhart & Grant (1996) estimate that short-lived plants harbor on average 10–30 taxa of parasites and herbivores, compared to over 200 for larger long-lived species, resulting in far greater complexity of selection in the latter. These parasites and herbivores can exert different selection pressures at different life stages, from seed to seedling, juveniles, and mature stages. Although this is not unique to trees, the heterogeneity of selection pressures is exacerbated by trees' longevity and by the diversity of organisms with whom they are interacting (Boege & Marquis 2005, Linhart & Grant 1996). Similarly, extreme climatic events are likely to occur within trees' lifetimes (Gutschick & BassiriRad 2003). This allows a complex interplay of frequency-dependent, balancing or episodic selection pressures that could contribute to the maintenance of genetic diversity.

Following foundation of a new population by a single individual, a loss of diversity is expected, even in self-incompatible species. However, genetic diversity can then be quickly re-established if seeds sired by immigrant pollen have greater fitness (Richards 2000), which is another form of frequency-dependent selection. Perhaps as a consequence of this preserved store of variation, invasive populations of trees can adapt within a few generations to new conditions (Petit et al. 2004a).

Finally, and most importantly, extensive gene flow does not seem to compromise local adaptation in trees. Trees commonly combine substantial genetic differentiation at quantitative traits (Q_{ST}) with little differentiation at molecular markers (F_{ST}) (McKay & Latta 2002). Computing average Q_{ST} and F_{ST} values for allogamous

herbs and trees from table 1 of McKay & Latta (2002) shows that although trees have much lower differentiation at molecular markers (F_{ST} of 0.05 versus 0.17), indicating higher gene flow among tree populations, differentiation at quantitative traits was similar in the two groups (Q_{ST} of 0.34 versus 0.35). Trees' large fecundity and the resulting strong selection of recruits could account for this observation (Le Corre & Kremer 2003).

3.6. Age at maturity

Delayed maturity in trees could dramatically reduce founder events during invasions, thereby preserving genetic diversity (Austerlitz et al. 2000). At the time when the first individuals start to reproduce, a non-negligible part of the space available for establishment will already be occupied by juveniles from seeds that arrived years before. In contrast, an annual plant colonizing an empty site can reproduce the first year and quickly fill the available space with its offspring. Everything else being equal, this should result in a much sharper loss of diversity and much greater differentiation in annuals. Simulations show that the key factor in avoiding founder effects is indeed delayed reproduction and not overlapping generations (Austerlitz et al. 2000).

4. PACE OF EVOLUTION IN TREES

Sinnott (1916) first argued that generation time should affect the rapidity of evolutionary change in trees as compared to herbs. Here we consider whether trees are indeed characterized by different mutation rates, nucleotide substitution rates, and patterns of diversification in comparison with other plants.

4.1. Mutation Rates

The large genetic diversity identified during population genetic surveys of trees has led some researchers to infer that trees have higher mutation rates than herbaceous plants (e.g., Linhart 1999). Trees' high genetic load (Klekowski 1988) seems to support this prediction. However, although trees might be expected to have higher per-generation mutation rates than other plants (because of the "chemostat-like" postzygotic accumulation of somatic mutations in the apical initials during plant growth; Klekowski & Godfrey 1989), it does not follow that they accumulate more mutations per unit of time. The arguments are as follows: (a) Metabolic rates seem to be lower in trees than in other plants (see Section 2.2.2). (b) Trees experience less recombination events per unit of time because of their longer generation time. (c) Assuming that mutations occur predominantly at cell division, trees should accumulate less mutations per unit of time compared to short-lived plants, because cell divisions corresponding to germination and flowering occur on a per-generation, not on a per-growth-season, basis. (d) Ontogenetic patterns of cell divisions could promote genomic stasis by allowing mutant cells to be eliminated (thereby compensating for the absence of an immune surveillance system capable of eliminating cells with deviant phenotypes, as is found in some animals). In trees, such ontogenetic pathways include logarithmic

cell divisions and highly branched phenotypes, as well as particular patterns of branch senescence (Klekowski et al. 1989). The extension in girth of the cambium, accomplished through the initiation of new radial cell files in excess of the number needed to achieve growth, has also been interpreted as a mechanism destined to facilitate the elimination of somatic mutations from the meristematic population (Mellerowicz et al. 2001).

