

Disturbance regimes, gap-demanding trees and seed mass related to tree height in warm temperate rain forests worldwide

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ABSTRACT

For tropical lowland rain forests, Denslow (1987) hypothesized that in areas with large-scale disturbances tree species with a high demand for light make up a larger proportion of the flora; results of tests have been inconsistent. There has been no test for warm temperate rain forests (WTRFs), but they offer a promising testing ground because they differ widely in the extent of disturbance. WTRF is dominated by microphylls *sensu* Raunkiaer and has a simpler structure and range of physiognomy than tropical or subtropical rain forests. It occurs in six parts of the world: eastern Asia, New Zealand, Chile, South Africa, SE Australia and the Azores. On the Azores it has been mostly destroyed, so we studied instead the subtropical montane rain forest (STMRF) on the Canary Islands which also represents a relict of the kind of WTRF that once stretched across southern Eurasia. We sought to find whether in these six regions the proportion of tree species needing canopy gaps for establishment reflects the frequency and/or extent of canopy disturbance by wind, landslide, volcanic eruptions (lava flow and ash fall), flood or fire. We used standard floras and ecological accounts to draw up lists of core tree species commonly reaching 5 m height. We excluded species which are very rare, very localized in distribution, or confined to special habitats, e.g. coastal forests or rocky sites. We used published accounts and our own experience to classify species into three groups: (1) needing canopy gaps for establishment; (2) needing either light shade throughout or a canopy gap relatively soon (a few months or years) after establishment; and (3) variously more shade-tolerant. Group 1 species were divided according the kind of canopy opening needed: tree-fall gap, landslide, lava flow, flood or fire. Only some of the significant differences in proportion of Group 1 species were consistent with differences in the extent of disturbance; even in some of those cases other factors seem likely to have had a major determining influence during evolution. We also sought to determine whether the species that are at least ‘short-term persistent’ in the soil seed bank (lasting 2–4 years) are all species needing canopy gaps for establishment. The answer was negative; large numbers of seeds of some shade-tolerants accumulate in the soil, and these species are able to benefit from soil disturbance in deep shade. We found a significant and strong positive relationship in Japan between mean seed mass and mature tree height, a weak positive relationship in New Zealand and no relationship in any of the other four regions. When comparing the seed mass values of Group 1 and Group 3 species we obtained different answers depending on whether or not we confined ourselves to taxonomically controlled contrasts. In only two of the four regions with an appreciable number of species in Group 1 is the mean seed mass of such species significantly lower than that of Group 3 species when taxonomic relatedness is ignored.

Key words: rain forest, disturbance, wind-throw, landslides, fire, flood, light-demand, shade-tolerance, seed banks, seed size.

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CONTENTS

I. Introduction	702
II. Preliminaries	704
(1) Lists of core species	704
(2) Penetration of light through WTRF canopies	705
(3) Groups of species based on light demand and type of disturbance needed	706
(4) Studies on soil seed banks	710
(5) Sources of seed dry mass values	710
(6) Comparisons of seed size	715
III. Disturbance regimes and species dependent on them	716
(1) Japan	716
(2) New Zealand	719
(3) Chile	721
(4) South Africa	722
(5) SE Australia	722
(6) Canary Islands	723
(7) Summary and statistical analysis	724
IV. Comparisons of seed mass	724
(1) Seed mass related to mature height	724
(2) Species Groups 1, 2 and 3 compared	725
(3) The ranges of seed mass within functional groups, and extreme values	725
V. Discussion	726
(1) Definition of disturbance regimes	726
(2) Disturbance regime and proportion of species gap-demanding for establishment	727
(3) Other issues of forest dynamics	732
(4) Soil seed banks	733
(5) Differences between functional groups in seed mass	733
VI. Conclusions	734
VII. Acknowledgements	735
VIII. References	735
IX. Supporting Information	744

I. INTRODUCTION

It has long been established that in tropical lowland rain forest (TLRF) on most soils there is a suite of species which need canopy gaps for establishment (Swaine & Whitmore, 1988). Such gap-demanding species are absent from lowland rain forests only on the poorest soils where the trees are relatively short, many of the taller trees die standing, and substantial canopy gaps made by tree-fall are few, e.g. in Amazonian caatinga on seasonally waterlogged white sand soils (Coomes & Grubb, 1996) and heath forests on well-drained sands in SE Asia (L. Nagy, personal communication; Ashton, 2013). Gap-demanders depend on rapid growth for their persistence in the community, and this is made difficult when paucity of nutrient supply and/or periodic dry spells combine with root competition in relatively small canopy gaps. The reality of such competition was shown experimentally for Amazonian caatinga by Coomes & Grubb (1998).

Concerning the forests on more fertile soils, Denslow (1987, p. 436) wrote ‘tree species that have a high demand for light are a larger proportion of the flora’ in ‘forests subject to large-scale disturbances’. Whitmore (1989) accepted that there are many more individuals of gap-demanding trees in areas with a greater extent of disturbance, e.g. Papua

New Guinea compared with Borneo, but emphasized that in both these areas only a small minority of the tree species are gap-demanding for establishment. However, a smaller-scale comparison is informative. Within the island of Borneo there is a strong contrast in the incidence of gap-demanding species between the geologically young area in Brunei where the slopes are steep and landslips are common, and the geologically older Danum area of Sabah with subdued slopes, few strong winds and few tree-fall gaps. In the former area a comparatively large number of gap-demanding species is present in the forest (e.g. at least 11 species of *Macaranga*) and in the soil seed bank (Mitchell, 1994), while in the latter area there are few gap-demanding species and very little seed of such species in the soil seed bank (Kennedy & Swaine, 1992). This comparison gives support to Denslow’s (1987) suggestion.

Warm temperate rain forest (WTRF) is found at a wide range of latitudes, usually within the limits 26–43° north or south of the Equator but at 24–32°N in China. There have been numerous studies of the dynamics of the forest, and the regions are known to differ in the extent of disturbances opening up the canopy, but there has been no comparison of all the different regions in terms of the incidence of gap-demanding species.

We define WTRF as built from evergreen trees able to establish away from canopy gaps and gap-demanding trees that are either evergreen or deciduous (depending on the region), with the most numerous leaf-size class among the evergreen species being microphyll *sensu* Raunkiaer (1934). WTRF is usually 15–40(–45) m tall. Almost no tree species have buttress roots, few or none are cauliflorous or ramiflorous (depending on region), and relatively few species (*c.* 10–20%) have compound leaves. In all regions bar East Asia few or no species have leaves or leaflets with drip-tips. The forest contains numerous individuals and species of small trees and treelets and/or herbs (angiosperms or ferns, depending on site). Climbers can be common, but very few species make stems of diameter at breast height (dbh) > 10 cm. Vascular epiphytes vary greatly in abundance but in most regions make up only a small biomass. WTRF varies greatly in the role played by conifers, depending on region. In New Zealand and South Africa conifers are among the species reaching the greatest heights and girths; in New Zealand they often form a prominent emergent layer of crowns, and the same is seen locally in South Africa. In eastern Asia only conifers reaching moderate to small size are present. In Chile conifers in the upland part of the core WTRF reach moderate size, and only the species of waterlogged sites attain great heights and girths. In the Azores there is one conifer of moderate height that invades tree-fall gaps. In Australian WTRF no conifer is present. Tree monocots are generally absent. Bamboo is abundant in Chile, but otherwise absent. Tree-ferns are absent in Chile, uncommon in Japan and China, and limited to wetter facies in Australia and South Africa, but are widespread and common in New Zealand.

The distinctions between WTRF and the most similar forest formation-types (both dominated by microphylls) are set out as supplementary material in online Appendix S1, where we also note species in WTRF that are exceptions to the statements above about buttresses, tree monocots, cauliflory, girth-size in climbers, and incidence of prominent epiphytes. We define cool temperate rain forest (CTRF) as differing from WTRF through having a clear dominance of nanophylls *sensu* Raunkiaer (1934) among the taller trees.

The climatic conditions experienced by the various regions of WTRF, which commonly occurs up to an altitude of 600–800 m, are shown in Table 1. Near sea level the warmth index of Kira (1991) ranges from 70–80°C.month in Chile to *c.* 150 in the Azores. In all regions other than eastern Asia the cold index of Kira (1991) is zero. In Japan it varies from 0 to –5°C.month, rarely down to –10°C.month, as shown in Fig. 2 of Hämet-Ahti, Ahti & Koponen (1974). The mean annual rainfall is most often in the range 1000–2000 mm, but can be as low as 700 mm or as high as 4000 mm. The seasonality of rainfall varies from a summer maximum *via* a rather even distribution through the year to a summer minimum. There is usually no ‘dry month’ *sensu* Walter & Lieth (1960–1967), but in the northern part of the Chilean WTRF region there are one to two dry months in summer.

Before human intervention WTRF covered a large area in Japan and China, substantial areas in New Zealand, Chile and South Africa, and smaller areas on the Azores, and in SE Australia (Fig. 1). Because most of the WTRF on the Azores has been lost and the remainder badly damaged (Fernández-Palacios *et al.*, 2011) we consider the situation in the floristically related subtropical montane rain forest (STMRF) of southern Macaronesia (Canary Islands) which also resembles floristically the WTRF of southern Europe lost during the last few million years (Axelrod, 1975). The STMRF is similar in structure and physiognomy to the WTRF but – apart from being exclusively montane – it generally differs in being richer in bryophytes on the trees and the ground, a result of the frequent cloud cover; the dominant leaf-size class may be microphyll or notophyll (see online Appendix S2).

Several authors have used, or continue to use, the term ‘subtropical’ for what we call WTRF (see online Appendix S1), but we consider that the term subtropical lowland rain forest (STLRF) should be confined to those forests which are structurally and physiognomically like TLRF except for being dominated by notophylls *sensu* Webb (1959), best exemplified by the lowland rain forest that stretches discontinuously on favourable soils from 22 to 34°S in eastern Australia.

Species-richness is much lower in WTRF than in TLRF or STLRF. Major families typical of tropical forests in the strictest sense are absent: Dipterocarpaceae, Lecythidaceae and Myristicaceae. In addition certain dicot families and subfamilies typical of both tropical and subtropical forests are absent or represented by very few species: Annonaceae, Bignoniaceae, Burseraceae, Clusiaceae, Malpighiaceae, Melastomataceae, Meliaceae, Moraceae, Phyllanthaceae, Putranjivaceae, Rhizophoraceae, Sapotaceae, Vochysiaceae, Dilleniaceae–Delinoideae, and –Dolioscarpoideae, Malvaceae–Bombacoideae and Sterculioideae, Sapindaceae–Sapindoideae, old Flacourtiaceae (now part of Salicaceae), and tree Apocynaceae, Euphorbiaceae and Urticaceae. The Lauraceae are notable as providing major shade-tolerant species in all areas of WTRF bar that in SE Australia; in that area too the family may well have been prominent before the extent of WTRF became much reduced in the Pliocene (see Byrne *et al.*, 2011) as leaf fossils suggest that Lauraceae were co-dominant in the Miocene in the area immediately to the north (Owen, 1975; Lange, 1982).

Our first objective in this paper is to review the proportion of species needing canopy-gaps for establishment, or soon after establishment, in the four major regions of WTRF, the small area in SE Australia, and the STMRF of the Canary Islands, and to determine whether or not they can be related to differences in the extent or types of disturbance opening up the forests.

Our second objective is to review the evidence for a seed bank in the soil. In earlier studies in TLRF it seemed that persistent seed in the soil was a characteristic of gap-demanding species (Swaine & Whitmore, 1988), but later work showed that some shade-tolerant species also build

Table 1. The latitudinal and altitudinal ranges of warm temperate rain forest (WTRF) in six regions and subtropical montane rain forest (STMRF) in one, plus the ranges of the Kira warmth and cold indices* near sea level for WTRF and at *c.* 550 m for STMRF, mean annual rainfall, time of maximum rainfall, and number of dry months *sensu* Walter & Lieth (1960–1967)

	Japan	New Zealand	Chile	South Africa	Australia	Azores	Canary Is.
Latitudinal range	26°30'– 38°00'N 800(–1200)	34°20'– 41°40'S 800	37°00'– 43°30'S 700(–950)	33°30'– 34°20'S 600(–1050)	37°20'– 37°45'S 80	36°50'– 40°00'N 800	27°40'– 28°50'N 1200 [Lower limit 600(–400)]
Maximum altitude (m) in that part of range nearer the equator	100–140 (–180)	88–120	70–80	125–137	100–110	<i>c.</i> 150	<i>c.</i> 135
Kira's warmth index: °C.month	0 to –5 (rarely –10)	0	0	0	0	0	0
Kira's cold index: °C.month	1150–2000 (–4000)	1000–2100 (–2300)	1200–2200 (–3500)	700–1200	700–1200 (–1500)	1000–2400	500–850 (+50 to 150 fog intercepted; locally 400–900)
Season of maximum rainfall	Summer	Rather less in summer but still wet then	Winter; summer wet in most of range	Spring to autumn	Rather even through year	Winter	Winter
Number of dry months	0	0	0 generally; 1–2 in the northern part	0	0	0	5

Values in parentheses are extreme values found at only a few sites.

*The warmth index is the sum of the positive differences between 5°C and the monthly mean temperatures; the cold index is the sum of negative differences between 5°C and the monthly mean temperatures. Meteorological data are taken from Walter & Lieth (1960–1967).

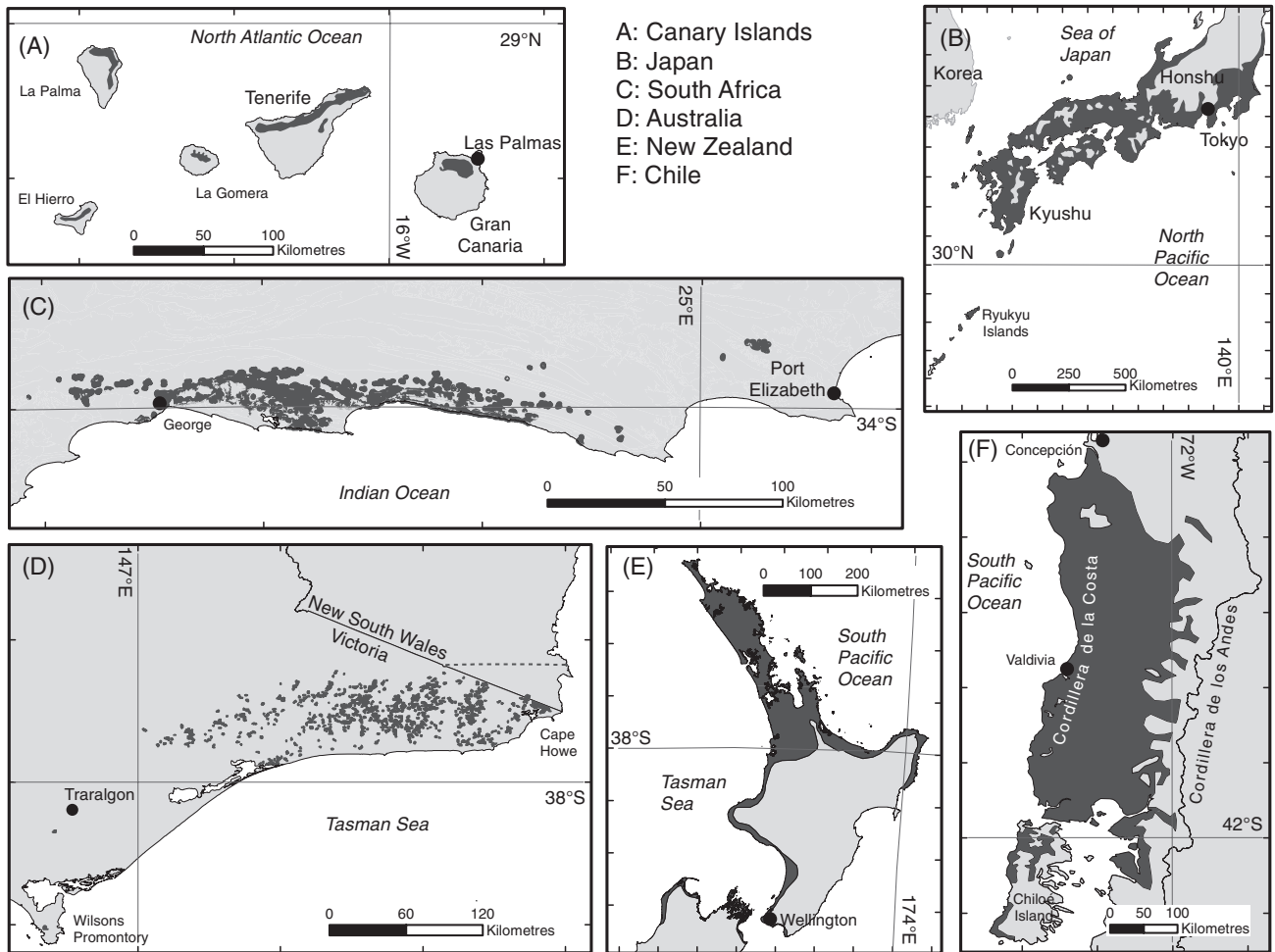


Fig. 1. Maps of the potential extent of (A) subtropical montane rain forest (STMRF) in the Canary Islands, and (B–F) warm temperate rain forest (WTRF) in five countries. In South Africa the WTRF is naturally restricted to patches by fire in the surrounding fynbos heathlands, and in Australia it is found in patches surrounded by sclerophyll forest. In all countries except South Africa the present-day cover is a small fraction of the potential cover. Scales differ among maps; latitudes and longitudes are denoted at one-degree intervals in all maps. Sources of information used to determine the extents: (A) Canary Islands, Santos (1990); (B) Japan, Satoo (1983); (C) South Africa, Mucina *et al.* (2006); (D) South-eastern Australia: within Victoria, Peel (1999); within New South Wales, a site of Melick & Ashton (1991), with a dashed boundary defining the zone in which other sites are likely to occur; (E) New Zealand, Webb (1978), Wardle (1991) and P.J. Bellingham, unpublished data; (F) Chile, Veblen *et al.* (1983), with the northern limit amended; the southern limit according to Kalin Arroyo *et al.* (1995); the upper altitudinal limit on the Cordilleras set at 900 m, and the extent on Chiloé Island following Armesto *et al.* (2011).

up a considerable soil seed bank (Jankowska-Błaszczuk & Grubb, 2006). Is the WTRF similar in this respect?

Our third objective is to determine whether or not mean seed mass increases significantly with mature tree height in each area of WTRF, as is found in global comparisons made without respect to vegetation type (see Moles *et al.*, 2005). This is a necessary background to any comparison of seed mass between gap-demanding and shade-tolerant species; past comparisons have not allowed for any differences in mature height between the two groups.

Our fourth objective is to find the extent of variation in seed size among both the species that need canopy gaps for establishment and those that do not. Early studies in TLRF emphasized the idea that gap-demanders have smaller

seeds on average than shade-tolerators (Swaine & Whitmore, 1988). However, for Japanese WTRF, Kohyama & Grubb (1994) documented a wide range in seed dry mass among shade-tolerators, and the existence of tiny-seeded species that benefit from being able to come to rest in minute ‘picosites’ on steep micro-slopes free of litter. For the same forest Grubb (1996) noted that among gap-demanders the range was narrower because of a lack of tiny-seeded species (<1 mg dry mass), and that the largest-seeded species had seeds a little larger than those of the largest-seeded shade-tolerator. Large seed size in gap-demanders was related to attraction of relatively large animals that disperse the seeds. Does WTRF in other areas contain notably small-seeded shade-tolerators and/or notably large-seeded gap-demanders?

II. PRELIMINARIES

(1) Lists of core species

For each of the six regions we used standard floras and published floristic accounts of forest remnants to produce a long list of woody species normally reaching a height of at least 5 m that might be in the core list. We then excluded (*i*) those not or doubtfully native; (*ii*) those which are scandent; (*iii*) those which are rare and localized in distribution; (*iv*) those typically found at specialized sites (lower rainfall, rocky, very wet, river-edge, coastal, high-altitude or forest-edges) and (*v*) those confined to one edge of the range of WTRF (e.g. the subtropical or high-altitude margin). We accepted as core species those with a wide geographical range but a strong tendency to occur only on lower slopes or only on ridges; likewise we accepted as core species those with a wide geographical range despite being absent from a considerable part of the total range of the WTRF in a region. The full details are set out in online Appendix S2, where the species that we have excluded from the core are listed. In our tables angiosperm species are assigned to families recognized by Stevens (2012), and conifers to families recognized by Farjon (2010). The sources of our nomenclature for species are given in online Appendix S2; where there has been a recent change in the accepted name, the earlier name is given in parentheses in the appropriate table.