We therefore expect that fewer somatic mutations should get fixed per unit of time in perennials than in annuals. In other words, the per-generation increase in mutation rate in perennials would be less than predicted from their difference in generation time. This seems supported by the work of Klekowski & Godfrey (1989) who estimated that mutation rate in mangrove trees is 25 times that of annual plants, although differences in generation times would predict a mutation rate >100 times as large. Future molecular studies might provide data on somatic mutation rates in annuals versus perennials, as indicated by a few promising attempts relying on microsatellites in long-lived trees (Cloutier et al. 2003, O'Connell & Ritland 2004). Similarly, if more studies confirm that trees have lower nucleotide diversity than expected from surveys based on genetic markers (Neale & Savolainen 2004), this would support the idea that trees accumulate fewer mutations per unit of time than do other plants (see Sidebar).

4.2. Substitution Rates

Although estimates of mutation rates remain rare in trees, evidence has now accumulated that shows perennials evolve more slowly at the DNA sequence level, for chloroplast, mitochondrial, and nuclear genes, particularly at silent sites (Table 3). Differences can be quite pronounced, but their causes are still under discussion. Some researchers consider the generation-time effect is an unlikely explanation for plants because cells continue to divide throughout their lives and do not rest like germline cells in animals (but see Section 3.1). Another (nonexclusive) hypothesis is that substitution rates would be driven by speciation events. Rates of substitution and diversification are correlated in angiosperms (Barraclough & Savolainen 2001, Jobson & Albert 2002, Xiang et al. 2004). This might be caused by differences in population

ARE MUTANT CELLS SUBJECT TO POSITIVE SELECTION WITHIN THE CROWN OF TREES?

Although the diploid (or polyploid) nature of plants and the presence of stratified meristems should lower the immediate phenotypic impact of somatic mutations, there have been repeated claims that somatic variation can play a role in generating immediately selectable variation among plant parts, especially in long-lived tree species. However, the evidence is not compelling and the topic remains highly controversial (reviewed in Gill et al. 1995; see also the discussion in the *Journal of Evolutionary Biology*, 2004, volume 17, issue 6).

Table 3 Comparison of nucleotide substitution rates in long-lived versus short lived plants

Dataset	Sample size	DNA sequences	Main conclusion	Ref.
<i>Lupinus</i> (Fabaceae)	44 taxa	ITS	Most taxa on long branches of the phylogenetic tree are annuals	1
<i>Sidalcea</i> (Malvaceae)	28 taxa	ITS and ETS	Annual species have up to 7 times higher molecular evolutionary rates than perennials	2
Seed plants	43 species	<i>rbcL</i>	Annuals evolve more rapidly than perennials, especially at nonsynonymous sites, owing to a recent acceleration of substitution rates	3
Seed plants	33–63 spp.	<i>atpB</i> – <i>rbcL</i>	Significant negative correlation between substitution rates and perenniality, especially at silent sites	4
Grasses versus palms	3 spp.	<i>rbcL</i> , <i>Adb</i> , <i>atpA</i>	Grasses evolve more rapidly than palms at silent sites at all three genes corresponding to the three plant genomes: ~3.7 times for <i>rbcL</i> , ~2.5 times for <i>Adb</i> , and ~6.7 times for <i>atpA</i>	5
Lentibulariaceae	69 spp.	7 loci from the three genomes	No relationship between substitution rate and generation time	6
Angiosperms	15 spp.	<i>rps3</i> intron	Annual taxa evolve up to 10–15 times faster than perennials for substitution and indel rates; first demonstration of differences between annuals and perennials in noncoding DNA	7
Angiosperms	24 spp. pairs	ITS1 and ITS2	Annual species evolve faster in 60% of the cases but the trend is not significant	8

1. Ainouche & Bayer (1999), 2. Andreasen & Baldwin (2001), 3. Bousquet et al. (1992), 4. Duminil, Grivet, Ollier, Jeandroz & Petit, unpublished results, 5. Eyre-Walker & Gaut (1997), 6. Jobson & Albert (2002), 7. Laroche & Bousquet (1999), 8. Whittle & Johnston (2003).

size, as speciation represents a form of bottleneck. In fact, large population sizes and extensive gene flow have been suggested as the causes of the low rates of evolution in trees (e.g., Bousquet et al. 1992). Other explanations rely on body size, which would, along with temperature, affect the rate of DNA evolution through their relation with metabolic rate (e.g., Gillooly et al. 2005; but see Reich et al. 2006).

4.3. Diversification Rates

Slow sequence evolution is often associated with morphological stasis (Barraclough & Savolainen 2001, Soltis et al. 2002), so trees are predicted to have lower diversification rates than other plants. Reduced rates of diversification in trees have been suggested long ago by comparing species richness at similar taxonomic levels, and they were explained by the generation-time effect (Sinnott 1916). Subsequently, growth form has been included in most treatments of diversification of angiosperms, along with mode of pollen and seed dispersal. An early study that confirmed a reduced rate of diversification in trees while controlling for the age of lineage is that of Levin & Wilson (1976). However, the first study that used phylogenetically independent contrasts to investigate the effects of the growth habit on diversification was conducted by Dodd et al. (1999). They found that a majority of transitions in growth form (75–84%) were from woody to herbaceous modes and that diversification in these new

herbaceous lineages was consistently more rapid. There was no major exception to the rule that the change from woodiness to herbaceousness results in increased species richness. Verdú (2002) extended these analyses by focusing on woody angiosperms only and by classifying the plants according to their age at maturity (as a surrogate for generation time), while controlling for pollination and seed dispersal mode. He could confirm the relationship at all taxonomic levels considered, implying that trees have lower diversification rates than shrubs. Trees have also low rates of karyotypic evolution (an order of magnitude lower than herbs according to Levin & Wilson 1976). Tree species are therefore much older than herbaceous species (e.g., Levin & Wilson 1976, Magallón & Sanderson 2001). These prolonged species life spans imply low rates of extinction, given the low rates of speciation.

Nevertheless, tree species can appear rapidly under some circumstances, such as in islands (e.g., Baldwin & Sanderson 1998, Böhle et al. 1996). In Hawaii, most evolutionary changes are from herbaceous to woody growth forms (Price & Wagner 2004). However, several of the woody taxa there have retained characteristics of herbaceous plants such as short generation time and specialization to ephemeral habitats. There are also a number of tree genera that are relatively species-rich (*Acacia*, *Eucalyptus*, *Prunus*, *Quercus*, *Salix*. . .), but they generally include shrubs or treelets that might have driven the radiation. Similarly, there has been a recent report of extraordinary rapid diversification in a neotropical tree genus (*Inga*), but the corresponding species are considered to have low generation times for trees (Richardson et al. 2001), so all these examples do not contradict the rule. In fact, many widely distributed rain forest tree species appear to be of great age and to have experienced morphological stasis, as is suggested by phylogeographic studies and by comparisons of the woody flora of the New World and Old World tropics (Dick et al. 2003a).

As for substitution rates, various explanations have been proposed to explain these differences in diversification rates. Trees shape the communities and buffer their own environment, which could reduce their evolutionary rates. The observation that forest herb species experience morphological stasis (Ricklefs & Latham 1992) suggests that the stability of forest environments could contribute to the reduced extinction rates. This hypothesis deserves further investigation. High intra- and interspecific gene flow and large population sizes could also reduce the likelihood of divergence and speciation, whereas the elevated individual life span should allow trees to persist under difficult conditions, thereby reducing extinction risks arising from demographic stochasticity (Hampe & Petit 2005). On the contrary, the suggestion that increased level of within-species genetic variability promotes speciation (because it is available for conversion to species differences) does not appear to be supported by the available evidence (Avice 1977).

4.4. Tree Evolution and Biotic Interactions

Arms races between host trees and their pathogens and herbivores are expected, thereby promoting fast rates of evolution, as illustrated by the Red Queen model (Van Valen 1973). However, antagonistic organisms generally have much shorter generation times than trees and may easily evolve new features within the lifetime

of their host. This asymmetry could be compensated for in various ways: (a) There might be differences in the amount of segregating genetic variation. For instance, trees could rely on rapid adaptive changes thanks to their increased levels of genetic diversity compared to that of their pathogens. (b) Trees also maintain populations of enemies of their pathogens and herbivores; in particular, mutualist microorganisms with similarly short generation times could mediate defense against antagonists, as in the case of protective ant-plant interactions corresponding to antiherbivore defenses “worn on the outside” (Heil & McKey 2003) or in fungal endophytes that limit pathogen damages (Arnold et al. 2003). (c) Specialized antagonists generally exert a weaker selective pressure on the host tree than vice versa (see, e.g., Benkman et al. 2003 for an elegant case study involving crossbills, which rely strongly on conifer seeds, and lodgepole pine).