(2) Penetration of light through WTRF canopies

It is not possible to make a critical comparison of the five regions of WTRF in respect of the proportion of daylight penetrating the canopy away from gaps because no single standardized technique for measuring light has been used in all of the regions. For Japan Kira (1975) and Yoda (1978) used matched selenium photocells in one type of WTRF (oak-dominated) and found that 0.5–1.0% of daylight reached the seedling layer, while Kusumoto (1957) obtained a value of 1–2% in another oak stand further north. At one New Zealand WTRF site (35°S) D.F.R.P. Burslem & P.J. Bellingham (unpublished data) found that seedlings in the deepest shade experienced 1.6% ‘canopy openness’ (measured using hemispherical photos analysed using GLA 2.0 software; see Frazer, Canham & Lertzman, 1999). At a second New Zealand WTRF site (38°S) (Lusk, Duncan & Bellingham, 2009) found that the commonest value for ‘canopy openness’, measured using Li-Cor ‘canopy analyzers’ under overcast conditions, was 1–2%. This may equate to 1–2% penetration of photosynthetically active radiation (PAR), but that needs to be checked. For Chilean WTRF the same method was used by Lusk (2002) and Lusk *et al.* (2008); they found that seedlings in the deepest shade experienced approximately 2% canopy openness. We have not traced any modern measurement of light penetration for WTRF in South Africa, but Phillips (1931, pp. 44–45 and 72) reported 1% penetration of diffuse light using Clements’s stopwatch photometer method. There appears to be no published work on light penetration in WTRF in Australia.

Aschan *et al.* (1994) reported 2% of PAR penetrating to the forest floor of STMRF on Tenerife (Canary Islands).

To summarize, it seems likely that in general the proportion of daylight penetrating to the most shaded sites in WTRF is 1–2%, i.e. slightly greater than in TLRF, but sometimes the proportion is the same as in TLRF (0.5–1%), which would be consistent with the lower but overlapping values for leaf area index reported (5–9 *versus* 7–9; see Coomes & Grubb, 2000). The absolute amounts of PAR penetrating will, of course, depend on degree of cloudiness, slope and aspect.

(3) Groups of species based on light demand and type of disturbance needed

For each region we have assigned species to three groups. Those in Group 1 need a canopy gap for establishment. Those in Group 2 either establish in deep shade but for survival and onward growth need a canopy gap within a relatively short period after establishment (a few months to a few years) or can tolerate only light shade at the time of establishment. Group 3 species can establish and persist in deep shade for long periods though most benefit from canopy gaps as they grow toward their full height.

Group 1 species are placed in sub-groups based on the kind of canopy gap that favours them: 1A, wind-induced tree-fall; 1B, landslides or new volcanic deposits; 1C, flood-deposits; 1D, opening by fire; and 1E, fire or flood or tree-fall. In some forests most canopy gaps arise from trees dying standing rather than being blown down, swept away or consumed by fire; among the different WTRF regions this phenomenon is seen most often in South Africa. The one tree species that uses the gaps so formed is placed in Group 1A. A more subtle effect occurs on very steep slopes where trees gradually bend downhill, becoming nearly horizontal, and let much more light reach ground level. The one tree known to use such gaps is placed in Group 1A.

The species invading the upper parts of landslides, new volcanic deposits and flood deposits do not face immediate competition from established seedlings and saplings or herbs (angiosperms or ferns), but must be able to grow on a substratum containing no organic matter or very little. Nitrogen is thus likely to be a primary limiting nutrient (Walker & del Moral, 2003). Pioneers on soil parent materials containing high concentrations of phosphorus are likely not to be limited by phosphate supply (Vitousek & Farrington, 1997), but on substrata poor in P or basic cations one or more of these elements may co-limit with nitrogen (Bishop *et al.*, 2010; Vitousek *et al.*, 2010). For a seedling on bared mature soil in a canopy gap the primary limiting nutrient is likely to depend on rooting density, changing from phosphate to nitrate as rooting density increases (see Grubb, 1986*b*). The species invading burnt-forest sites may face shortage of nitrogen from the start, while benefitting from an enriched supply of cations (and in some cases P) from the ash (Demeyer, Voundi Nkana & Verloo, 2001).

A potential difficulty arises in assessing dependence of species on disturbance events that have a long return time

(on the order of once per century) but have major effects on the forest. There is increasing evidence for TLRF in SE Asia that exceptional blow-downs and very severe droughts can have lasting effects as a result of gap-formation (Ashton, 2013), and it is possible that this will prove to be true for WTRF and STMRF as well.

A different problem arises where human intervention has been all-pervasive in the forest remnants found today. This is the case for most of the STMRF on the Canary Islands. The possibility arises that the gap-demanders in the STMRF today played no part in that forest before the impact of humans; an extreme view is that they existed only in the heath forest found at higher altitudes than the STMRF and on rock outcrops in the STMRF zone. The idea becomes plausible by observations made in other rain forest areas where it has been possible to see primary forest opened up after being hardly impacted by humans until the 20th century.

Grubb & Stevens (1985) reported what happened in a lower montane rain forest in an isolated valley in Papua New Guinea, little affected by humans until a saw mill was opened, and the forest was clear felled. Of the five most abundant tree species in the secondary forest up to 20 years old in 1970, only one was also found in tree-fall gaps in the primary lower montane forest, and it was very rare in that forest. Two came from upper montane rain forest, and two from naturally unforested river gravels. Many of the dominant and occasional species were seen at the edges of lower montane forest against semi-natural grassland on waterlogged soils. Clearly in cases like that of the STMRF in the Canary Islands observations on the stands least affected by humans are vitally important for the assignment of species to the core Group 1.

The definition of species as needing canopy gaps for establishment is not straightforward. For some species seen as adults only at edges and in tree-fall gaps within the forest, it is found by critical observation that they not infrequently become established under canopy shade, but die if a gap is not formed within a relatively short time. Examples in Chilean WTRF are *Embothrium coccineum* and *Lomatia hirsuta* (Figueroa & Lusk, 2001).

For plants of TLRF in Australia and SE Asia Grubb & Metcalfe (1996) and Jankowska-Błaszczuk & Grubb (2006) identified a small group of species unable to establish in the full shade of the understorey (diffuse site factor 0.4–2.0%) but able to establish in ‘micro-gaps’, i.e. where a limb has fallen rather than a whole crown or at a site a little distance from a crown-fall (diffuse site factor 2–4%, to be compared with >4% in single-tree-fall gaps). We have not been able to identify a corresponding group of species in WTRF. This means that there is a clear disjunction between species in Groups 1 and 2 in WTRF, but not in TLRF.

For species not demanding canopy gaps for establishment, classification into more and less shade-tolerant groups is made difficult by changes in relative shade tolerance that occur as plants become older and taller. The potential

importance of this issue has been emphasized for TLRF by Clark & Clark (1992), Hawthorne (1993), Grubb (1996) and Poorter *et al.* (2005), and for WTRF by Lusk *et al.* (2008, 2011). The issue was not considered by those who formulated tolerance indices for tree species in northern temperate deciduous forests, e.g. Baker (1945) and Ellenberg (1963). For WTRF some clear examples of the problem are known. At a site in Chile Figueroa & Lusk (2001) reported the mean percentage canopy openness under which the juveniles (up to 1 m tall) of 26 species were found; they showed that both *Laureliopsis philippiana* and *Aextoxicon punctatum* were among the most shade-tolerant. However, Veblen, Ashton & Schlegel (1979) found that at a later stage in the life cycle the *Laureliopsis* needed a canopy gap for onward growth, while the *Aextoxicon* did not. When we describe species as ‘strongly shade tolerant’, and assign them to Group 3B, we indicate either an ability to mature in deep shade (relevant to tall shrubs and small trees) or an ability to grow to full height without the formation of a canopy gap above (relevant to medium-height and tall trees).

Assignments of species to gap-response groups are based on the relevant literature indicated in each of the tables, on the advice of ecologists who have long experience of the forests in question (acknowledged in the headings to the tables) and on personal observations. T.S.K. has 26 years of experience of working in WTRF in Japan, P.J.B. 21 years in WTRF in New Zealand, and F.I.P. 6 years in WTRF in Chile. P.J.G. has worked briefly in all six study areas, P.J.B. in all areas bar SE Australia, and A.V. on Madeira in addition to the Canary Islands.

(4) Studies on soil seed banks

Many Group 1A species in TLRFs are known to have seed banks in the soil that persist for at least a few years (Dalling, Swaine & Garwood, 1994; Jankowska-Błaszczuk & Grubb, 2006; Dalling & Brown, 2009), and we sought to determine how far this is true of such species in WTRF. Beveridge (1967), who worked with Podocarpaceae in New Zealand, made the only study which attempted to separate species persisting for different lengths of time in the soil in a way that meets the criteria of Thompson, Bakker & Bekker (1997). The basis of our analysis of such evidence as is available is given in online Appendix S3.

(5) Sources of seed dry mass values

A commentary on all the sources from which we obtained values for seed mass is given in online Appendix S4, and the sources are listed in Tables 2–7.

We present new values for dry seed mass for species in Japan, New Zealand, Chile and the Canary Islands. With the exception of one data set (see online Appendix S4), we defined a seed as a single mature, fertilized ovule including the testa plus the fibrous inner part of the fruit wall when present. Any aril, sarcotesta or fleshy part of the fruit wall, and any wing, was removed.

Table 2. The core tree and tall shrub species of warm temperate rain forest (WTRF) in Japan arranged in groups according to their requirement for canopy gaps, together with sources of requirements for gaps and presence in soil seed bank, whether deciduous, and values given by various authors for mature height and seed dry mass (values in square brackets are for seeds removed from pyrenes); species with no maximum height recorded in the literature are known by one of the authors (T.S.K.) to grow to >5 m

	Sources of requirements for canopy gaps (key to numbers is at foot of table)	Sources of soil seed bank	Deciduous (D) or evergreen (E)	Max. height (m) <i>Flora of Japan</i> (Satake <i>et al.</i> , 1989)	Max. height (m) <i>Flora of Japan</i> (on web)	Max. height (m) Yakushima (Aiba & Kobayama, 1997)	Mean seed mass (mg)	Sources of seed mass values
1A. Establish in multiple- or single-treefall gaps								
<i>Aralia elata</i>	See 24 re landslides See 25 re lava flows	17	D	5	—	—	0.75, 1.0	41, 42
<i>Idesia polycarpa</i>	9, 10, 13, 16, 20, 34	—	D	15	15	—	1.8	38
<i>Carpinus lasiflora</i>	26, 30, 33, 36	17	D	15	—	—	3	41
<i>Mallotus japonicus</i> *†	11, 12, 16, 26	16, 17	D	15	15	—	8.2	42
<i>Acer capillipes</i> var. <i>morifolium</i>	9, 10, 13, 16, 18, 26, 34	—	D	15	15 (20)	—	9	42
<i>Carpinus tschonoskii</i>	1, 11	—	D	15	—	—	12	41
<i>Zanthoxylum ailanthoides</i>	4, 13, 33, 36	—	D	15	—	—	12	42
<i>Acer rufinerve</i>	11, 13, 16, 20, 26, 33, 36	17	D	15	—	—	12	42
<i>Euscaphis japonica</i>	16	16, 17	D	12	15	—	26	41
<i>Saxida controversa</i>	11, 13	—	D	6	6 (10)	—	30, 47	41, 42
<i>Clerodendrum trichotomum</i>	16, 26, 33	—	D	15	24	—	44	41
<i>Stewartia monadelpha</i>	10, 18, 20, 34	—	D	3	6	—	55	41
<i>Sapium japonicum</i>	1, 4, 11, 20, 30, 36	—	D	15	—	—	75	42
<i>Lindera umbellata</i>	Theaceae	—	D	6	—	—	88	41
<i>Diospyros japonica</i>	4, 12	16	D	—	—	—	110	41
<i>Syrax japonica</i> *†	4, 16	—	D	—	10 (15)	—	130	42
	11, 33	—	D	—	8 (10)	—	150	42
	1, 3, 4, 12, 13, 19, 21, 26, 34	—	D	8	—	—	—	—
<i>Aleurites cordata</i>	20	—	E	15	15	—	730	42
<i>Sapindus mukorossi</i>	26, 30, 33	—	D	25	25	—	890	41
<i>Rhus succedana</i>	11, 13, 17, 26	17	D	10	—	—	—	—
<i>Rhus sylvestris</i>	11	—	D	6	6 (10)	—	—	—
<i>Ilex micrococca</i>	16	16	D	10	10 (25)	—	—	—
<i>I. rotunda</i>	36	—	E	10	10 (20)	—	—	—
<i>Ehretia acuminata</i>	11	—	D	—	10 (20)	—	—	—
<i>Aphananthe aspera</i>	9, 10, 13, 15, 30	—	D	20	—	—	—	—
<i>Celtis sinensis</i>	10, 13, 15	—	D	20	—	—	—	—
<i>Lindera erythrocarpa</i>	20, 26	—	D	—	—	—	—	—
<i>Ficus erecta</i>	11, 12, 13, 15, 20, 36	17	D	5	—	—	—	—
<i>Schoepfia jasminodora</i>	21	—	D	10	—	—	—	—
<i>Prunus jamaicensis</i> *†	1, 3, 13, 16, 20, 21, 26, 33	—	D	25	—	—	—	—
<i>Tetradium glabrifolium</i>	11	—	D	15	10	—	—	—
<i>Acer nipponicum</i>	33	—	D	18	15	—	—	—
<i>Villebrunnea pedunculata</i>	6	—	E	—	—	—	—	—
1B. Pioneer on lower altitude landslides								
<i>Abies firma</i> †	See 24 re landslides See 25 re lava flows	—	D	15	40	—	0.6	41
	—	—						
	See 24 re landslides	—	D	15	40	—	0.6	41
	—	—						
	See 24 re landslides	—	D	15	40	—	0.6	41
	—	—						

Table 2. Continued

	Sources of requirements for canopy gaps (key to numbers is at foot of table)	Sources of soil seed bank	Deciduous (D) or evergreen (E)	Max. height (m) <i>Flora of Japan</i> (Satake <i>et al.</i> , 1989)	Max. height (m) <i>Flora of Japan</i> (on web)	Max. height (m) Yakushima (Aiba & Kohyama, 1997)	Mean seed mass (mg)	Sources of seed mass values
<i>Pinus thunbergii</i> †	—	—	E	40	35	—	14	41
<i>Lindera citriodora</i>	9	—	D	—	—	—	110	41
<i>Salix sieboldiana</i>	—	—	D	—	—	—	—	—
2. Can establish in shade but need early canopy gap for persistence and onward growth (at least some benefit from landslides where they invade with shade-tolerant spp. but outgrow them	For invasion of landslides see 24 For persistence on landslides see 27	—	—	—	—	—	—	—
<i>Photinia glabra</i>	14, 15, 20	—	E	5	—	—	2.9	41
<i>Daphniphyllum macropodum</i>	22, 33	—	E	—	15	—	42, 50	38, 41
<i>Diospyros morrisiana</i>	7	—	E	—	10	—	90, 120	41, 42
<i>Elaeocarpus sybuestris</i> var <i>ellipticus</i>	11, 14, 15	—	E	20	20	—	290	41
<i>Castanopsis cuspidata</i> †	1, 16, 21, 27, 31, 33, 35	—	E	20	—	—	370	39
<i>C. sieboldii</i>	20, 22, 28, 29	—	E	20	—	—	620	39
<i>Quercus glauca</i> †	21, 30, 33, 35	—	E	18	—	—	530, 750	39, 41
<i>Q. myrsinaefolia</i>	21, 30, 35	—	E	20	—	—	810, 1100	39, 41
<i>Q. gilva</i> ‡	21, 30, 31, 32, 33	—	E	30	—	—	1100	39
<i>Q. salicina</i> §	1, 4, 16, 20, 21, 22, 29, 31, 32, 33, 34, 35	—	E	20	—	—	1100	39
<i>Lithocarpus glabra</i>	18	—	E	15	—	—	1200	39
<i>Quercus sessilifolia</i>	16, 21, 32, 35	—	E	20	—	—	1400	39
<i>Q. acuta</i> §	1, 4, 20, 21, 22, 29, 30, 32, 33	—	E	20	—	—	1600	39
<i>Lithocarpus edulis</i> †	1, 20, 22, 33, 34, 36	—	E	15	—	—	1700	39
<i>Dendropanax trifidus</i>	1, 2, 3, 36	—	E	7	—	—	—	—
<i>Daphniphyllum ijesmanii</i>	7, 34	—	E	—	—	—	—	—
<i>Elaeocarpus japonicus</i>	7, 26, 34	—	E	7	7	—	—	—
<i>Persea thunbergii</i>	9, 10, 22, 23, 27, 29, 30, 33, 35	—	E	—	—	—	—	—
<i>Michelia compressa</i>	7, 30	—	E	15	—	—	—	—
<i>Myrica rubra</i>	1, 8, 11, 34	—	E	10	—	—	—	—
<i>Ardisia sieboldii</i>	7	—	E	—	5	—	—	—
<i>Helicia cochinchinensis</i>	7, 34	—	E	10	—	—	—	—
<i>Prunus spinulosa</i>	7	—	E	7	—	—	—	—
<i>P. zippeliana</i>	7	—	E	15	—	—	—	—
<i>Meliosma rigida</i>	7, 9, 34	—	E	7	7	—	—	—

Table 2. Continued

	Sources of requirements for canopy gaps (key to numbers is at foot of table)	Sources of soil seed bank	Deciduous (D) or evergreen (E)	Max. height (m) <i>Flora of Japan</i> (Satake <i>et al.</i> , 1989)	Max. height (m) <i>Flora of Japan</i> (on web)	Max. height (m) Yakushima (Aiba & Kohyama, 1997)	Mean seed mass (mg)	Sources of seed mass values
3A. To varying degrees more shade-tolerant than Group 2								
<i>Vaccinium bracteatum</i> †	—	—	E	5	5	—	0.53	41
<i>Ilex latifolia</i>	—	—	E	10	10 (20)	—	8.6	41
<i>I. chinensis</i>	—	—	E	10	10 (15)	—	9	37
<i>I. orenata</i>	4	—	E	16	6	—	12	41
<i>I. pedunculosa</i>	—	17	E	7	5 (10)	—	14	41
<i>Ternstroemia gymnanthera</i>	—	—	E	10	—	—	14	42
<i>Viburnum odoratissimum</i> var. <i>acabuki</i>	—	—	E	20	20	—	16	41
<i>Ilex integra</i>	—	—	E	10	10 (30)	—	17, 30	41, 42
<i>Osmanthus heterophyllus</i>	—	—	E	8	8	—	59	41
<i>Cephalotaxus harringtonia</i>	—	—	E	10	10	—	360	38
<i>Podocarpus macrophyllus</i>	—	—	E	20	—	—	390, 440	38, 41
<i>Viburnum japonicum</i>	—	—	E	6	6	—	—	—
<i>Ilex goshimensis</i>	—	—	E	10	10 (15)	—	—	—
<i>Cinnamomum tenuifolium</i>	30	—	E	—	—	—	—	—
<i>Litsea coreana</i>	—	—	E	—	—	—	—	—
<i>Neolitsea sericea</i>	4	17	E	—	—	—	—	—
<i>Syzygium buxifolium</i>	—	—	E	15	10 (15)	—	—	—
<i>Osmanthus insularis</i>	—	—	E	15	10 (20)	—	—	—
<i>Symplocos lancifolia</i>	—	—	E	—	—	—	—	—
<i>S. lucida</i>	—	17	E	—	—	—	—	—
<i>S. theophrastifolia</i>	—	17	E	—	—	—	—	—
3B. Strongly shade-tolerant ('Reverse-J populations' reported by authors quoted)								
<i>Rhododendron tashiroi</i>	1, 5, 28	28	E	2	4	10	0.074	40
<i>Eurya japonica</i> †	1, 4, 5	16, 17	E	—	—	11	0.32	40
<i>Cleyera japonica</i>	1, 5	17	E	—	—	15	3.2	40
<i>Symplocos prunifolia</i>	1, 5	16, 17	E	—	—	15	[4]	40
Gap-demanding in northern WTRF								
<i>Distylium racemosum</i>	1, 5, 23, 29, 33, 35	28	E	10	—	21	19	40
<i>Myrsine nerifolia</i>	1, 5	17	E	10	5 (10)	14	21	40
<i>Symplocos tanakae</i>	5	—	E	—	—	15	[26]	40
<i>Illicium religiosum</i>	1, 4, 5, 30	17	E	10	—	15	32	40

Table 2. Continued

	Sources of requirements for canopy gaps (key to numbers is at foot of table)	Sources of soil seed bank	Deciduous (D) or evergreen (E)	Max. height (m) <i>Flora of Japan</i> (Satake <i>et al.</i> , 1989)	Max. height (m) <i>Flora of Japan</i> (on web)	Max. height (m) Yakushima (Aiba & Kohyama, 1997)	Mean seed mass (mg)	Sources of seed mass values
<i>Symplocos glauca</i>	1, 5, 19, 35	17	E	—	—	14	[75]	40
<i>Neolisea aciculata</i>	1, 5	17	E	—	—	17	[110]	40
<i>Camellia sasanqua</i>	1, 5, 35	—	E	5	—	16	340, 510	40, 41
<i>Litsea acuminata</i>	1, 5, 30	—	E	—	—	19	[670]	40
<i>Nageia nagi</i>	5, 19	—	E	20	20	17	340, 880	37, 41
<i>Camellia japonica</i>	1, 5, 30	17	E	15	—	15	680, 970, 1100	37, 41, 42
<i>Persea japonica</i>	1, 30, 33	—	E	—	—	—	—	—

1, Aiba *et al.* (2001); 2, Enoki & Abe (2004); 3, Ishida *et al.* (2005); 4, Isogai & Okutomi (1991); 5, Kohyama (1986); 6, T.S. Kohyama (unpublished observations); 7, Kohyama & Aiba (1997); 8, Kohyama *et al.* (1984); 9, Maesako (1991); 10, Maesako (1999); 11, Miyawaki (1980b); 12, Miyawaki (1980a); 13, Miyawaki (1982); 14, Miyawaki (1983); 15, Miyawaki (1984); 16, Naka & Yoda (1984); 17, Nakagoshi (1984); 18, Nakagoshi & Suzuki (1977); 19, Nanami *et al.* (2011); 20, Ohsawa (1984); 21, Omura *et al.* (1978); 22, Saito (2002); 23, Sato *et al.* (1994); 24, Shimokawa (1984); 25, Tagawa (1964); 26, Tagawa (1978); 27, Tagawa, 1979; 28, Tagawa *et al.* (1984); 29, Takyu & Ohsawa (1997); 30, Takyu & Ohsawa (1997); 31, Tanouchi (1996); 32, Tanouchi *et al.* (1994); 33, Tanouchi & Yamamoto (1995); 34, Tezuka & Kusumoto (1960); 35, Yamada *et al.* (2012); 36, Yamamoto (1992); 37, Earle & Jones (1962); 38, Jones & Earle (1966); 39, Hiroki & Matsubara (1982); 40, Kohyama & Grubb (1994); 41, Royal Botanic Gardens Kew (2008); 42, P.J. Grubb & T.S. Kohyama (Unpublished results).

*Also invades landslides early.

†Also invades lava flows early.

‡Noted in Ref. 24.

§Noted in Ref. 33.

Sampling was haphazard and often limited to a single fruiting individual. No conscious bias was employed in the terms of the size of the seed or fruit collected, except that an effort was made to cover the full range of size in apparently healthy fruits/seeds. A minimum of 10 seeds was collected for each species, with larger numbers for species with very small seeds. For species on the Canary Islands a more rigorous pattern of sampling was adopted. No more than five seeds were collected from any one tree, and at least 80 seeds were collected per species. All seeds were cleaned and dried for 48 h at 80°C. Dry mass values were determined for single seeds or known numbers of seeds on an electronic balance to a precision of 0.1 mg. The values quoted have been rounded off to two significant figures.

The only critical information we have found concerning variation in seed mass in a single collection for WTRF species is that recorded by Glenny (1986) who used *c.* 100–300 seeds per species for 10 New Zealand trees and tall shrubs. The coefficient of variation ranged from 12% for *Sophora microphylla* to 43% for *Prumnopitys ferruginea*. The distribution was positively skewed for six species, negatively skewed for two species, and without skew for two species.

(6) Comparisons of seed size

We first determine whether there is any significant relationship between mean seed mass and mature height of a species within each of the six forest regions considered. Several of our sources for normal mature height use mostly or exclusively 5 m intervals, at least for species over 10 m tall. Only for New Zealand has there been a critical study of mature heights for all the core species of WTRF differentiating them at intervals of 1 m; for Japan and Chile we have similarly precise values for some species. For the plot of log mean seed dry mass against 'log normal maximum height', if more than one value is available for one or both variables, we use arithmetic mean values for seed mass, and the highest values reported for tree height except where those are given in parentheses (as in Tables 2–5 and 6) indicating that they are reached only exceptionally.

We compare species in Groups 1 and 3 in respect of seed size firstly without reference to phylogeny or mature plant height, and then analyze the seven cases in which intrafamilial intergeneric comparisons can be made between Groups 1 and 3, and the single case in which an intrageneric comparison is possible. When there is more than one recorded mean seed mass for a species we use the arithmetic mean, but when we have two or more species in a shade-tolerance group in the comparison we use the logarithmic mean.

Where there are sufficient Group 1 species in the forest to make the exercise worthwhile, we go on to compare species in Groups 1 and 3 at the same height in order to find whether any consistent pattern emerges. Finally we compare species in Groups 2 and 3.

Table 3. The core tree and tall shrub species of warm temperate rain forest (WTRF) in New Zealand arranged in groups according to their requirement for canopy gaps, together with sources of requirements for gaps and presence in the soil seed bank, mature heights (from McGlone *et al.*, 2010) and seed dry mass values recorded by various authors; the new values are from the New Zealand Plant Traits data base of Landcare Research; species marked with an asterisk are also found as pioneers on landslides [Smale *et al.*, 1997 (only records for 'younger' landslides accepted) and P.J. Bellingham, unpublished data]

	Papers reporting degree of requirement for gaps (key to numbers at foot of table)	Papers reporting appreciable occurrence in soil seed bank (key to numbers at foot of table)		Normal maximum height (m) (McGlone <i>et al.</i> , 2010b)	Mean seed dry mass (mg)				
		Transient	Persistent		(Glenny, 1986)	(Wardle, 1991)	(Burrows, 1995a-d, 1996a-e, 1999a-b)	(Moles <i>et al.</i> , 2000)	New values (unpublished data)
1A. Species needing tree-fall gaps or forest-edges for establishment									
<i>Akamia rosifolia</i>	3	61	—	12	—	—	—	—	0.03
<i>Kunzea ericoides*</i>	1, 5, 16, 33, 34, 51	62	57, 60	25	—	0.063	—	—	0.05
<i>Fuchsia excorticata</i>	10	59, 61	60	14	0.054	0.07	0.06	—	0.08
<i>Leptospermum scoparium*</i>	34	—	—	10	—	0.2	—	—	0.09
<i>Ascarina lucida</i>	18, 39, 40	—	—	8	—	0.72	—	—	1.1
<i>Entelea arborescens</i>	5, 21	—	58	6	—	2	—	—	2.2
<i>Aristotelia serrata</i>	11	59, 60, 61, 62	—	10	—	4.1	3.7	—	—
<i>Plagianthus regius</i>	15	60	—	17	3.8	4.2	4.5	—	—
<i>Coprosma robusta</i>	11	59	60	6	4.6	14	6	7.9	—
<i>Dodonaea viscosa*</i>	13	—	—	8	—	—	9.5	—	—
1B. Species needing a fresh volcanic deposit for establishment									
<i>Metrosideros robusta</i> (on young lava flows)	36	—	—	30	—	0.06	—	—	0.05
<i>Coriaria arborea</i> (on young tephra and scoria)	23	59, 61	—	8	—	0.4	0.58	—	—
2. Species able to establish in shade but need either light shade or an early canopy gap for persistence and onward growth									
<i>Quintinia serrata</i>	44	—	—	12	—	—	—	—	0.03
<i>Brachyglottis repanda</i>	2, 34	59	58	7	—	—	—	—	0.05
<i>Olearia rani</i>	48	—	—	8	—	—	0.12	—	0.07
<i>Metrosideros umbellata</i>	53	—	—	20	—	—	—	—	0.12
<i>Dracophyllum latifolium</i>	34	—	—	10	—	—	—	—	0.15
<i>Olearia fuifurcata</i>	2, 48	—	—	7	—	—	—	—	0.44

Table 3. Continued

	Papers reporting degree of requirement for gaps (key to numbers at foot of table)	Papers reporting appreciable occurrence in soil seed bank (key to numbers at foot of table)		Normal maximum height (m) (McGlone <i>et al.</i> , 2010b)	Mean seed dry mass (mg)			New values (unpublished data)	
		Transient	Persistent		(Glenny, 1986)	(Wardle, 1991)	(Burrows, 1995a-d, 1996a-e, <i>et al.</i> , 1999a-b)		(Moles <i>et al.</i> , 2000)
<i>Carpodetus serratus</i>	15, 26, 30	—	—	10	—	0.4	0.56	0.48	—
<i>Libocedrus plumosa</i>	3	—	—	25	—	1.6	—	—	2.5
<i>Manoao colensoi</i>	46	—	—	15	—	1.8	—	—	2.7
<i>Pseudopanax crassifolius</i>	15, 24	—	—	15	—	3.2	4	—	—
<i>Agathis australis</i>	6, 7, 25, 42, 44	—	—	40	—	9.5	—	—	2.6
<i>Leucopogon fasciculatus</i>	33, 48	—	—	6	—	—	—	—	7.3
<i>Pseudopanax arborens</i>	15	59	—	8	—	9	8.4	6.3	—
<i>Halocarpus tikia</i>	3	—	—	25	—	12	—	—	5.1
<i>Nothofagus truncata</i>	25, 48	—	—	30	—	7.7	—	—	12
<i>Pittosporum tenuifolium</i>	15, 23	—	—	10	—	11	14	13	—
<i>Melicope ternata</i>	21	—	58	8	—	—	—	—	14
<i>Phyllocladus trichomanoides</i>	6, 9, 25, 34, 45	—	—	25	—	16	—	—	—
<i>Podocarpus totara</i>	37	—	—	35	—	—	—	—	16
<i>Pennantia corymbosa</i>	13	—	—	12	—	14	20	—	—
<i>Coprosma lucida</i>	15	—	—	6	—	—	24	—	21
<i>Dacrycarpus dacrydioides</i>	22, 47	—	—	30	—	10	—	30	—
<i>Kinghtia excelsa</i>	9, 33, 50	—	—	50	—	19	—	30	22
<i>Grisehlmia littoralis</i>	10, 23	60	—	15	—	26	31	—	—
<i>Sophora microphylla</i>	2	60	—	25	—	58	—	—	67
<i>Prumnophyts taxifolia</i>	43	—	56	30	—	110	—	100	—
<i>Toronia toru</i>	23, 35	—	—	12	—	—	—	—	150
<i>Vitex lucens</i>	1, 2, 27, 49	—	—	20	—	—	—	680	520
3A. Species to varying degrees more shade-tolerant									
<i>Weinmannia siticcola</i>	44	—	—	20	—	—	—	—	0.1
<i>Schefflera digitata</i>	11	61	—	8	—	0.6	0.52	—	—
<i>Melictytus ramiflorus</i>	5, 10, 38, 47, 49, 51	59, 62	58, 60	10	—	0.76	1.5	0.8	—
<i>Macropiper excelsum</i>	10, 49	59	58	7	—	—	2.4	1.9	1.6
<i>Phyllocladus toatoa</i>	3	—	—	20	—	—	—	—	2.1
<i>Raukawa edgerleyi</i>	3	—	—	14	—	—	—	—	2.5
<i>Melictytus micranthus</i>	3	—	—	5	—	4.2	—	—	2.8
<i>Melictytus macrophyllus</i>	3	61	—	6	—	—	—	—	4.4
<i>Alseuosmia macrophylla</i>	20	—	—	5	—	—	4.1	—	5.1
<i>Dacrydium cupressinum</i>	22, 26, 33, 38	—	—	40	—	4.8	—	4.8	—
<i>Ixerba brexioides</i>	38, 44	—	—	17	—	—	—	—	5.7
<i>Melicope simplex</i>	14	—	—	8	—	—	5.9	—	5.9
<i>Hobertia populnea</i>	27	—	—	11	—	6.6	—	—	5.5

Table 3. Continued

	Papers reporting degree of requirement for gaps (key to numbers at foot of table)	Papers reporting appreciable occurrence in soil seed bank (key to numbers at foot of table)		Normal maximum height (m) (McGlone <i>et al.</i> , 2010b)	Mean seed dry mass (mg)			
		Transient	Persistent		(Glenny, 1986)	(Wardle, 1991)	(Burrows, 1995 <i>a-d</i> , 1996 <i>a-e</i> , 1999 <i>a-b</i>)	(Moles <i>et al.</i> , 2000)
<i>Nestegis lanceolata</i>	48	—	—	15	—	—	—	7.2
<i>Lophomyrtus bullata</i>	20	—	—	8	—	—	—	6.8
<i>Laurelia novae-zelandiae</i>	47	—	—	36	—	12	—	9.8
<i>Podocarpus cunninghamii</i> (formerly <i>P. hallii</i>)	4	—	—	24	—	—	—	12
<i>Coprosma arborea</i>	48	—	58	10	—	—	—	13
<i>Myrsine australis</i>	1, 2, 17	—	—	7	—	—	14	17
<i>Streblus heterophyllus</i>	13	—	—	12	—	—	27	11
<i>Nestegis montana</i>	3	—	—	15	—	—	—	20
<i>Coprosma grandifolia</i>	18, 33	—	—	6	—	—	17	27
<i>Myrsine salicina</i>	34	—	—	10	—	29	—	37
<i>Syzygium maire</i>	3	—	—	16	—	—	—	130
<i>Lilsea calicans</i>	49, 50	—	—	18	—	—	—	140
<i>Alectryon excelsus</i>	16, 49	60	—	14	—	—	230	180
<i>Elaeocarpus hookerianus</i>	31	—	—	13	—	—	—	220
<i>Prumnopitys ferruginea</i>	22, 38, 44	—	56	30	320	200, 480	—	480
<i>Elaeocarpus dentatus</i>	9, 38	—	—	21	—	360	—	660
3B. Most shade-tolerant								
<i>Pseudowintera axillaris</i>	33	—	—	8	—	—	—	3.8
<i>Pseudowintera colorata</i>	13	—	—	10	3.8	3.7	5.5	4.1
<i>Dysoxylum spectabile</i>	8, 19, 28, 29, 33	—	—	16	—	—	220	110
<i>Hedycarya arborea</i>	13	—	—	15	—	170	190	140
<i>Rhopalosiphis sapida</i>	13, 32	61, 62	—	10	—	230, 260	170	240
<i>Beilschmiedia tawa</i>	19, 22, 38, 50, 55	—	—	25	1400	1100	960	900
<i>B. tarairi</i>	2, 27, 41	—	—	22	—	—	—	1800
<i>Corynocarpus laevigatus</i>	1, 2, 16, 27	—	—	16	1900	2700	2400	—

1. Atkinson (2004); 2. Bellingham (1984); 3. P.J. Bellingham & B.R. Burns, unpublished data; 4. Bellingham & Richardson (2006); 5. Bellingham *et al.* (2010); 6. Bielecki (1959*a*); 7. Bielecki (1959*b*); 8. Buddenhagen & Ogden (2003); 9. Burns & Smale (1990); 10. Burrows (1995*c*); 11. Burrows (1995*d*); 12. Burrows (1995*e*); 13. Burrows (1995*f*); 14. Burrows (1996*a*); 15. Burrows (1996*b*); 16. Burrows (1996*c*); 17. Burrows (1996*d*); 18. Burrows (1996*e*); 19. Burrows (1996*f*); 20. Burrows (1999*a*); 21. Cameron *et al.* (1987); 22. Carswell *et al.* (2007); 23. Clarkson & Clarkson (1995); 24. Clearwater & Gould (1995); 25. Collins & Burns (2001); 26. Coomes *et al.* (2009); 27. Court (1978); 28. Court & Mitchell (1988); 29. Court & Mitchell (1989); 30. Day (1998); 31. Day *et al.* (1997); 32. Enright (1985); 33. Enright *et al.* (1993); 34. Esler & Astridge (1974); 35. Hamilton & Atkinson (1961); 36. Knightbridge & Ogden (1998); 37. Lusk & Ogden (1992); 38. Lusk *et al.* (2009); 39. Martin & Ogden (2002); 40. Martin & Ogden (2005); 41. Myers (1984); 42. Ogden (1983); 43. Ogden & Stewart (1995); 44. Ogden *et al.* (1987); 45. Pook (1979); 46. Rogers (1999); 47. Smale (1984); 48. Smale & Gardner (1999); 49. Smale & Kimberley (1983); 50. Smale & Kimberley (1983); 51. Smale *et al.* (1995); 52. Walker *et al.* (2003); 53. Wardle (1971); 54. Wardle (1991); 55. West (1995); 56. Beveridge (1967); 57. Enright & Cameron (1988); 58. Grant-Hoffman (2009); 59. Moles & Drake (1999); 60. Partridge (1989; forest sites only); 61. Sem & Enright (1995); 62. Sem & Enright (1996).

Table 4. The core tree and tall shrub species of warm temperate rain forest (WTRF) in Chile arranged in groups according to their requirement for canopy gaps, together with values given by various authors for normal maximum height and seed dry mass; requirements for canopy gaps based principally on Lusk (2002), Saldaña & Lusk (2003), Lusk & Kelly (2003), Lusk *et al.* (2008, 2011), but also on Weinberger (1974), Veblen *et al.* (1979, 1983), Armesto & Figueroa (1987), Armesto & Fuentes (1988), Donoso (1989, 2006), Figueroa & Lusk (2001), Lusk & Del Pozo (2002), Christie & Armesto (2003), Gutiérrez *et al.* (2008) and F.I. Piper, personal observations; species marked with an asterisk are also found as pioneers on landslides (Veblen & Ashton, 1978)

	Normal maximum height (m)			Mean seed dry mass (mg)				
	(Hoffmann, 2005)	(Parada <i>et al.</i> , 2003)	(Donoso, 2006)	(Donoso & Cabello, 1978)	(Donoso, 1989)	(Lusk & Kelly, 2003)	(Donoso, 2006)	(F.I. Piper, unpublished data)
1B. Needs areas of bared ground to persist in the landscape; most often colonizes landslides but is thought to have benefitted from human-induced clearance on a large scale	40	40	40	7	—	—	6.4–10	6.6
<i>Nothofagus obliqua</i>								
2. Can establish in shade but need light shade or a canopy gap early in life for persistence and onward growth								
<i>Nothofagus domboeyi</i>	40	49	—	2.3	1.9	—	—	—
<i>Lomatia hirsuta</i>	15	—	15	7.1	5.3	—	4.1	4.8
<i>Aristotelia chilensis</i>	5	8.4	10	9.6	—	—	7.7–10	—
<i>Embothrium coccineum</i>	15	—	—	11	13	—	10–14	—
<i>Sophora cassioides</i>	10	—	10	65	—	—	59–71	87
3A. To varying degrees shade-tolerant for onward growth								
<i>Caldecluvia paniculata</i> *	20	18.7	20	—	—	—	0.11	—
<i>Weinmannia trichosperma</i> *	40	34	—	0.11	0.12	—	—	—
<i>Eucyphia cordifolia</i> *	40	38	—	2	1.4	—	1.1	—
<i>Dasylphyllum diacanthioides</i>	15	35.8	10–30 ^a	—	—	—	—	—
<i>Raukautia laetivirens</i>	6	—	—	3.5	—	—	—	—
<i>Laurelia sempervirens</i>	40	—	40	5	—	—	3.5	4.1
<i>Drinys wintieri</i>	30	—	—	4.2	3.7	—	2.7–5.2	6.2
<i>Lomatia ferruginea</i>	10	9.9	15	6	5.9	—	4.2	7.7
<i>L. dentata</i> *	10	—	10	7.4	—	—	—	8.4
<i>Saxegothaea conspicua</i>	15	—	—	—	9.1	10	—	—
<i>Rhaphitamnus spinosus</i>	6	11.2	6	13	—	—	—	—
<i>Luma apiculata</i>	15	—	25	—	19	—	8.5	14
<i>Anomyrtus meli</i>	20	—	20	40	40	—	30–31	—
<i>Peumus boldus</i>	ND ^b	—	20	70	—	—	—	65
<i>Persia lingue</i>	ND ^b	—	30	870	950	—	—	530, 750

Table 4. Continued

	Normal maximum height (m)		Mean seed dry mass (mg)				
	(Hoffmann, 2005)	(Parada <i>et al.</i> , 2003)	(Donoso, 2006)	(Donoso, 1989)	(Lusk & Kelly, 2003)	(Donoso, 2006)	(F.I. Piper, unpublished data)
<i>Cryptocarya alba</i>	20	—	20	—	—	—	520
<i>Guevinia avellana</i>	20	23.3	20	2400	—	—	—
3B. Strongly shade-tolerant for onward growth							
<i>Laurelopsis philippiana</i>	30	34	>30	1.8	—	1.6	—
<i>Anomyrtus luma</i>	20	21.9	20–25 ^a	34	—	26–31	—
<i>Myrcogenia planipes</i>	8	16.8	8	—	46	34	—
<i>Aextoxicon punctatum</i>	25	33.4	25	340	—	200–500	—
<i>Podocarpus nubigena</i>	30	—	—	270	450	—	—

^aDifferent normal maximum heights in different areas.