In contrast to antagonistic interactions, mutualistic interactions could favor low rates of evolution in trees. The Red King model of Bergstrom & Lachmann (2003) uses a game-theoretical approach to show that the “slowest runner” can dominate the coevolutionary process. On an evolutionary timescale, slow evolution effectively ties the hands of a species, allowing it to “commit” to threats and thus “bargain” more effectively with its mutualistic partner over the course of the coevolutionary process. Because mutualistic and antagonistic relationships are often not easily differentiated under natural conditions and transitions from mutualism to antagonism may be frequent (Thompson 2005), a component of each model might apply to many real-world interactions.

The longevity of trees relative to that of their associated microorganisms could also directly select for the formation of mutualisms: Favoring tree performance benefits the microorganisms by preserving a stable environment for its offspring, especially in taxa that experience limited dispersal. This idea is very similar to the notion that spatial structure tends to favor mutualism, a well-established principle (Yamamura et al. 2004).

5. CONCLUSIONS

Trees have dominated terrestrial ecosystems for over 370 million years (Niklas 1997), a testimony to their evolutionary success. We have shown that the rapid rate of microevolution often reported in tree populations is not incompatible with their slow rate of macroevolution: Trees possess features that allow them to preserve genetic diversity during extended periods of time. This, in combination with their large juvenile population sizes, enables strong and variable selection. Such a strategy, which results in great potentials for local adaptation despite low evolutionary rates, appears to be the key to their success from an evolutionary standpoint. Yet, explaining the origin of this seemingly paradoxical evolutionary strategy proves difficult, as the effects of size, generation time, longevity, age at maturity, fecundity, and other potential explanatory factors are often difficult to tease apart. For instance, the predominantly allogamous mating system of trees have been interpreted to be the consequence of either their great longevity or their large size; similarly, the lower nucleotide substitution rates of trees have been attributed to increased generation time but also

to decreased metabolic rate. Further comparative studies are needed to disentangle these factors, allowing a better understanding of the way plant evolution scales with size and longevity.

Compared with studies of short-lived herbaceous plants, a change in timescale is needed to investigate the factors that shape tree evolution: Rare and extreme events become inevitable when life span increases. They should therefore shape trees' physiology and ecology and determine their resilience as populations and species. Because the lifetime of most trees by far exceeds the professional lifetime of biologists, innovative interdisciplinary approaches are required to better understand their evolution.

SUMMARY POINTS

1. Trees are an extremely polyphyletic assemblage, but they share key characters such as great size, height, and longevity, which explain their ecological success.
2. In demographic terms, trees (and other large plants) have little in common with large animals. Most importantly, they experience much less senescence effects and their often prodigious fecundity increases continually with increasing size.
3. Trees have high levels of genetic diversity within populations but little differentiation among populations, due to their outcrossed mating system, their aptitude for extensive gene flow and diversifying selection, and their large population sizes.
4. Trees experience markedly slower mutation, nucleotide substitution, and speciation rates than other plants.
5. As a consequence, the tree growth form combines a great potential for rapid microevolution with slow rates of macroevolution.
6. Identifying the major causes of tree evolution is difficult, because potential factors such as longevity, size, or fecundity are often tightly interconnected.

FUTURE ISSUES

1. More comparative studies (including phylogenetic corrections) are required to disentangle the various factors affecting the ecology and evolution of trees.
2. Further studies on allometric scaling should help distinguishing between true compensatory adaptations to the tree habit and mere consequences of trees' size and longevity.
3. Model species with their complete genomes sequenced will provide a powerful tool for identifying the genetic mechanisms that are involved in growth form changes.
4. Further comparisons with the evolutionary consequences of size and longevity in animals should be of great interest.

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