^bNot determined.

III. DISTURBANCE REGIMES AND SPECIES DEPENDENT ON THEM

(1) Japan

Typhoons, which occur every year, create canopy gaps by tree-fall at a relatively high rate (Saito, 2002), but several authors have noted that most gaps are relatively small and inadequate for the most light-demanding species (Naka, 1982; Naka & Yoneda, 1984; Miura *et al.*, 2001). Japan lies in a seismically active zone, and landslides are also relatively common, though not as frequent as tree-fall gaps (Tanouchi & Yamamoto, 1995; Masaki *et al.*, 1999). Fresh lava flows from active volcanoes are only of local importance, and the plants favoured by them overlap with those favoured by landslips (see Tagawa, 1964).

Thirty-two Group 1A species, i.e. species establishing only in tree-fall gaps and at forest edges against streams, rivers and/or bluffs), or mostly there and only occasionally on landslides or lava flows, have been recorded in 35 ecological studies spread from Yakushima at *c.* 30°N to near Mt Fuji at *c.* 35°N (Table 2), and these make up 33% of the total list of core species. Almost all are deciduous (Table 2). In hilly and mountainous country the deciduous species are most abundant along the gullies where there is more frequent disturbance; the forest along narrow ridges lets in more light than that on slopes and favours more light-demanding species but is not subject to especially frequent disturbance.

One evergreen species (*Symplocos prunifolia*) is gap-demanding for establishment in the northern part of the WTRF, but shade-tolerant in the southern, on Yakushima (Kohyama, 1986); we count it in the not gap-demanding category in the summary in Table 8.

We recognize only four Group 1B species, those that are earliest to invade landslides and lava flows (Table 2). One is an evergreen conifer and three are deciduous dicots. *Pinus thunbergii* is probably the species that benefits most by landslides. *Alnus firma* and *Salix sieboldiana* also establish on periodically flooded soils at scoured sites on floodplains. These days *Lindera citriodora* is most often seen as an invader along roadsides. The key feature of the micro-sites on which these four species become established is the inorganic nature of the substratum – the absence or near-absence of organic matter. By contrast, Group 1A species generally invade soil containing some organic matter, even though they are commonest on tip-ups (see Grubb, 1992).

A few Group 1A species are relatively early invaders of landslides and lava flows in addition to establishing in tree-fall gaps (*Mallotus japonicus*, *Prunus jamasakura*, *Styrax japonicus*), but they do not invade as abundantly as *Pinus thunbergii* and *Alnus firma* (Shimokawa, 1984).

Of the 25 Group 2 species, i.e. those routinely establishing in canopy shade but with a limited ability to persist and continue growing unless in light shade, 10 are oaks. We review in online Appendix S5 the evidence for a gradient in light-demand among them.

One laurel species is assigned to Group 2: *Persea thunbergii* which is very common. It was shown by Sato, Tanouchi

Table 5. The core tree and tall shrub species of warm temperate rain forest (WTRF) in South Africa arranged in groups according to their requirements for canopy gaps, together with normal maximum heights (values in parentheses are reached only exceptionally), mean seed dry mass values (from Geldenhuys, 1996, except original values for *Cunonia capensis*), and mean largest dimensions of seeds (from Phillips, 1926a, b); requirements for canopy gaps based on Geldenhuys (1994), Midgley *et al.* (1990, 1995, 1997), Seydack (1995) and J. J. Midgley (personal communication, January 2003)

		Normal maximum height (m)	Mean seed air-dry mass (mg)	Largest dimension of seed (mm)					
				<1	1–2	2–5	6–10	11–15	16–20
1A. Needs at least a single-treefall gap for establishment									
<i>Zanthoxylum davyi</i>	Rutaceae	30	15	—	—	+	—	—	—
1D. Needs fire for establishment									
<i>Virgilia divaricata</i>	Fabaceae	10	60	—	—	—	—	+	—
2. Can establish in shade but need an early canopy gap for persistence and onward growth									
<i>Cunonia capensis</i>	Cunoniaceae	30	0.28	+	—	—	—	—	—
<i>Nuxia floribunda</i>	Stilbaceae	10 (15)	ND	+	—	—	—	—	—
<i>Platylophus trifoliatus</i>	Cunoniaceae	30	ND	—	+	—	—	—	—
<i>Psyrax obovata</i>	Rubiaceae	17	ND	—	—	+	—	—	—
<i>Pterocelastrus tricuspidatus</i>	Celastraceae	10	13	—	—	+	—	—	—
<i>Rothmannia capensis</i>	Rubiaceae	14 (20)	50	—	—	+	—	—	—
<i>Olinia ventosa</i>	Penaeaceae	20	150	—	—	—	+	—	—
<i>Ekebergia capensis</i>	Meliaceae	20 (30)	220	—	—	—	+	—	—
3A. To varying degrees shade-tolerant									
<i>Ilex mitis</i>	Aquifoliaceae	30	2.7	—	—	+	—	—	—
<i>Burchellia bubalina</i>	Rubiaceae	5 (10)	2.8	—	—	+	—	—	—
<i>Gonioma kamassi</i>	Apocynaceae	6	23	—	—	+	—	—	—
<i>Apodytes dimidiata</i>	Icacinaceae	20	51	—	—	—	+	—	—
<i>Rapanea melanophloeos</i>	Primulaceae	20	63	—	—	—	+	—	—
<i>Curtisia dentata</i>	Curtisiaceae	20	70	—	—	—	+	—	—
<i>Maytenus peduncularis</i>	Celastraceae	8	72	—	—	+	—	—	—
<i>Ochna arborea</i>	Ochnaceae	12	370	—	—	—	+	—	—
<i>Faurea macnaughtonii</i>	Proteaceae	20	ND	—	—	—	+	—	—
3B. Most shade-tolerant									
<i>Podocarpus latifolius</i>	Podocarpaceae	30	300	—	—	—	+	—	—
<i>Ocotea bullata</i>	Lauraceae	30	450	—	—	—	—	—	+
<i>Olea capensis</i> ssp. <i>macrocarpa</i>	Oleaceae	40	510	—	—	—	—	—	+
<i>Afrocarpus falcatus</i>	Podocarpaceae	60	710	—	—	—	—	—	+

ND = no data.

& Takeshita (1994) that seedlings of this species become established in large numbers on the forest floor, but rather few grow into saplings and they need a gap above them for onward growth. Earlier Tagawa (1979) had shown that the seedlings of *Persea thunbergii* have a higher mortality rate than those of *Castanopsis cuspidata*, especially in their first year; the key difference seemed not to concern shade but to be their greater sensitivity to late-summer drought.

Eleven species are assigned to Group 2 largely on the basis of their being more abundant in secondary forest than in primary forest in the same area (Kohyama & Aiba, 1997; Aiba, Hill & Angetsuma, 2001), and three on the basis of other studies of forest dynamics listed in Table 2.

The only long-term study of changes in composition of WTRF after severe disturbance is that of Yamada *et al.*

(2012). This emphasizes the rise of the Fagaceae after clear-felling, their subsequent decline, and their failure to increase markedly as a result of typhoon damage. The study reveals little about Group 1 species or non-Fagaceae Group 2 species as they are too sparse. More details are provided in online Appendix S5.

Many of the 36 Group 3 species, i.e. those variously more shade-tolerant, have not been studied critically in terms of their relative light demands. In Table 2 we have separated those species for which 'reverse J' distributions of plant size have been documented, mostly by Kohyama (1986), but in one case by Tanouchi & Yamamoto (1995).

The strongly shade-tolerant, tiny-seeded species *Eurya japonica* and *Rhododendron tashiroi* are effective pioneers in full daylight on rocky roadside cuttings where there is very

Table 6. The core tree and tall shrub species of warm temperate rain forest (WTRF) in south-eastern Australia arranged in groups according to their requirements for canopy gaps of different kinds (based on Melick & Ashton, 1991, and D.G. Cameron & R. Kooyman, personal communication), together with normal maximum heights (from Costermans, 2000), and mean seed dry mass values from various sources

		Normal mature height (m) (from Costermans, 2000)	Mean seed dry mass (mg)	Source of seed mass (key at foot of table)
1C. Establish in gaps made by floods				
<i>Tristaniopsis laurina</i>	Myrtaceae	20	10	1
1D. Establish in gaps made by fire				
<i>Olearia argophylla</i>	Asteraceae	8	0.17	2
<i>Olearia livata</i>	Asteraceae	5	0.32	3
<i>Pomaderris aspera</i>	Rhamnaceae	8	0.56	3
<i>Prostanthera lasianthos</i>	Lamiaceae	8	1.3	3
<i>Bedfordia arborescens</i>	Asteraceae	7	2.3	2
<i>Eucalyptus botryoides</i> ^a	Myrtaceae	40	1.9, 2.6	3, 4
<i>E. elata</i>	Myrtaceae	40	4.4, 4.7	4, 3
<i>E. cypellocarpa</i>	Myrtaceae	60	7.1	4
<i>E. obliqua</i>	Myrtaceae	70	7.9, 11.4	3, 4
<i>E. globulus</i> ^b	Myrtaceae	53	9.4, 12.8	3, 4
<i>Acacia melanoxydon</i>	Fabaceae	30	11, 13	1, 3
1E. Establish in gaps made by flood or fire, but also establish in endogenous gaps in forest				
<i>Acacia mearnsii</i>	Fabaceae	15	13	3
<i>Notelaea venosa</i>	Oleaceae	7	140	2
<i>Elaeocarpus reticulatus</i>	Elaeocarpaceae	10	210	1
3. To varying degrees more shade-tolerant				
<i>Hedycarya angustifolia</i>	Monimiaceae	6	5.4	2
<i>Acronychia oblongifolia</i>	Rutaceae	10	5.9	1
<i>Pittosporum undulatum</i>	Pittosporaceae	14	11	1
<i>Eupomatia laurina</i>	Eupomatiaceae	8	22	1
<i>Rapanea howittiana</i>	Primulaceae	10	43	2
<i>Acmena smithii</i>	Myrtaceae	30	150	1

1, Floyd (2008); 2, R. Kooyman (personal communication) based on three dimensions following Moles *et al.* (2005); 3, Royal Botanic Gardens Kew (2008); 4, Turnbull & Doran (1987).

^aRecorded growing to 50 m by Melick & Ashton (1991).

^bArithmetic mean values for ssp. *globulus* and *pseudoglobulus* which are approximately equally frequent.

little soil; they cannot compete with the herbaceous and shrubby species that dominate stretches of roadside where the soils are deep. On Yakushima one of us (T.S.K.) made two comparisons of the densities of saplings (>50 cm tall; <2 cm dbh): (i) between tree-fall gaps and closed stands in forest, and (ii) between a rocky roadside and closed stands (Fig. 2). In the first case there was no correlation between density quotient and seed mass for 14 species (Fig. 2A), but in the second case tiny-seeded species were overwhelmingly important, four larger-seeded species were absent, and five had only one to two saplings on 90 m² of roadside (Fig. 2B). As expected, tiny-seededness facilitates invasion. The failure of the faster-growing competitors on the most infertile soil, and consequent invasion by *Eurya japonica* and *Rhododendron tashiroi*, enabled us to see that strong shade-tolerance does not necessarily imply shade-requirement; before the road was built this important point would not have been apparent.

The extent to which species have been recorded in the seed bank is summarized in Table 2, with additional detail given in online Appendix S3. Nine of the 32 Group 1A species have

been recorded, and it is thought that some are 'short-term persistent', lasting at least 2–4 years in the soil. No Group 1B species or Group 2 species has been reported in the soil seed bank in more than trace quantities, but 14 of the 36 Group 3 species. One of these (*Symplocos prunifolia*) behaves as a gap-demonstrator in the northern part of the WTRF, where the seed-bank study was made. Another (*Eurya japonica*) was described by Naka & Yoda (1984) as 'intermediate between pioneer and late successional species'. Manabe & Yamamoto (1997) showed that it recruits strongly in canopy gaps, but also establishes commonly in deep shade. We suspect that most of the other Group 3 species are present in the seed bank only transiently, except for *Rhododendron tashiroi* which has a recruitment pattern like that of *Eurya japonica* (see Tagawa *et al.*, 1984).

(2) New Zealand

Cyclones that originate in the tropical southwest Pacific Ocean affect the warm temperate regions of New Zealand more frequently than the rest of the country (Shaw, 1983).

Table 7. The core tree and tall shrub species of subtropical montane rain forest (STMRF) in the Canary Islands arranged in groups according to their requirements for canopy gaps, together with normal maximum heights (from Bramwell & Bramwell, 1974, except that for *Erica scoparia* ssp. *platycodon* from A.B. Fernández-López, personal communication), and mean seed dry mass values from various sources; requirements for gaps based on Arévalo & Fernández-Palacios (1998, 2007), Arévalo *et al.* (1999), Fernández-Palacios & Arévalo (1998), Fernández-Palacios *et al.* (2004), and A.B. Fernández-López (personal communication)

		Normal maximum height (m)	Mean seed dry mass (mg)	Source of seed dry mass (key at foot of table)
1A. Need canopy gaps for establishment (greatly increased as a result of human impact)				
<i>Erica arborea</i>	Ericaceae	15	0.15	1
<i>E. scoparia</i> ssp. <i>platycodon</i>	Ericaceae	6 (11)	0.03	2
<i>Morella faya</i> (formerly <i>Myrica faya</i>)	Myricaceae	10	27	3
2. Need light shade throughout or a canopy gap soon after establishment				
<i>Ilex canariensis</i>	Aquifoliaceae	10	21, 25	4, 3
3A. Shade-tolerant to varying degrees				
<i>Rhamnus glandulosa</i>	Rhamnaceae	10	26	3
<i>Viburnum rigidum</i> (formerly <i>V. tinus</i>)	Adoxaceae	5	45	3
<i>Prunus lusitanica</i> ssp. <i>hixa</i>	Rosaceae	10	90	3
<i>Picconia excelsa</i>	Oleaceae	10	310	3
<i>Laurus azorica</i>	Lauraceae	20	—	—
(Tenerife)	—	—	560	3
(La Gomera)	—	—	1000	3
<i>Persea indica</i>	Lauraceae	20	980	3
3B. Most shade-tolerant				
<i>Ilex perado</i> ssp. <i>platyphylla</i> (formerly <i>I. platyphylla</i>)	Aquifoliaceae	15	33	3
<i>Heberdenia excelsa</i> (formerly <i>H. bahamensis</i>)	Primulaceae	10	130	3
<i>Ocotea foetens</i>	Lauraceae	40	800	3
<i>Apollonias barbujana</i> ssp. <i>barbujana</i>	Lauraceae	25	1000	3

Sources of seed mass values: 1, Royal Botanic Gardens Kew website (2008); 2, Fagúndez & Izco (2003); 3, A. Valido (unpublished data); 4, P.J. Bellingham & P.J. Grubb (unpublished data).

Severe cyclones reach New Zealand about every 10 years (Martin & Ogden, 2006), and can cause tree-fall gaps to occur in old-growth forests, sometimes over extensive areas (Conway, 1959; Ogden & Stewart, 1995). The trajectory of extra-tropical cyclones is affected by the phase of the El Niño Southern Oscillation (ENSO). Those formed in La Niña years are more likely to track over or close to New Zealand but the strongest cyclones tend to affect New Zealand when the ENSO cycle is between El Niño and La Niña (Sinclair, 2002). Extra-tropical cyclones and other major storms cause local wind and high-intensity rainfall events that result in floods, landslides and tree-falls. Although most of New Zealand is seismically active, the warm temperate zone is generally the least affected by earthquakes (Anderson & Webb, 1994). However, some areas are directly affected by small-scale volcanism (e.g. on and near the Auckland Isthmus) on which primary successions occur (Clarkson, 1990; Smale & Gardner, 1999). Secondary successions after human clearance are widespread throughout much of the

region (Wardle, 1991). In New Zealand there has been a very short history of human occupation (only since *c.* 1280 AD; Wilmshurst *et al.*, 2008). Natural lightning-induced fires were very rare throughout the Holocene and virtually non-existent in the WTRF (Ogden, Basher & McGlone, 1998). Fires caused by volcanic eruptions (Wilmshurst & McGlone, 1996) were also very infrequent and local. Human-induced fire kills almost all the rain forest trees.

There are 10 Group 1A species, i.e. species that establish only in tree-fall gaps and at forest margins, or mostly there and occasionally on landslides (Table 3). Three of these species are fully deciduous (*Aristotelia serrata*, *Fuchsia excorticata*, and *Plagianthus regius*), a characteristic more typical in New Zealand of tree species that grow at forest margins and on nutrient-rich soils than of species subject to greater winter cold (McGlone *et al.*, 2004).

Although fire was a negligible form of disturbance in the WTRF before human intervention, two Group 1A species (*Kunzea ericoides* and *Leptospermum scoparium*, both Myrtaceae)

Table 8. The numbers and percentages of core species of trees and tall shrubs in various canopy-gap response categories in warm temperate rain forest (WTRF) in five regions and in subtropical montane rain forest (STMRF) in one

	Japan	New Zealand	Chile	South Africa	Australia	Canary Islands
1. Establish only in canopy gaps						
1A. Need treefall gaps or trees leaning over or trees dying standing	32	10	—	1	—	3
1B. Need landslides or new volcanic deposits	4	2	1	—	—	—
1C. Needs flood	—	—	—	—	1	—
1D. Need fire	—	—	—	1	11	—
1E. Need fire or flood or treefall canopy gaps	—	—	—	—	3	—
2. Need canopy gap relatively soon after establishment (or light shade from the start)	25	28	5	8	—	1
3. To varying degrees more shade-tolerant	36	37	22	13	6	10
Total	97	77	28	23	21	14
Group 1 species as a percentage of Groups 1, 2 and 3	37	16	3.6	9	71	21
Group 2 species as a percentage of Groups 2 and 3	41	43	19	36	0	9

are notable for being commonly dominant initially in post-fire successions today. The *Leptospermum* has capsules with a degree of serotiny, i.e. retention of seed until heated in a fire. A fuller account of these species is given in online Appendix S5.

Of the two Group 1B species, pioneers on volcanic deposits, *Metrosideros robusta* is rarely a terrestrial tree, but it colonises bare lava (Clarkson, 1990); otherwise it establishes in the crowns of mature rain forest trees in old-growth forests as a strangler (Wardle, 1991). *Coriaria arborea*, which is nitrogen-fixing, colonises not only recent volcanic tephra and scoria but also landslides (Clarkson, 1990) and denuded floodplains (Bellingham, Peltzer & Walker, 2005).

The 28 Group 2 species include eight conifers, some of which grow to very large size and can be very long-lived, notably *Agathis australis* (Ogden & Stewart, 1995). Some conifer species are highly dependent on disturbance for regeneration, with disturbances ranging from the very large scale, e.g. after catastrophic eruption (Wilmshurst & McGlone, 1996) to individual tree-fall gaps (Cameron, 1955; Ogden & Stewart, 1995). Regeneration of most of these conifers takes place through an overstorey of short-lived angiosperm trees, typically species in Groups 1 and 2 (Esler & Astridge, 1974; Pook, 1978), and also *Weinmannia silvicola* (Group 3, Burns & Smale, 1990). The tall conifer *Dacrycarpus dacrydioides* can also establish directly on denuded floodplains (Smale, 1984; Duncan, 1991). In contrast to the tall, long-lived conifers, most of the angiosperm trees in Group 2 are

short-stature, fast-growing short-lived species. Exceptions are considered in online Appendix S5.

The separation of the 37 Group 3 species into Groups 3A and 3B is not sharp. Our assignment of some species, e.g. *Coprosma grandifolia* and *Prumnopitys ferruginea* should be seen as tentative. Typically species in Group 3A show discontinuous regeneration, exemplified by most of the podocarps (Wardle, 1963; Coomes & Bellingham, 2011), while species in Group 3B have a continuous reverse-J distribution of tree sizes, exemplified by *Beilschmiedia tawa* (West, 1995).

The smallest-seeded of the Group 3 species, especially *Weinmannia silvicola* (0.1 mg), *Schefflera digitata* (0.5–0.6 mg) and *Raukaua edgerleyi* (2.5 mg) establish preferentially on fallen logs and the trunks of tree ferns (Pope, 1924; Bellingham & Richardson, 2006; Gaxiola, Burrows & Coomes, 2008). The same is seen for the smallest-seeded Group 2 species, especially *Quintinia serrata* (0.03 mg).

The studies of the soil seed bank are the best that have been made for any WTRF (see online Appendix S3). Of the 10 Group 1A species seven have been recorded as having an appreciable occurrence in the soil seed bank, four in the short-term persistent category (Table 3). One of the two Group 1B species, *Coriaria arborea*, can have a transient seed bank. Only 6 of the 28 Group 2 species and 8 of the 37 Group 3 species have been reported to have an appreciable soil seed bank (Table 3). There is evidence of a short-term persistent seed bank for only three Group 2 species (*Brachyglottis repanda*, *Melicope ternata* and *Prumnopitys taxifolia*), and only four Group 3 species (*Coprosma*

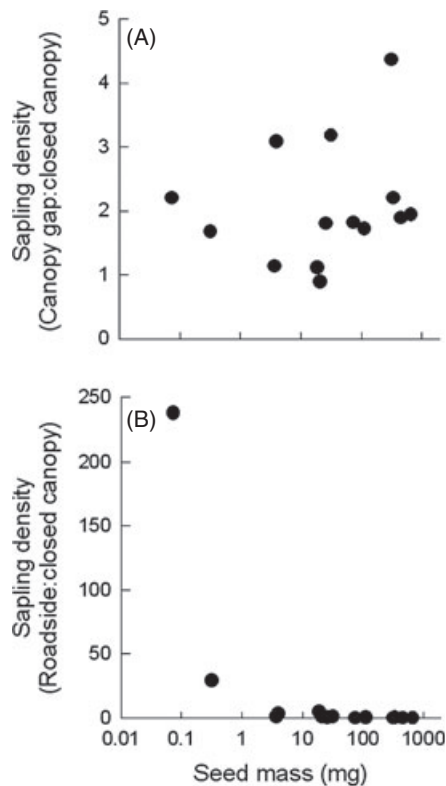


Fig. 2. The relationship between sapling density quotients and mean dry seed mass for 14 highly shade-tolerant tree species of warm temperate rain forest (WTRF) on Yakushima in southern Japan. (A) Density in tree-fall gaps/density in closed stands and (B) density on rocky roadside cuttings/density in closed stands; tree-fall gaps (totalling 650 m²) and closed stands (2000 m²) in Segire River Basin, and roadside cuttings (90 m²) on same rock type in Ohko River Basin. The species ordered by increasing seed mass are *Rhododendron tashiroi*, *Eurya japonica*, *Cleyera japonica*, *Symplocos prunifolia*, *Distylium racemosum*, *Myrsine nerifolia*, *Symplocos tanakae*, *Illicium religiosum*, *Symplocos glauca*, *Neolitsea aciculata*, *Camellia japonica*, *C. sasanqua*, *Nageia nagi* and *Litsea acuminata*.

arborea, *Macropiper excelsum*, *Meliclytus ramiflorus* and *Prumnopitys ferruginea*).

A few Group 2 species have been recorded as pioneers in full daylight on landslides. For example Smale, McLeod & Smale (1997) recorded *Leucopogon fasciculatus*, *Olearia rani*, *Pittosporum tenuifolium* and *Pseudopanax crassifolius* on Tertiary mudstones in the warm temperate zone of New Zealand; they were accompanied by two Group 3 species (*Meliclytus ramiflorus* and *Myrsine australis*). In cool temperate southern New Zealand, Mark *et al.* (1964) and Mark, Dickinson & Fife (1989) found that young (<15 years old) landslide surfaces of exposed gneiss were colonized by a Group 2 species (*Griselinia littoralis*) and a Group 3 species (*Podocarpus cunninghamii*, formerly *P. hallii*) accompanied by *Weinmannia racemosa*, which is closely related to the Group 3 species *W. silvicola*. Thus, as in Japan, shade-tolerance does not necessarily imply shade-demand.

(3) Chile

The WTRF of Chile is not subject to damage by cyclones, but severe storms do occur. Natural tree-fall gaps vary greatly in size. Veblen (1985) worked at three sites, and found the range to be *c.* 80–1060 m² with median values for different gap-making species of 80–200(–500) m². Vallejos (2004) found gaps to vary from *c.* 40–50 to *c.* 400–700 m², depending on the species of gap-maker. In forests where some canopy gaps are natural and others are caused by selective felling *c.* 20–30 years earlier, the size ranged from *c.* 20–30 to *c.* 240–540 m² in one study (González *et al.*, 2002) and from 274 to 970 m² in another (Muñoz & González, 2009). Veblen (1985) recorded the mean incidence (across species) of different causes of gap formation: uprooting 33–64% depending on site, wind-snap 33–50% and branch breakage 0–17%. For the one gap-maker encountered >10 times at each of two sites (*Eucryphia cordifolia*) uprooting ranged from 27 to 58%, wind-snap from 33 to 55% and branch breakage from 8 to 18%.

In contrast to the situation in Japan or New Zealand, there are bamboos (*Chusquea* spp.) that are very widespread, grow to >5 m tall, invade most gaps and severely suppress the growth of other species (Veblen, Schlegel & Oltremari, 1983); *C. quila* is the major species at lower altitudes, and *C. culeou* at higher altitudes. Larger-scale disturbances caused by landslides probably occur more often in Chile than in Japan or New Zealand; certainly it was suggested by Veblen *et al.* (1996) that the incidence of landslides is greater in inland southern Chile than in any other part of the world except perhaps New Guinea. There are significant differences between the area of WTRF along the Coastal Cordillera and that on the Andes; the former experiences less frequent disturbances by landslides but is still subject to wind disturbances that cause large canopy gaps (Veblen *et al.*, 1981).

Disturbances also occur in Chilean WTRF as a result of heavy ash showers from the nearby volcanoes (Jara & Moreno, 2012). These have a greater effect on and near the Andes than on the Coastal Cordillera. Most recently the Caulle volcano has spread ash over a very large area. On 15 June 2011 it was estimated by remote sensing that the area affected within 30 km of the crater was *c.* 2600 km² (Comisión Nacional de Medio Ambiente, Chile), but significant falls of ash occurred much further away in both Chile and Argentina. The area affected has declined since June 2011.

The WTRF was probably affected less often by catastrophic floods; it was possibly affected by lightning-induced fires (Veblen *et al.*, 1983). Fresh lava flows are frequent on the flanks of volcanoes above the altitudinal limit of WTRF; they are uncommon lower down but are found, e.g. on Volcán Llaima (Segura Uauy, 1999).

We recognize no Group 1A species, and only one Group 1B species, *Nothofagus obliqua* (Table 4). This species is different in nature from any Group 1B species seen in Japan or New Zealand. It can establish in the shade of bamboo, and even grow to about 1 m tall, but such plants all die, and therefore the species effectively needs areas of bare ground for its early

life if it is to persist in the landscape (Veblen *et al.*, 1983, 1996). The only possible chance otherwise is to establish in a canopy gap in one of the rare years when the bamboo dies all across the landscape. However, observations made in the early 1990s after such a mass death of bamboo showed that the seedlings of bamboo grew faster than those of the *Nothofagus obliqua* which again succumbed to shading (González *et al.*, 2002). It is probable that, before the arrival of humans, effective invasion by *Nothofagus obliqua* occurred most often on landslides, where it may form almost pure stands initially (Veblen & Ashton, 1978; Veblen *et al.*, 1983). This is true even for the coastal regions (Armesto, Mitchell & Villagrán, 1986), where the largest earthquakes can have huge impacts (in the last 60 years two had a moment magnitude scale, $M_w > 8$; Chapron *et al.*, 2006; Moreno, Rosenau & Oncken, 2010). *Nothofagus obliqua* probably also invaded land covered in deep ash, and alluvial deposits from catastrophic floods. Veblen *et al.* (1983) and Veblen (1989) tentatively explained the present abundance and widespread distribution of the species in WTRF as the result of past forest clearance by aborigines using fire.

Five species which are widespread in forest gaps and at forest edges must be placed in Group 2 because critical observations show that, although they require light shade or formation of a new canopy gap for persistence, they do become established in shade. Three species (*Aristotelia chilensis*, *Embothrium coccineum* and *Lomatia hirsuta*) occur in both lower- and higher-altitude forests, *Sophora cassioides* at lower altitudes, and *Nothofagus dombeysi* at higher altitudes. Observations on their shade tolerance were published by Figueroa & Lusk (2001), Lusk (2002), Belov, Lavruchin & Martin (2005–2009) and Lusk *et al.* (2011). Figueroa & Lusk (2001) reported that *Aristotelia chilensis* and *Lomatia hirsuta* germinated freely under canopy shade (68 and 57%, respectively, in the understorey versus 93 and 83% in a canopy gap of c. 80 m²), while *Embothrium coccineum* was more inhibited (11% versus 93%). There is one non-core Group 2 species with a very different kind of life history: *Gomortega keule*; it has very large seeds, and sprouts freely, forming multi-stemmed individuals believed to be very long-lived (Muñoz-Concha & Davey, 2011; see online Appendix S5).

The 22 species assigned to Group 3 vary greatly in the amount of light needed for onward growth (Donoso, 1989, 2006; Lusk *et al.*, 2008). However, even the least shade-tolerant can establish and persist for a significant time in the understorey. Many shoots of *Anomyrtus luma*, *Caldcluvia paniculata*, *Eucryphia cordifolia*, *Laureliopsis philippiana* and *Lomatia dentata* seen on the forest floor are from root-suckers, but careful inspection shows that there are also many seedlings (González *et al.*, 2002; Lusk & Piper, 2007; Lusk *et al.*, 2008). We have separated five species into Group 3B; the evidence for this is given in online Appendix S5.

The four smallest-seeded species in Group 3 (*Caldcluvia paniculata*, *Weinmannia trichosperma*, *Eucryphia cordifolia* and *Laureliopsis philippiana*; 0.06–2.0 mg) all become established preferentially on fallen trunks (Veblen *et al.*, 1981; Lusk, 1995; Christie & Armesto, 2003; Lusk & Kelly, 2003). *Raukaua*

laetivirens (3.5 mg) also establishes on logs, but more often grows as a hemi-epiphyte on large living trees (Veblen *et al.*, 1981).

Four of the five species in Group 2 (not *Sophora cassioides*) and 4/22 species in Group 3 were recorded by Veblen & Ashton (1978) as invading recent landslides (exposed bedrock or pumiceous lapilli) at altitudes <500 m (Table 4). Those found most widely were *Eucryphia cordifolia* (5/5 sites, sometimes with a higher frequency at a given site than the Group 1 species *Nothofagus obliqua*) and *Lomatia hirsuta* (3/5). Of the eight invasive species seven have wind-dispersed seeds; *Aristotelia chilensis*, being bird-dispersed (Armesto & Rozzi, 1989), is the only exception. The largest-seeded of the seven species are close to *Nothofagus obliqua* in seed dry mass (Table 4). Veblen & Ashton (1978) emphasized that high dispersibility is not enough to make invasion of young landslides possible, and some species with very small seeds (*Dasyphyllum diacanthoides*, *Laurelia sempervirens*, *Laureliopsis philippiana* and *Saxegothaea conspicua*) establish only rarely, presumably because of intolerance of the wholly open conditions and/or the nutrient-poor substratum. Vera *et al.* (2008) found a very high mortality in new germinants of *Laureliopsis philippiana* when they were grown in open conditions. By contrast, survival was almost 100% under light shade. In the same experiment seedlings of the same age of *Aextoxicon punctatum* had a very high survival rate under both light regimes.

At least two of the Group 2 species (*Embothrium coccineum* and *Lomatia hirsuta*) and one Group 3A species (*Lomatia ferruginea*) can invade young lava flows found at higher altitudes than WTRF, e.g. seen at c. 800–1000 m on Volcan Osorno (P.J. Grubb, personal observations, November 2006). Veblen *et al.* (1977) earlier recorded the *Embothrium* invading higher-altitude flows. Segura Uauy (1999) recorded *Lomatia ferruginea* on young lava flows within the altitudinal zone of WTRF where such flows are uncommon. Thus the assertion of Alberdi *et al.* (2009) that *L. ferruginea* does not invade volcanic deposits is untrue.

There has been little research on the possibility of a soil seed bank in Chilean WTRF; this issue is considered in online Appendix S3.

(4) South Africa

Violent winds are rare in the WTRF, and there is a contrast with the more northerly subtropical forests in eastern South Africa where cyclones play a role (Midgley *et al.*, 1997; Mucina *et al.*, 2006). Geldenhuys & Maliapaard (1983) found that most gaps in the canopy are small, and most trees die standing as a result of old age, disease or 'stress' – 70% in an extensive study by Midgley, Cameron & Bond (1995). The latter authors found that in their plots the trees had almost never established on a fallen trunk, or on a tip-up mound or in a pit caused by tree uprooting. There is also a virtual lack of seismic activity and landslides, and an absolute lack of any volcano producing fresh lava flows.

Fire plays a dominant role in restricting the distribution of the WTRF, and in the dynamics of the surrounding

communities (fynbos heathland and grassland) and of the forest edges, but it plays a very limited role in the dynamics of the forest (Geldenhuys, 1994; Midgley *et al.*, 1997). Again there is a contrast with other forest types to the north-east (Everard, 1985). Lightning sometimes kills small groups of trees, but seems not to start a forest fire, and the commonly accepted view is that the forest is 'virtually unburnable' (Mucina *et al.*, 2006). However, exceptional fires fanned by 'bergwinds' do burn into forests, as happened in 1996 and 1998, and the legume *Virgilia divaricata* can then form dense stands, recruited from the soil seed bank (*c.* 160–250 seeds m⁻²), much of it at depth and responding only to very high soil-surface temperatures; the other WTRF species re-establish in these stands (C.J. Geldenhuys, personal communication). The *Virgilia* is common at the forest-fynbos margin, but it seems likely that where the soil seed bank inside the forest is dense it results from a previous incursion of fire and subsequent dense stands of the *Virgilia*, perhaps >200 years earlier (Geldenhuys, 1994).

Elephants spend time in the forest, but there is no evidence that they initiate episodes of regeneration by felling or killing trees; the nearby fynbos heathland may well be their major source of food.

Our assignment of species to groups follows Midgley *et al.* (1990, 1995, 1997) and Professor J.J. Midgley (personal communication). The single species recorded as needing tree-fall gaps for establishment (Group 1A in Table 5), *Zanthoxylum davyi*, is sparse in the forest, not even recorded in the extensive study of Midgley *et al.* (1995) on gap-making and gap-filling.

There are eight species in Group 2, and nine in Group 3A. Within both groups there are probably significant differences in the extent to which they need canopy gaps to reach full size. In Group 3B we have placed the four species considered by Professor J. J. Midgley to be the most shade-tolerant.

There is generally a negligible soil seed bank apart from the *Virgilia divaricata* mentioned above (Midgley *et al.*, 1997; C.J. Geldenhuys, personal communication).

(5) SE Australia

The significant forms of disturbance were reviewed critically by Melick & Ashton (1991). Violent winds are not a major cause of forest gaps, in contrast to the situation further north on the east coast of Australia (see Adam, 1992). The gaps formed by death or fall of one or more trees are 5–30 m across. Although there is little seismic activity, landslides are a significant means of disturbance on steep rocky slopes. There is no extant volcano in the area producing fresh lava flows. Periodic floods affect the forest patches along valley floors, killing sensitive species through soil anoxia, ripping out trees and creating new sediments. The greatest differences from the situation in South Africa are that (i) the forest patches are smaller and (ii) periodically they are penetrated deeply by fire from the surrounding sclerophyll forest or human-induced vegetation.

Our assignment of species to Groups 1C–E in relation to disturbance regime (Table 6) is based wholly on the account

of Melick & Ashton (1991). There is no species assigned to Group 1A, i.e. establishing only in or almost only in gaps made by tree death or tree fall within the forest ('endogenous gaps' in the terminology of Melick & Ashton, 1991).

The single Group 1C species *Tristaniopsis laurina* generally dominates valley floor sites, and in the runs of years between significant floods the shade-tolerant, flooding-intolerant species establish beneath it and may grow to large size. The *Tristaniopsis*, which is confined to valley floors by its drought-intolerance, establishes only in gaps, but after a disturbance it may respond by producing sprouts as well as giving rise to new seedlings. It commonly leans over in the direction of water flow, and in extreme cases will 'layer' (produce new roots on shoots) where it touches the ground.

Group 1D contains eleven species of 'sclerophyll' vegetation (particularly 'wet sclerophyll forest') that invade after fire has opened the rain forest. *Pomaderris aspera* is the most consistent invader (see online Appendix S5).

Group 1E contains three species, all invaders typical of the matrix of 'sclerophyll' vegetation in which the patches of WTRF are found; they all need a gap created by fire or flood or an 'endogenous gap'.

None of the six Group 3 species is regarded as especially shade-tolerant like the species in Group 3B in New Zealand, Chile and South Africa. At least two of the species are able to establish in full daylight: *Acmena smithii* and *Pittosporum undulatum*, which sometimes colonize talus slopes. The resistance and resilience of Group 3 species in the face of periodic fire is summarized in online Appendix S5.

Only the most skeletal information is available concerning the soil seed bank of species in Australian WTRF; the Group 3 species seem to have little or none, while the available evidence (mainly from other forest types) suggests that species of *Acacia* and *Pomaderris aspera* have persistent seed banks in the soil, those of *Eucalyptus* have shorter-lived seed banks in the canopy, and species of *Olearia* and *Tristaniopsis laurina* have no persistent seed bank (see online Appendix S3).

The general perspective of Melick & Ashton (1991) is that in the absence of an increase in frequency and intensity of fires resulting from human activity, the WTRF and sclerophyll forest can persist in a long-term alternation and balance rather like the better known system in Tasmania, where cool temperate rain forest dominated by *Nothofagus cunninghamii* alternates with wet sclerophyll forest dominated by *Eucalyptus regnans* (see Howard, 1981).

(6) Canary Islands

In most years violent winds are not a major cause of forest gaps, but occasionally they have a big impact, especially in rugged areas with narrow ridges; in 2004 storm Delta flattened *c.* 150 ha of forest on the Enchereda massif of La Gomera (A.B. Fernández-López, personal communication). Another infrequent cause of gaps, perhaps experienced on the order of once every hundred years, could be killing of trees by exceptionally severe drought; unlike most areas of WTRF the STMRF of the Canary Islands regularly suffers a 5-month 'dry season' (Table 1) and some extreme droughts

are likely to occur. At the present time some areas of forest on La Gomera are suffering die-back from an unknown cause or causes, with a concomitant increase in gap-demanders (A.B. Fernández-López, personal communication); how far such die-back occurred before invasion by humans is hard to assess. Landslides are rare and generally confined to the steepest slopes, and despite the volcanic origin of the islands, there has not been any new lava flow in the montane rain forest zone for at least a million years (Fernández-Palacios & Arévalo, 1998).

It is virtually certain that before the arrival of humans about 2000–2500 years ago fire was a part of the natural disturbance regime in the vegetation types found above the montane rain forest belt, where it is much drier, but there is no evidence that it was significant in the rain forest. Fire was definitely important in the forest of *Pinus canariensis* which is one of those pines that regenerate from epicormic buds after being burnt (Keeley & Zedler, 1998; Climent *et al.*, 2004). Following the exceptionally dry period from autumn 2011 to summer 2012, fires in early August 2012 (almost certainly started by humans) spread into the STMRF, destroying 20–25% of the Garonajay National Park on La Gomera where the best areas of forest remain. Thus the forest can burn in exceptional years, and might conceivably have done so before human intervention as a result of fires spreading from the drier pine forest above it or the drier broad-leaved forest below it (now largely cleared – see online Appendix S2), but there is no definite evidence that it did so.

In two areas of forest on Tenerife, Arévalo & Fernández-Palacios (1998) found the canopy gaps to be mostly small; the mean for gaps >10 m² in area was found to be *c.* 40 m². On La Gomera the trees are bigger and create larger gaps, many in the range 40–160 m² (A.B. Fernández-López, personal communication). On Tenerife, Arévalo & Fernández-Palacios (1998) found that many gaps are filled by sprouts rather than by trees newly established from seed. Arévalo & Fernández-Palacios (2007) found that in the rare large gaps (>100 m²) in their study area there was a trend toward a negative effect of increased irradiance on juveniles of shade-tolerant species, and no increase in the establishment of shade-intolerant species.

So great has the human impact on the Canary Islands been (see online Appendix S2) that we have to consider the possibility that the gap-demanding plants in the forest today (*Erica arborea*, *E. scoparia* and *Morella faya*; Table 7) played no part originally in the STMRF (see Section II.3). There is no doubt that in the semi-natural remnants of STMRF on the Canary Islands today they need well-lit micro-sites to become established (Fernández-Palacios & Arévalo, 1998; Arévalo & Fernández-Palacios, 1998). In addition, at a site on La Palma where coppicing is practised, and plots up to 60 years old were studied, it was found that establishment of new seedlings of *Erica arborea* and *Morella faya* ceased within 3 years, as shade intensified (Bermúdez *et al.*, 2007). Viable seeds of all three species can be found in appreciable quantity in the soil (and that is not true of any of the other tree species), but new work is needed to determine whether

they form even a short-term persistent seed bank (see online Appendix S3).

There is no doubt that the abundance of all three species has increased greatly as a result of human utilization of the forest. Also all three species have declined markedly where forests have been protected from human exploitation over the last four decades (A.B. Fernández-López, personal communication). It is tempting to take the view that the three species have invaded the STMRF as a result of human impact, but we reject this extreme view, and we place all three species in Group 1A on the basis of their behaviour in the forest that has been least disturbed by humans, that on La Gomera.

Erica scoparia occurs there on very steep slopes where the trees gradually bend over to form a ‘horizontal forest’ that lets much more light penetrate to ground level; *Erica scoparia* then establishes on the moss-covered soil (A.B. Fernández-López, personal communication). *Morella faya* produces sucker shoots freely, leading to successive ‘generations’ of trunks that enable individuals to last for many years – long enough by hypothesis for the species to invade new gaps made by rare disturbance events such as large blow-downs and exceptional droughts. *Erica arborea* is the species least understood. A study in northernmost Morocco found that healthy mature plants can be found under considerable shade (not deep shade) from the sclerophyll *Quercus suber* on drier sites and the semi-deciduous *Q. canariensis* on moister, deeper-soil sites (Ojeda, Arroyo & Marañón, 2000). By contrast, in a study of forest, woodland and open woodland sites in extreme south-western mainland Spain, dominated by these two oak species, seedlings of *Erica arborea* were found only in open woodland with a mean global site factor (proportion of full daylight) of 27% at 0.5 m above the soil, and then only rather few (Pérez-Ramos & Marañón, 2012). The latter authors concluded that *Erica arborea* behaves as a ‘pioneer’ *sensu* Swaine & Whitmore (1988), being recruited from the soil seed bank where a canopy gap is formed by a tree falling or by fire. We suggest that in view of the species surviving appreciable shade as an older plant it should be regarded as a ‘late-tolerant’ *sensu* Oldeman (1990). We hypothesize that (i) in the STMRF of the Canary Islands the requirements are essentially similar to those found in the western part of the Mediterranean Basin, except that fire was not involved in the natural forest and (ii) the canopy gaps necessary for long-term persistence in the landscape have arisen in the past from the causes suggested for *Morella faya*.

There appears to be only one Group 2 core species. *Ilex canariensis* is described as intermediate in tolerance between shade-intolerants and shade-tolerants by Arévalo, Fernández-Palacios & Palmer (1999), who showed that it survives largely as a result of basal sprouting; projection models of real stands reveal that without this asexual reproduction it becomes extinct. In this respect it is like the *Lithocarpus* spp. in Japanese WTRF. There are three non-core species that are probably best placed in Group 2 (see online Appendix S5).

There are 10 Group 3 species, all of them encountered as shaded seedlings in the critical studies of Arévalo & Fernández-Palacios (1998) and Fernández-Palacios & Arévalo (1998). The *Prunus* encroaches strongly on canopy gaps by lateral spread of the crown (P.J. Bellingham and P.J. Grubb, unpublished observations), and was found by Fernández-Palacios & Arévalo (1998) to produce many more effective sprouts than seedlings. Six other Group 3 species have basal sprouting ('suckers'): all four laurels (*Apollonia barbuiana*, *Laurus azorica*, *Ocotea foetens*, *Persea indica*), *Ilex perado* ssp. *platyphylla* and (less often) *Viburnum rigidum* (Fernández-Palacios & Arévalo, 1998; Arévalo *et al.*, 1999; Fernández-Palacios *et al.*, 2004). *Ocotea foetens* is the rarest of the laurels (Bramwell & Bramwell, 1974), grows tallest and is centred on gully sites, where it can create deep shade and is often dominant; on Tenerife the stands are typically rich in ferns, of which 15 species were recorded by Rivas-Martínez *et al.* (1993). A single stand on La Palma, described by Lohmeyer & Trautman (1970) was different in kind, having abundant *Hedera canariensis* on the ground, and only scattered individuals of the few other species. In the experience of A.B. Fernández-López (personal communication) four species are particularly shade-tolerant (Table 7).

The one study of the dynamics of WTRF on the Azores (Elias & Días, 2009) revealed two species needing canopy gaps for establishment: *Erica azorica* (shorter-lived) and *Juniperus brevifolia* (long-lived). The Group 3 species include *Frangula azorica* and *Laurus azorica* which establish in shade but need canopy gaps to grow tall, and *Ilex azorica* able to regenerate wholly in the understorey. In a glasshouse experiment lasting 2 years many seedlings of *Erica azorica* grew from soil samples, but no *Juniperus brevifolia*.

(7) Summary and statistical analysis

The numbers of species in Groups 1, 2 and 3 in each of the six regions are shown in Table 8. The extent of statistically significant differences in the incidence of Group 1 species was determined using Fisher's Exact Test (Table 9); following Moran (2003) we did not make Bonferroni corrections for multiple comparisons. The Australian and Japanese forests do not differ significantly from each other, but both have a significantly greater incidence of Group 1 species than the forests in New Zealand, South Africa and Chile. The forest on the Canary Islands does not differ significantly in incidence of Group 1 species from any of the other forests.

As to the incidence of Group 2 species among the Group 2 plus Group 3 species, none of the forests is significantly different from any of the others.

IV. COMPARISONS OF SEED MASS

(1) Seed mass related to mature height

As shown in Fig. 3, there is a significant and marked trend to greater log seed mass with greater log mature height for the

WTRF in Japan ($r^2 = 0.18$, $P < 0.001$). However, the trend is weaker for WTRF in New Zealand ($r^2 = 0.06$, $P = 0.04$) and there is no trend in the Canary Islands ($P = 0.11$), South Africa ($P = 0.29$), Australia ($P = 0.37$), or Chile ($P = 0.68$). For New Zealand the species occupy a 'wedge-shaped' space on a graph, with the largest mean seed size increasing markedly with maximum tree height while the smallest mean seed size increases little or not at all (Fig. 3). By contrast, for Chile and South Africa the species occupy a 'fan-shaped' space on the graph, with the largest mean seed size increasing markedly and smallest mean seed size decreasing markedly (Fig. 3).

The general lack of a significant relationship between mean seed mass and mature height within a region results in a general lack of significant differences in seed mass among regions, despite there being some significant differences in mature height.

The Group 3 species differed in mean heights among the six regions studied ($F_{5,111} = 4.84$, $P = 0.001$), with those in South Africa (23.6 m) and those in Chile (22.5 m) taller than those in Japan (13.0 m) and New Zealand (14.8 m; $P < 0.05$, Tukey tests; Fig. 4). The mean heights of the Group 3 species in the remaining regions were not significantly different (Fig. 4).

An ANOVA on log-transformed data for the mean seed mass values of the Group 3 species showed that there were significant differences among the regions ($F_{5,111} = 2.48$, $P = 0.037$), but *post-hoc* Tukey tests did not support this result ($P > 0.05$). For Group 1 species the means for New Zealand (2.5 mg) and the Canary Islands (9 mg) are significantly lower than that for Japan (119 mg; $F_{3,47} = 9.89$, $P < 0.001$; Tukey test $P < 0.02$), but the means for the other regions (not including Chile and South Africa with only one or two Group 1 species) are not significantly different.

(2) Species Groups 1, 2 and 3 compared

We first compare the values for Groups 1 and 3 without respect to taxonomic relatedness or mature height, then make comparisons allowing for these potentially important complicating factors. Finally, we compare species in Groups 2 and 3.

The simplest kind of comparison yields different answers depending on the region studied. For two of the regions with an appreciable number of species in Group 1 there is no significant difference between the mean seed mass values for Group 1 and Group 3 species (Japan $t_{44} = 0.15$; $P = 0.88$; Australia $t_{19} = 1.52$, $P = 0.15$; both using log-transformed data; Fig. 5). However, for New Zealand and the Canary Islands the mean values for Group 1 species are markedly lower ($t_{47} = 4.66$, and $t_{11} = 4.50$ respectively, both $P < 0.001$; log-transformed data). For the two regions with very few Group 1 species (Chile 1, South Africa 2) they clearly have much lower seed mass than the mean for Group 3 species in the corresponding region (Fig. 5).

In seven intrafamilial intergeneric comparisons across three regions, Group 1 species had smaller seeds than

Table 9. The probabilities of the differences between regions in the proportion of Group 1 species in the total list of core species, determined by Fisher's Exact test (two-tailed)

	Japan	Canary Is.	New Zealand	South Africa	Chile
Australia	0.1037	0.1227	0.0013	0.0041	0.0003
Japan	—	0.5610	0.0195	0.0431	0.0059
Canary Is.	—	—	0.7051	0.3795	0.1354
New Zealand	—	—	—	0.7313	0.1822
South Africa	—	—	—	—	0.5908

those in Group 3 (Table 10; ANCOVA, tolerance category $F_{1,29} = 5.442$, $P = 0.027$, covariate family $F_{1,29} = 0.005$, $P = 0.95$, covariate region $F_{1,29} = 0.003$, $P = 0.96$, seed-mass data log-transformed). Only one intrageneric comparison was possible, and the trend was the same for this genus as for all the intergeneric comparisons (Table 10). Two of the seven intrafamilial comparisons were made in regions where the means considered without reference to taxonomic relatedness were not significantly different (one in Japan, one in Australia).

Before considering any differences in seed mass between species in Groups 1 and 3 compared at a given height, we must consider any differences among the Groups in mean height. As shown in Fig. 4, the mean heights of the species in Groups 1 and 3 are not significantly different in Japan (15.2 *versus* 13.0 m; unpaired Student's $t_{58} = 1.33$, $P = 0.19$), New Zealand (12.8 *versus* 14.8 m; $t_{47} = 0.73$, $P = 0.47$), Australia (25.4 *versus* 13.0 m; $t_{19} = 1.32$, $P = 0.20$), or the Canary Islands (11.2 *versus* 16.5 m; $t_{11} = 0.86$, $P = 0.41$). In the regions with just one or two Group 1 species (Chile and South Africa) they are not notably taller or shorter than the Group 3 species (Tables 4 and 5).

For the three regions with an appreciable number of species in Group 1, two different patterns are seen in the relationship between the Group 1 and Group 3 species. For Japan the scatter in log seed mass against log mature height is essentially similar in the two groups (Fig. 6), and there is no significant difference between the means (see above). For Australia with fewer species there is considerable overlap as for Japan (Fig. 6), and the means are not significantly different (see above). However, for New Zealand (Fig. 6) there is no significant difference in seed mass between Groups 1 and 3 among the species of low stature (<10 m tall; $t_{13} = 1.10$, $P = 0.29$) but among the taller-growing species the shade-tolerators have seeds of much greater mass (279 mg *versus* 1.2 mg for gap demanders); the overall means are very different ($t_{32} = 5.01$, $P < 0.001$; Fig. 4).

In New Zealand, Group 2 species have significantly smaller seeds on average than those in Group 3 ($t_{63} = 2.27$, $P = 0.027$), and Chile and South Africa tend to have smaller seeds in Group 2 but not significantly so ($P < 0.71$). In Japan the reverse is true ($t_{37} = 3.81$, $P = 0.001$; Fig. 5), chiefly because all the Fagaceae have relatively large seeds. The range of means for the 10 species of Fagaceae is 370–1700 mg, and 7 have means of 1000 mg or more (Table 2).

(3) The ranges of seed mass within functional groups, and extreme values

Where the number of species in a functional group is appreciable there is a strikingly wide range of values. The broadest ranges were found for the Group 3 species; they covered between four and five orders of magnitude in Chile, and four in New Zealand. These ranges parallel that of four orders published earlier for shade-tolerators in Japan (Kohyama & Grubb, 1994). The range for shade-tolerant core species in Australia (of which there are only six) is much smaller, between 2 and 3 orders of magnitude. However, if two non-core species are admitted, the range increases to about four orders of magnitude. These species are *Eucryphia moorei* (Cunoniaceae, mean dry seed mass 0.19 mg) and *Livistona australis* (Arecaceae, 2000 mg; seed mass values are taken from Floyd, 2008).

The various regions differ in whether or not the smallest-seeded Group 1 core species has seeds smaller than the smallest-seeded Group 3 core species. It is the case in the WTRF of New Zealand (Table 3) and Australia (Table 6), and in the STMRF of the Canary Islands (Table 7), but it is not the case in Japan (even though there are many Group 1 species; Table 2) or South Africa (two Group 1 species; Table 5) or Chile (one Group 1 species; Table 4). If the non-core species *Eucryphia moorei* is admitted (see preceding paragraph), then in Australia also the seed of the smallest-seeded gap-demander is larger than that of the smallest-seeded shade-tolerator.

In Japan, as shown in Table 2, the largest-seeded Group 1 species (*Aleurites cordata* with mean value 730 mg and *Sapindus mukorossi* 890 mg) have larger seeds than all but two of the Group 3 species (*Camellia japonica* 680–1100 mg and *Nageia nagi* 340–880 mg). There is no Group 1 species with such relatively large seeds in any of the other five forest regions studied. On the other hand one of the Group 1 species in SE Australian WTRF has a much bigger seed than the majority of gap-demanders in tropical lowland rain forests (*Elaeocarpus reticulatus* 210 mg).

In WTRF outside Japan the only Group 2 core species with a mean seed mass >300 mg is seen in New Zealand (*Vitex lucens* 680 mg), and the next largest is *Ekebergia capensis* in South Africa (220 mg). However, in Chile the non-core Group 2 species *Gomortega keule* has a 'seed' (including endocarp) of mean dry mass *c.* 4000 mg (Muñoz-Concha & Davey, 2011).

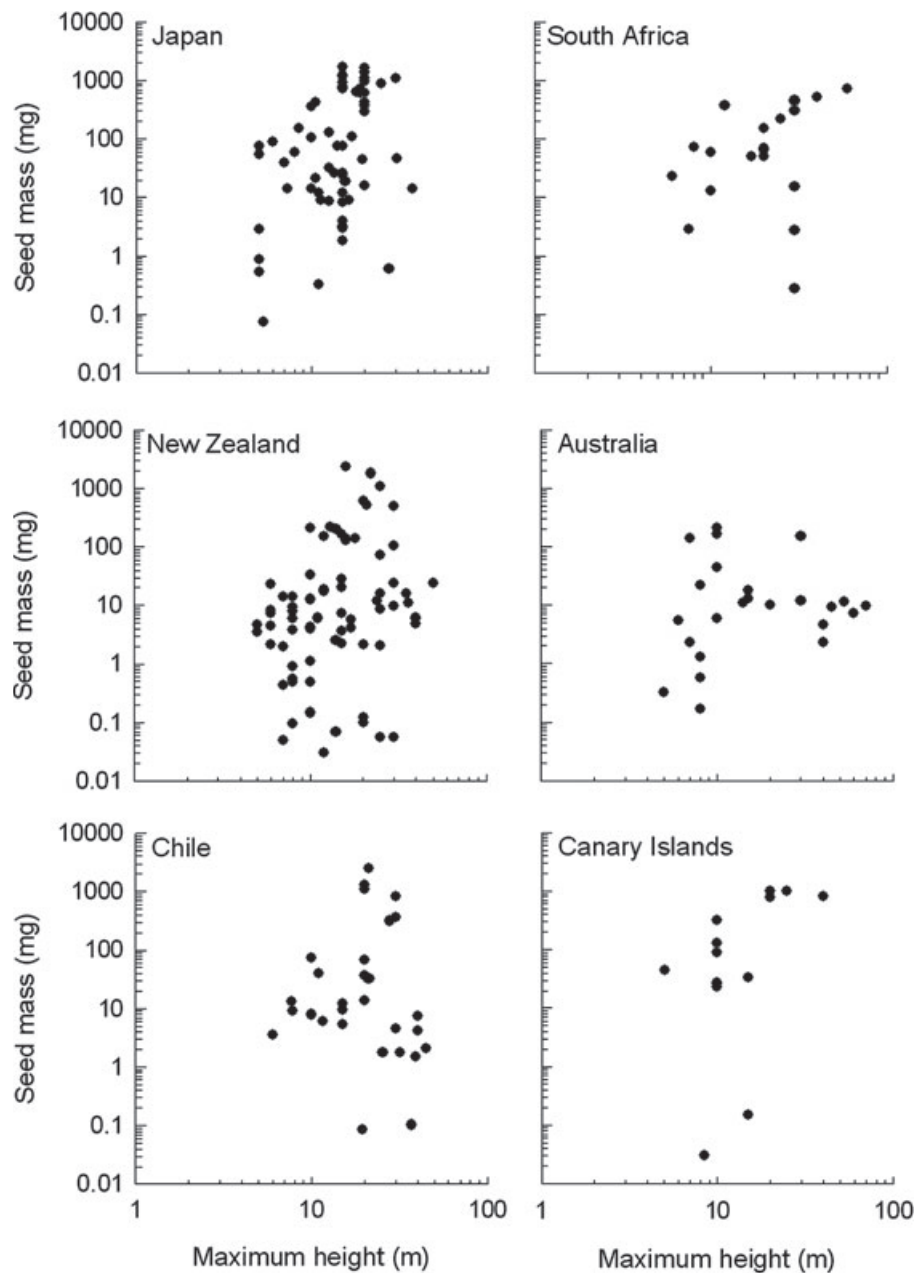


Fig. 3. The relationships between dry seed mass and mature height (both on log scales) for species of trees and tall shrubs in five warm temperate rain forests and in subtropical montane rain forest on the Canary Islands.

V. DISCUSSION

(1) Definition of disturbance regimes

Disturbance regimes in general cannot be summarized wholly satisfactorily in single values because they are multi-dimensional, involving variation in frequency, intensity, timing and extent (White, 1979; Grubb & Hopkins, 1986; Loehle, 2000). In the specific case of WTRF and STMRF no single measure of disturbance is wholly satisfactory because gap-demanding species exploit qualitatively different kinds of gap: tree-fall gaps caused by wind, landslides, lava flows,

ash falls, gaps made by fires or floods etc. Nevertheless, if the relevant data were available, it might still be useful to have a single index based on the sum of the proportions of the forest changing into gap per (say) century as a result of all the various causes. In this way the forests of concern would be separated into those highly disturbed (Japan, New Zealand, Chile and Australia) and those experiencing little disturbance (South Africa and Canary Islands).

There next arises the question of the extent to which different kinds of disturbance have led to the local evolution of, or invasion from elsewhere by, specialist species. A striking feature of Table 8 is how few specialists there are on landslides

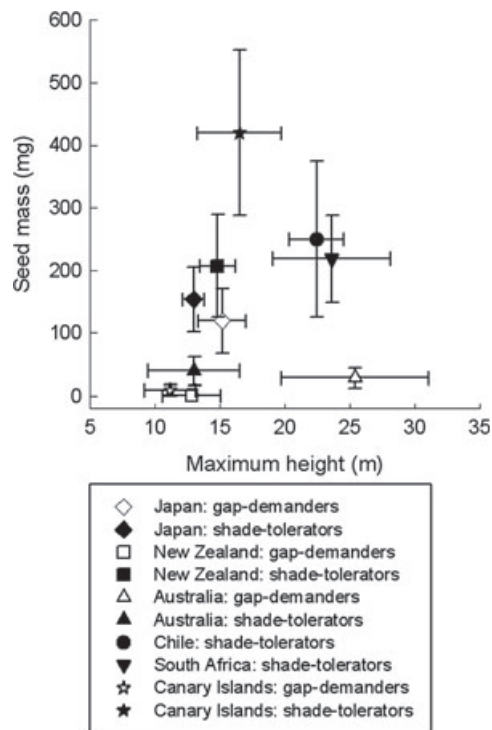


Fig. 4. The mean values for mean seed dry mass and mature height (± 1 S.E.M) for Group 1 species (gap-demanders) and Group 3 species (shade-tolerators) in four regions, and for Group 3 species alone in two regions where there are only one or two Group 1 core species. The means for tree height are calculated using only the species for which seed mass values are also available. The numbers of species are as follows: for Group 1 $N = 18$ for Japan, 12 for New Zealand, 15 for SE Australia, and 3 for the Canary Islands; for Group 3 $N = 20$ for Japan, 37 for New Zealand, 22 for Chile, 13 for South Africa, 6 for SE Australia and 10 for the Canary Islands.

or lava flows or deposits of scoria or flooded areas. In many areas, this situation may be explained at least partly by the shorter return-time of wind-driven tree-fall gaps compared with landslides etc., but this is doubtfully the case for the slopes of the Andes in Chile which are extremely active tectonically.

Landslides account for much larger areas than lava flows etc., but still a notable proportion of the gap-demanding species pioneering on them also occur in canopy gaps caused by wind-throw, *viz.* 3/7 in Japan and 3/4 in New Zealand (Tables 2 and 3). Moreover, in Chile all eight of the major pioneer trees on landslides also become established in forest, although the one Group 1 species does need landslides for persistence in the natural landscape (Table 4).

From the point of view of understanding the proportion of gap-demanding species in WTRF in different regions, a reasonable approximate index of the extent of disturbance in WTRF would generally be the proportion of forest going into the gap phase per unit time as a result of wind-throw, provided it was based on studies covering a large enough area and a long enough period. Unfortunately for most regions

we do not have the data needed to create such an index. With such an index one could reasonably plot incidence of gap-demanding species against incidence of canopy gap-formation. Two areas stand out as needing different treatment: for the WTRF in Australia the proportion going into the gap phase as a result of fire should be added to that caused by wind, and for that part of the WTRF in Chile on the slopes of the Andes the proportion subject to landslides should be added.

(2) Disturbance regime and proportion of species gap-demanding for establishment

We leave aside initially the region with the highest incidence of Group 1 species (Australia 71%), conscious that this high incidence might reflect to a significant degree the fact that the rain forest occurs in small fragments within an extensive matrix of sclerophyll vegetation which provides most of the Group 1 species. Instead we consider first the contrast in Tables 8 and 9 between the region with the next highest incidence of Group 1 species (Japan 37%) and the two regions with the lowest incidence (South Africa 9% and Chile 4%).

The lower incidence of Group 1 species in South African WTRF than in Japanese is consistent with the much smaller degree of disturbance (no typhoons and almost no landslides). However, there is reason to believe that another factor has been influential. The paucity of Group 1 species in South African WTRF may be a result chiefly of the extremely low fertility of the soils (see Van Daalen, 1984), an evolutionary result paralleling the effect seen in certain tropical forests and cited at the start of Section I. It is significant that the one Group 1A species in our list of core species for the South African WTRF (*Zanthoxylum davyi*) is much more abundant in STMRF ('Southern Mistbelt Forest') which occurs on more fertile soils (Mucina *et al.*, 2006). In this forest there is at least one other gap-demanding tree, *Ptaeroxylum obliquum* (see Geldenhuys, 2010) and the forest is notably subject to invasion by gap-demanding aliens (*Rubus* spp. and *Solanum mauritianum*; Mucina *et al.*, 2006).

At first sight there is a problem with this approach in that some of the best-preserved WTRF in Japan with numerous species confined to tree-fall gaps (that on Yakushima) is found on highly leached, infertile soils over granite. However, the persistence of gap-demanders in the system may be dependent on the fact, emphasized by Grubb (1992), that establishment of gap-demanding species in single-treefall gaps is commonly confined to tip-up mounds, where – by hypothesis – root competition from established trees is significantly reduced. In the South African WTRF there are few tip-ups, and by hypothesis few micro-sites where root competition is not effective. In that case it is the interaction of nutrient paucity and the disturbance regime which has been important in inhibiting the evolution of species needing gaps for establishment.

A quite different kind of complication is involved in the much lower incidence of Group 1 species in the Chilean WTRF than in the Japanese (4% *versus* 37%). It is certainly

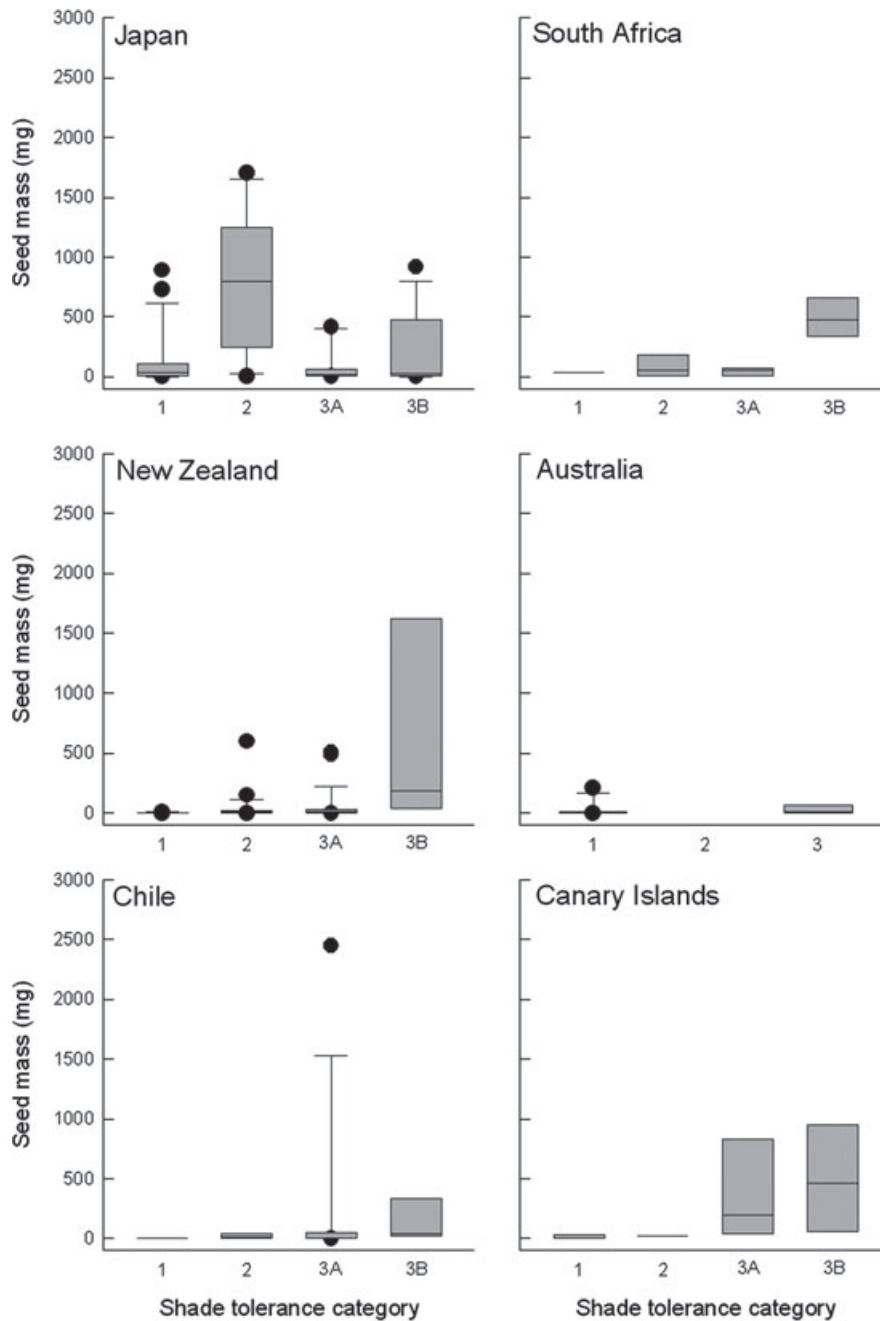


Fig. 5. The median values and ranges of seed dry mass for core species of trees and tall shrubs in five warm temperate rain forests and in subtropical montane rain forest on the Canary Islands, separated into groups according to their requirements for establishment and persistence (see text for details). The boundary of the box closest to zero indicates the 25th percentile, the boundary of the box farthest from zero indicates the 75th percentile, and the bar within marks the median. Error bars above and below the box indicate the 90th and 10th percentiles, with outliers denoted beyond.

not consistent with the hypothesis that the incidence of gap-demanders reflects the extent of disturbance, because the Chilean forest suffers a very high frequency of landslides considered on a world scale (Veblen *et al.*, 1996) and some significant strong winds, and yet there is only one Group 1 species among a core set of 28 species. We suggest that this is an evolutionary result of the all-pervading presence

of bamboos (*Chusquea* spp.) which invade canopy gaps effectively by vegetative spread, and grow both tall (5 m) and quickly. The five Group 2 species exploiting canopy gaps have evolved an ability to establish in a degree of canopy shade and persist in a little more shade than the one Group 1 species (*Nothofagus obliqua*).

Table 10. Data on mean seed dry mass used for comparisons between Group 1 and Group 3 species within families, and within a genus; the data are from Tables 2, 3 and 6, and arithmetic mean values are used here if multiple values are given in the earlier tables

Region	Family	Species	Shade tolerance group	Height (m)	Seed mass (mg)	
(a) Intrafamilial intergeneric comparisons						
Japan	Lauraceae	<i>Lindera citriodora</i>	1	ND	110	
		<i>Neolitsea aciculata</i>	3	17	[110]	
		<i>Litsea acuminata</i>	3	19	[670]	
New Zealand	Cunoniaceae	<i>Ackama rosifolia</i>	1	12	0.03	
		<i>Weinmannia silvicola</i>	3	20	0.1	
		<i>Aristolelia serrata</i>	1	10	3.9	
	Elaeocarpaceae	<i>Elaeocarpus hookerianus</i>	3	13	220	
		<i>Elaeocarpus dentatus</i>	3	21	510	
		Malvaceae	<i>Entelea arborescens</i>	1	6	2.1
			<i>Plagianthus regius</i>	1	17	4.2
			<i>Hoheria populnea</i>	3	11	6.1
		Myrtaceae	<i>Metrosideros robusta</i>	1	30	0.055
	<i>Kunzea ericoides</i>		1	25	0.057	
	<i>Leptospermum scoparium</i>		1	10	0.15	
	<i>Lophomyrtus bullata</i>		3	8	7.8	
	<i>Syzygium maire</i>		3	16	130	
	<i>Dodnaea viscosa</i>		1	8	9.5	
	Sapindaceae	<i>Alectryon excelsus</i>	3	14	210	
Australia		Myrtaceae	<i>Eucalyptus botryoides</i>	1	40	2.6
	<i>E. elata</i>		1	40	4.4	
	<i>E. cypellocarpa</i>		1	60	7.1	
	<i>E. obliqua</i>		1	70	9.7	
	<i>Tristaniopsis laurina</i>		1	20	10	
	<i>Eucalyptus globulus</i>		1	53	11	
	<i>Acmena smithii</i>		3	30	150	
	(b) Intrageneric comparison					
New Zealand	Rubiaceae	<i>Coprosma robusta</i>	1	6	8.1	
		<i>C. arborea</i>	3	10	13	
		<i>C. grandifolia</i>	3	6	23	

Values in square brackets were determined after removal of the endocarp.
ND = no data.

We now return to the area with the highest incidence of Group 1 species: Australia with 71%. The statistically significant contrasts with New Zealand, Chile and South Africa (Table 9) are undoubtedly compatible with the idea that incidence of such species parallels the incidence of disturbance because periodic disturbance by fires is so common and widespread in Australian WTRF, and no form of disturbance is so common and extensive elsewhere.

However, we must ask whether the proportion of Group 1 species in Australian WTRF is very high wholly as a result of the very high incidence of disturbance. Could the relatively small number of shade-tolerant species result partly from the stands of WTRF occupying in total a very small area, while the wet sclerophyll forest (dominated by various *Eucalyptus* spp. and containing almost all of the Group 1 species of the WTRF) occupies a large area? This issue is especially important because the area of WTRF in SE Australia has been small throughout the Quaternary, and is thus not a recent phenomenon resulting from human activity (see Kershaw *et al.*, 1991; Byrne *et al.*, 2011). Studies of Mediterranean-type Sclerophyll Forest and STMRF in South Africa yielded only a weak correlation between area of a forest fragment and number of species in it, and a

shallow slope for the relationship (Bond & Euston-Brown, 1993; Everard, Midgley & Van Wyk, 1993). However, there could still be a significant effect of area when the total area of a given forest type in a particular region is very small for a long time.

We now turn to a different kind of complication, possibly partly responsible for the significantly lower incidence of Group 1 species in the WTRF of New Zealand compared with that in Japan (16% *versus* 37%). It is tempting to explain the lower incidence of Group 1 species in terms of a lower incidence of disturbance. In Japan the WTRF suffers frequent disturbance by strong winds, and significant numbers of landslides. In New Zealand it suffers a lower incidence of strong winds (cyclones on the order of once a decade *versus* typhoons in Japan every year), and probably about the same incidence (or a lower one) of landslides. There is a lack of comparative data on incidence of landslide formation in New Zealand and Japan, and our expectation is based on the total rainfall, the frequency of very heavy falls and the extent of sloping topography. It seems likely that the WTRF in Japan has experienced during evolutionary time a greater incidence of disturbance overall.

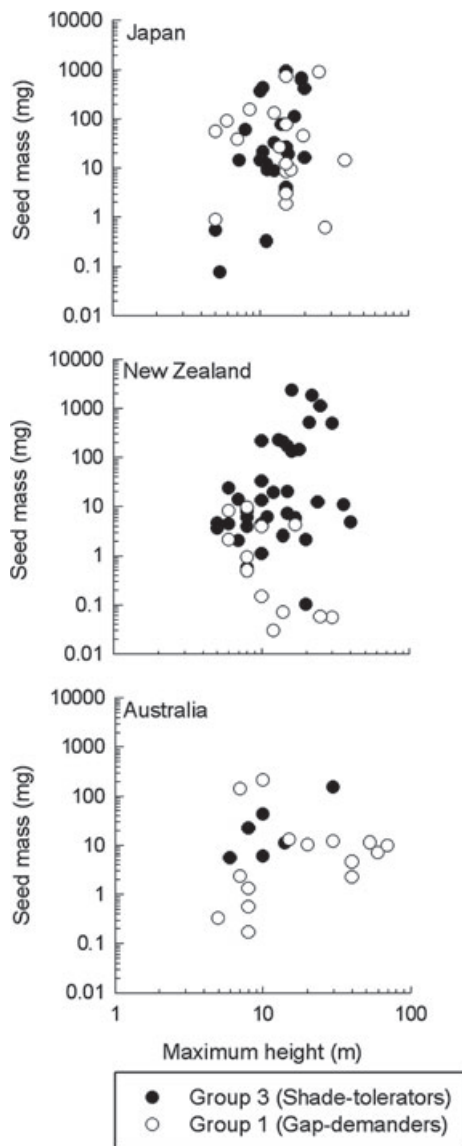


Fig. 6. The relationship between seed dry mass and maximum height (both on log scales) for Group 1 species (gap-demanders) and Group 3 species (shade-tolerators) in three warm temperate rain forests.

Despite this potential fit with the incidence of disturbance, we suspect that a quite different factor has played a significant part: the great difference between Japan and New Zealand in the availability of floristic groups with the potential to give rise to Group 1 species.

Japan has been continuously close to land that provided a connection with the subtropical and tropical areas to the south (Hope *et al.*, 2004), reflected in the presence today among the Group 1 species of 10 genera that are most speciose in the tropical lowland regions (Table 2): *Aleurites*, *Mallotus* and *Sapium* (Euphorbiaceae), *Aphananthe* (Cannabaceae), *Clerodendrum* (Lamiaceae), *Ehretia* (Boraginaceae), *Ficus* (Moraceae), *Lindera* (Lauraceae), *Sapindus* (Sapindaceae–Sapindoideae)

and *Schoeffia* (Olacaceae). In Japan there is also a rich temperate deciduous flora to the north, which has been in contact with the WTRF for a very long time. Confining ourselves to genera occurring widely in cool temperate deciduous forest today, we find five among the Group 1 species: *Acer* (Sapindaceae–Aceroidae, three spp.), *Alnus* and *Carpinus* (Betulaceae, one and two spp., respectively), *Prunus* (Rosaceae, one sp.) and *Salix* (Salicaceae, one sp.).

By contrast the islands comprising New Zealand are at the present time isolated from the nearest land masses by 2150 km or more, and recent research suggests that most of their flora has been recruited by long-distance dispersal (McGlone, Duncan & Heenan, 2001; Winkworth *et al.*, 2002; McGlone, 2006). Almost all the species below the tree-line can be seen as having primarily warm or cool temperate lowland or tropical-subtropical montane affinities. There are only a few exceptions that have strong tropical-subtropical lowland affinities: the palm *Rhopalostylis*, the climbing pandan *Freycinetia*, the dicots *Alectryon* (Sapindaceae–Sapindoideae), *Dysoxylum* (Meliaceae), *Syzygium* (Myrtaceae), *Pisonia* (Nyctaginaceae), *Planchonella* (Sapotaceae) and *Vitex* (Verbenaceae) all with one species each, and *Beilschmiedia* (Lauraceae, two spp.). *Freycinetia*, *Pisonia* and *Planchonella* are not among the core tree species of the WTRF (see online Appendix S2). None of the Group 1 species in New Zealand (Table 3) belongs to a primarily tropical–subtropical lowland genus, except perhaps the *Dodonaea* (see Harrington & Gadek, 2009).

The small number of species with tropical–subtropical lowland affinity may well reflect not only the difficulty of access but also the fact that the WTRF was being constantly ‘squeezed’ into the northern tip of New Zealand during the Pleistocene glaciations (see McGlone, Newnham & Moar, 2010a).

A second contrast with Japan is the lack of a rich temperate deciduous flora in the south of Australasia. We suggest that easy access to Japanese WTRF of two contrasted floristic elements (tropical lowland and temperate deciduous) has played a significant part in the recruitment of proportionally more Group 1 species than are found in New Zealand.

It is possible that the lack of Group 1 species in Chilean WTRF, apart from *Nothofagus obliqua*, also results in part from the lack during geological time of a deciduous flora to the south comparable with *Acer*, *Alnus*, *Carpinus* and *Prunus* which have given rise to Group 1 species in Japanese WTRF. By contrast, the lack of Group 1 species in tropical–subtropical genera cannot be explained by a lack of connection to such a flora. It is true that the Atacama Desert to the north, and the Andes to the east of the WTRF, constitute barriers now. However, during the Palaeocene there were present in central Chile two families that are strictly tropical at the present time (Lecythidaceae and Myristicaceae) and there were several that are currently tropical–subtropical in distribution (as defined in Section I): Annonaceae, Arecaceae, Bignoniaceae, Erythroxylaceae and Vochysiaceae plus the sub-families Bombacoideae and

Sterculioideae of the Malvaceae (Hinojosa & Villagrán, 1997; Villagrán & Hinojosa, 1997). A number of these tropical-subtropical families persisted in the Eocene, when there was an increase in the representation of families prominent now in southern temperate forests (Villagrán & Hinojosa, 1997; Gayó, Hinojosa & Villagrán, 2005). There was then a decline in the representation of the tropical-subtropical families in the Oligocene and early Miocene, followed by an increase in the mid-Miocene (Hinojosa, 2005).

What is not known is when the various tropical-subtropical families were lost from central Chile. Troncoso & Encinas (2006) reported the presence of six genera of Annonaceae, two of Melastomataceae and one each of Caryocaraceae, Malpighiaceae and Sapotaceae as late as the Miocene-Pliocene junction (*c.* 5 million years ago). At least one of the genera persisting to this period includes many Group 1A species in the neotropics today: *Miconia* (Melastomataceae). The tropical-subtropical families that persisted to the end of the Pliocene were lost during the repeated glaciations of the Pleistocene, when there were severe reductions in forest area and in species richness (Villagrán & Hinojosa, 1997).

There is yet another possible complicating factor, the inhibition of mesomorphic gap-demanding species by a regular summer dry season; this particularly concerns the Canary Islands where the total number of core species in the STMRF is small and the incidence of Group 1 species is not significantly different from that in the WTRF of any region. The range of mean annual rainfall in the STMRF of the Canary Islands (*c.* 500–850 mm) is lower than in any of the WTRF regions; they have *c.* 700–2400 mm, leaving aside exceptionally wet areas (Table 1).

More significantly the whole of the STMRF in the Canary Islands suffers a lack of rain every summer. Höllermann (1981) pointed out that there are five dry months by the criterion of Walter & Lieth (1960–1967), i.e. when the mean rainfall in mm is less than twice the mean temperature in °C. The total rainfall for the months June–August is only *c.* 15–45 mm (Bañares *et al.*, 1991). Of the five WTRF regions only that in Chile regularly suffers a dry spell in summer, and it affects only about a third of the total area and lasts a much shorter time than that in the Canary Islands. At the northern margin of the WTRF zone, e.g. at Concepción, there is a season with two ‘dry months’ by the definition of Walter & Lieth (1960–1967) (January–February) and a mean total annual rainfall *c.* 1300 mm. Further south, e.g. at Temuco, there is just one ‘dry month’ (January) and a total of *c.* 1200 mm (Luebert & Plissock, 2006). The central and southern parts of the Chilean WTRF zone do not experience a ‘dry month’.

In Japan there is evidence of a short period of reduced rainfall in summer in one relatively small area. At some sites in north-western Shikoku, and on the opposing coast of Honshu (mean annual rainfall *c.* 1150–1450 mm), August is on average markedly drier than the other summer months,

but it is not a dry month by the definition of Walter & Lieth (1960–1967).

All of the rain forests of the Canary Islands are dependent on cloud: both interception of cloud water as an addition to rainfall, and reduction of evapo-transpiration. Accurate assessment of the interception of cloud water by plants is notoriously difficult. However, there have been recent critical measurements that range from 80 mm in three summer months (García-Santos, Marzol & Aschan, 2004) through 110 and 150 mm in two summers (García-Santos & Bruijnzeel, 2011) to 880 mm (Marzol, 2008). It seems likely that most of the forest receives 50–150 mm, and amounts as high as 400–900 mm are confined to certain ridge tops (Fernández, 2002).

The reality of summer water shortage for the plants despite the interception of cloud water has been shown by measurements of the rate of sap flow in some of the most abundant tree species (Jiménez *et al.*, 1996, 1999*b*), changes in osmotic potential and tissue elasticity (González-Rodríguez *et al.*, 1999), and closure of stomata and changes in fluxes of carbon dioxide (Jiménez *et al.*, 1999*a*; González-Rodríguez, Morales & Jiménez, 2002). It is no wonder that the three species found by Arévalo & Fernández-Palacios (1998) to be most abundant within the STMRF are either very closely related to widespread species of Mediterranean Sclerophyll Forest (*Laurus azorica* and *Viburnum rigidum*) or found in such forest at the western end of the Mediterranean Basin (*Prunus lusitanica*).

All of the Group 1 species included in the core list are sclerophylls: *Erica arborea*, *E. scoparia* ssp. *platycodon* and *Morella faya* which flourish at both drier and moister sites. The three soft-leaved relatively light-demanding species in the STMRF, which we have tentatively rated as at the more light-demanding end of the range of Group 2 species (see online Appendix S5), are all excluded from our core list because they are either ‘rather rare’ or ‘extremely rare’ (*Euphorbia mellifera*, *Gesnouinia arborea* and *Sambucus nigra* ssp. *palmensis*). All are absent from the drier forest sites, but the extreme rarity of *Euphorbia mellifera* and *Sambucus nigra* is apparently to a large extent a result of human activity, so that it is not possible to be sure of their tolerances in forest free of human interference (A.B. Fernández-López, personal communication). Nevertheless there is a *prima facie* case that the combination of root competition and summer drought has reduced the incidence of soft-leaved relatively light-demanding species.

To summarize, some of the differences in the incidence of Group 1 species among the six regions studied are likely to be explicable at least in part by the extent-of-disturbance effect (Australia *versus* New Zealand, South Africa and Chile, and Japan *versus* New Zealand and South Africa), but other factors are also important – sometimes more important: soil infertility, presence of aggressive gap-filling bamboo, ease of access to species-rich tropical evergreen and temperate deciduous floras, and possibly lack of water in summer.

(3) Other issues of forest dynamics

Here we consider briefly three disparate topics: the incidence of Group 2 species, variation in tolerance within Group 2 and Group 3 species, and invasion of open sites by shade-tolerators. There is no significant variation among regions in the incidence of Group 2 species among species of Groups 2 and 3 (Section III.7). We might have expected some parallel with the incidence of Group 1 species in the total set.

There is almost certain to be significant variation in the degree of shade-tolerance among both the Group 2 and the Group 3 species we have recognized. As yet there are critical data on the degree of shade tolerated at different stages of development only for Chile (Lusk *et al.*, 2008), and it is highly desirable that the same methodology be applied in other regions of WTRF. It should be accompanied by experimental work which reveals any interactions between the effects of shade and those of nutrient supply (see Grubb *et al.*, 1996) and/or water-shortage (see Sack, 2004).

In work on the temperate forests of the Northern and Southern Hemispheres the idea that species might benefit from shade rather than simply tolerating it was not much discussed in the older literature, but its importance has been demonstrated in more recent physiological and biochemical studies, e.g. those of Murchie & Horton (1997), Naidu & DeLucia (1997), Kitao *et al.* (2000) and Valladares *et al.* (2002) for plants of temperate deciduous forest in the Northern Hemisphere, and those of Tausz, Warren & Adams (2005) and Reyes-Díaz *et al.* (2009) for trees of cool temperate rain forest in the Southern Hemisphere. By contrast, in the wet tropics earlier researchers were more aware of benefit from shade for shade-tolerant species (see Murray & Nichols, 1966), and the phenomenon has been well established in more recent physiological studies, e.g. those of Krause & Winter (1996), Lovelock, Jebb & Osmond (1994), Scholes, Press & Zipperlen (1997) and Matsubara *et al.* (2008). Most of these studies have concerned transitions in growing conditions from shade to bright light, but some have concerned growth in bright light from the start.

While some species might benefit from shade rather than simply tolerating it, the converse applies to other species. Coomes & Bellingham (2011) argue that even long-term survival in deep shade counts for little unless accompanied by height growth. They reviewed data on comparative growth rates of temperate podocarps and angiosperms in deep shade and considered that even though survivorship of some podocarps in deep shade is high, growth into the canopy for some of them (e.g. *Dacrydium cupressinum*) is likely to depend on periodic openings in the canopy above them.

Despite the mounting evidence for photoinhibition of shade-tolerant species, some species that are seen to regenerate commonly in deep shade in TLRF can establish and grow healthily in the open, e.g. on the bared rock and subsoil of extensive roadside cuttings. A clear example in NE Australia is the wind-dispersed *Darlingia darlingiana* (Proteaceae) which was shown experimentally by Bloor & Grubb (2003) to be very shade-tolerant.

We have seen that at least a few Group 3 species of WTRF similarly invade road-cuttings (or landslides or talus slopes or lava flows) in full daylight: *Eurya japonica* and *Rhododendron tashiroi* in Japan, *Melicactus ramiflorus* and *Myrsine australis* in New Zealand, *Eucryphia cordifolia* and *Lomatia ferruginea* in Chile, and *Acmena smithii* and *Pittosporum undulatum* in Australia. As emphasized by Veblen & Ashton (1978), such species must combine ease of dispersal with an ability to grow in the open on a slender nutrient supply. This is especially true of those with very small seeds which fail to compete on roadsides with deeper soils where there is a greater supply of nutrients. The only studies we have found of experimental work on photoinhibition in species of WTRF are those of Castro-Arévalo *et al.* (2008) and Alberdi *et al.* (2009), who compared the light-demanding *Embothrium coccineum*, the intermediate *Gevuina avellana* and the shade-tolerant *Lomatia ferruginea*. The thermal dissipation of excess energy was saturated at a notably lower irradiance in *Lomatia ferruginea* than in the other two species, leaving unresolved the leaf-level mechanisms by which this species can be successful in completely open areas. New work is needed to understand its ability to grow and resist photodamage (as judged by leaf colour) in full daylight. A study on three STMRF species in the Canary Islands showed that the gap-demander *Morella faya* is most resistant to high light, while the shade-tolerant *Laurus azorica* and *Persea indica* were successively more sensitive (González-Rodríguez *et al.*, 2001). Studies on diurnal changes in components of the violaxanthin (V) and lutein epoxide (Lx) cycles in leaves of the four Canarian laurel species in the field were reported by Esteban *et al.* (2007). They found a functional V cycle in all four species but a functional Lx cycle only in *Ocotea foetens*. More work is needed to relate these findings to the extent of high-light tolerance in the various species at different stages of the life cycle.

(4) Soil seed banks

Our review has shown that much is yet to be learnt about soil seed banks in WTRF. There is some evidence that the most abundant species that are at least 'short-term persistent' in the soil are mostly gap-demanders, but some shade-tolerant species also persist in the soil as is often found in both TLRF and in northern temperate deciduous forests (see Jankowska-Błaszczuk & Grubb, 2006). Good examples are *Eurya japonica* and *Rhododendron tashiroi* in Japan and *Macropiper excelsum* and *Melicactus ramiflorus* in New Zealand.

The most general advantage of a seed bank for shade-tolerators is risk-spreading: avoidance of seedling loss to predators, disease, physical damage or unfavourable weather in any given year. Jankowska-Błaszczuk & Grubb (2006) presented evidence for risk-spreading in both temperate and tropical species, and considered the possible advantage to have been unduly neglected for plants in forests. Risk-spreading is most convincingly the chief advantage for shade-tolerators with larger seeds (say 100–500 mg) such as the two New Zealand *Prumnopitys* spp., the seeds of which were found by Beveridge (1967) to be alive after 5 years on the forest floor. For shade-tolerant species with small seeds

(say up to 1–2 mg) such as *Rhododendron tashiroi*, *Eurya japonica*, *Macropiper excelsum* and *Meliclytus ramiflorus*, a major advantage of a seed bank may be an ability to invade promptly various kinds of litter-free micro-sites on soil disturbed within the forest: pit-sides and mounds made by tipped-up standing dead trees, heaps and mounds made by animals, micro-landslides within the forest, and places where the litter has been scraped away by a thick heavy trunk sliding down a slope (see Fig. 1 in Grubb, 1996).

In view of the findings summarized by Jankowska-Błaszczuk & Grubb (2006) and by Dalling & Brown (2009), it would be particularly interesting to know whether, in general, the most persistent species in the soil seed bank of WTRF are among the largest present (as in TLRF) or among the smallest (as in northern temperate deciduous forest).

There is a need for not only further work on which species are in the persistent seed bank but also experimental work on the effective triggers to germination for species with different-sized seeds. Orozco-Segovia, Sánchez-Coronado & Vázquez-Yanes (1993), Kyereh, Swaine & Thompson (1999), Daws *et al.* (2002) and Pearson *et al.* (2002) reported evidence that in TLRF smaller-seeded species are stimulated to germinate by the amount of light and/or the red/far-red ratio (and are best suited to smaller canopy gaps) while larger-seeded species are stimulated by increased diurnal fluctuations in temperature (and best suited to larger canopy gaps). Will the same be found for trees in WTRF? Allowance should always be made for changes in sensitivity as the ungerminated seeds age, such as found by Orozco-Segovia & Vázquez-Yanes (1989) and Metcalfe (1996).

(5) Differences between functional groups in seed mass

It has long been known that at the world scale there is a trend to larger seed size in taller plants (Thompson & Rabinowitz, 1997), but from the time of Salisbury (1942) onward ecologists have generally made comparisons of seed size between more and less shade-tolerant species without regard for mature height (see Grubb, 1998*b*). This becomes a serious issue if, in a given forest type, the shade-tolerators and gap-demanders differ markedly in mature height. In fact, we did not find the usual significant trend in seed size with mature height in trees and tall shrubs in three of the five regions of WTRF that we studied (Chile, South Africa and Australia) or in the STMRF of the Canary Islands, only in the WTRF of Japan and New Zealand.

For the WTRF in New Zealand we found that the largest mean seed mass increased markedly with final plant height but the smallest mean seed mass did not do so, a pattern shown for TLRF by Grubb, Coomes & Metcalfe (2005). For the WTRF of Chile and South Africa a previously unrecorded pattern was found; the largest mean seed mass increased with increasing height, and the smallest mean seed mass decreased with increasing height. Both patterns can be interpreted in terms of the range of feasible seed sizes increasing dramatically with whole-plant size.

The fact that there is no significant difference in final height between species in Groups 1 and 3 in WTRF in the three regions where there are many Group 1 species (Japan, New Zealand and Australia) makes our interpretation of the comparison of seed mass values more secure. In New Zealand the Group 3 species had greater mean seed mass than the Group 1 species, the result found most often since the time of Salisbury (1942), and also suggested by the trend in WTRF in the regions where there are extremely few Group 1 species (Chile and South Africa). The same result was found in all seven intrafamilial intergeneric comparisons and the one intrageneric comparison made without reference to final height (Table 10).

More interesting are the results from Japan and Australia where the seed mass values of Group 1 and Group 3 species overlap widely and there is no significant difference between the means (Fig. 5). This result arises because there are small-seeded shade-tolerant species and large-seeded gap-demanders, a position that is common in TLRF (Grubb, 1998*a*).

The tiny-seeded shade-tolerators are unable to establish where the substratum is covered by litter. They need either steep 'pico-sites' at soil level from which litter is shed, as emphasized by Kohyama & Grubb (1994) for Japan and by Metcalfe, Grubb & Turner (1998) for SE Asia, or fallen logs and tree-fern trunks as noted by various authors reporting on WTRF in New Zealand and Chile from Pope (1924) onward (see Sections III.1 and III.2).

Plants tolerant of deep shade do not need especially large seeds in order to survive in low light. This point was already appreciated by Glenny (1986), and was independently emphasized by later authors: Kohyama & Grubb (1994), Metcalfe & Grubb (1995) and Grubb (1996). It is notable that in three of the five regions of WTRF the seeds of the smallest-seeded Group 3 core species are smaller than those of the smallest-seeded Group 1 species (Japan, Chile and South Africa; Tables 2–4 and 5); the same phenomenon is found in SE Australia if the non-core species *Eucryphia moorei* is admitted (see Section IV.2). Although none of the shade-tolerant trees on the Canary Islands has tiny seeds, one of the widespread shade-tolerant medium-height shrubs (*Hypericum grandifolium*, 2 m) was found by us to have a mean seed mass of 0.05 mg. This is still not as low as the value of 0.03 mg for the Group 1 taxon *Erica scoparia* ssp. *platycodon* (6 m).

It is also significant that Augspurger (1984), Boot (1996) and Bloor & Grubb (2003) all showed that among shade-tolerant species of TLRF survival of very deep shade (e.g. 0.2–1.0% daylight) was not correlated with seed size. Grubb & Metcalfe (1996) argued that the significance of greater seed mass in shade plants (where it is not primarily an attractant to large animals that disperse the seeds) is that it enables seedlings to emerge through litter, to root down through litter, to resist being scratched out of the soil by litter-feeding birds, to make possible recovery after being partially eaten, to resist more prolonged drought and to compete more effectively for light.

The twin advantages to a gap-demander of having smaller seeds are (i) they are likely to be more highly dispersible and (ii) there is an associated increase in the number of seeds. Together these two effects have the potential to increase the number of canopy gaps invaded. However, it is clear that some gap-demanders have evolved large seeds that are so attractive to disperser animals that they reach many gaps despite their larger size and reduced numbers. Two of the species with the largest seeds in Japanese WTRF are Group 1 species: *Aleurites cordata* and *Sapindus mukorossii* (Table 2). Dr T. Riyou (personal communication) found that seeds of *Aleurites cordata* that have turned black and fallen to the ground are taken by a rat (*Rattus* sp.), while Professor T. Yumoto (personal communication) suggested that the jungle crow (*Corvus macrorhynchos*) may also be involved in dispersal. Wakasugi *et al.* (2001) reported that a murine rat is the major disperser of *Sapindus mukorossii*. The North American *S. drummondii*, which also produces large one-seeded fruits, is dispersed by the ringtail, *Bassariscus astutus*, a member of the racoon family (Procyonidae) (Taylor, 1954). Neither *Aleurites cordata* nor *Sapindus mukorossii* was mentioned in the wide-ranging studies of Noma & Yumoto (1997) and Yumoto *et al.* (1998) on dispersal by birds and by macaque monkeys (*Macaca fuscata yakui*) on Yakushima.

Group 2 species were identified in five of the six regions studied. In New Zealand their mean seed mass was significantly smaller than that of the Group 3 species (unpaired $t_{63} = 2.27$, $P = 0.027$; Fig. 5). Although the means for Group 2 species were also lower in Chile and South Africa, they were not significantly so ($P > 0.2$). The exceptional region is Japan, where Group 2 species have greater seed mass than Group 3 species (unpaired $t_{36} = 4.09$, $P < 0.001$; Fig. 5); here the Fagaceae make up 10/25 Group 2 species. They are dispersed by animal species that destroy a large part of the crop, chiefly birds and rodents, but also macaques (Yumoto *et al.*, 1998).

VI. CONCLUSIONS

(1) There are significant problems in how to make a critical comparison of the different regions of WTRF: differences in the amount and type of research carried out on the light climate and forest dynamics, subjectivity in the classification of species (especially for those in Groups 2 and 3), lack of coverage of differences in regeneration behaviour (e.g. sprouting *versus* non-sprouting) across the ranges of individual species, cases where human impact has been so great that it is difficult to be sure whether or not the light-demanding tree species common in the forest today had a role in the forest under natural conditions, and most seriously lack of exactly comparable data on gap sizes and proportions of forest area entering the gap phase per unit time as a result of different kinds of disturbance, particularly disturbance events with a longer return time. Nevertheless a worthwhile preliminary analysis is possible because many of

the differences among regions in disturbance regime and in proportion of gap-demanding species are quite gross.

(2) The incidence of Group 1 species among the core species declines along the following series: Australia 15/21 species, Japan 36/97, Canary Islands 3/14, New Zealand 12/77, South Africa 2/23 and Chile 1/28. The differences between the Australian forest and the forests in New Zealand, South Africa and Chile (but not those in Japan or the Canary Islands) are statistically significant, as are the differences between the Japanese forest and the forests in New Zealand, South Africa and Chile. Some of these differences are consistent with the extent of opening up of the canopy by disturbance events, but we argue that other factors are also involved, and may be more important in some cases: soil infertility, presence of aggressive gap-filling bamboo, limited access during evolutionary time to lineages able to give rise to gap-demanding species, and possibly lack of water in summer.

(3) The incidence of Group 2 species among Groups 2 and 3 declines in the series: New Zealand 28/65, Japan 25/61, South Africa 8/21, Chile 5/27, Canary Islands 1/11 and Australia 0/6, but none of the differences is significant.

(4) Experiments in Japan and New Zealand show that the proportion of species probably in the 'short-term persistent' soil seed bank is greater for Group 1 species than for Group 2 and Group 3 species, but that some Group 3 species do build up large numbers of persistent seed in the soil. Preliminary studies for WTRF in South Africa and Australia have found only Group 1 species with an appreciable amount of persistent seed, and there may be none in the soil of STMRF in the Canary Islands. Very little is known as yet of the seed bank in Chilean forests.

(5) The trees of WTRF in Chile, South Africa and Australia, and of STMRF in the Canary Islands, do not carry significantly larger seeds on taller-growing species. The general trend in WTRF is for the largest mean seed mass to increase with tree height, while there is either no appreciable change in the smallest mean seed mass or it decreases with tree height.

(6) The trees of WTRF in Japan and Australia show that light-demanders do not always have on average significantly smaller seeds than shade-tolerators; in WTRF in New Zealand there are significant differences between Group 1 and Group 3 only among the taller species.

(7) Outside Japan the only Group 1 species in WTRF with a seed of mean dry mass > 100 mg is in Australia, and the only Group 2 species with a mean dry mass > 500 mg are in New Zealand and Chile. By contrast, Group 3 species with seed of mean dry mass < 1 mg are found in WTRF not only in Japan but also in New Zealand, Chile and Australia, and there are shade-tolerant shrubs with such seeds in STMRF on the Canary Islands. Evolution of gap-demanding species with large seeds (dependent on dispersal by larger animals) has been much less common than evolution of shade-tolerant species with very small seeds (dependent on exploitation of specialized micro-sites in adequately moist regions).

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Differences between warm temperate rain forest (WTRF) and other forests, deciduous species, and exceptions to generalizations about life forms present.

Appendix S2. Definition of extents of warm temperate rain forest (WTRF) and subtropical montane rain forest (STMRF) regions, notes on the vegetation of adjacent areas, human impacts, and how the lists of core species were made.

Appendix S3. Supplementary information on soil seed banks.

Appendix S4. Commentary on all sources from which seed mass values were obtained.

Appendix S5. Supplementary observations on regeneration and morphology of selected groups of species.

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