Article

Why Do Some Evergreen Species Keep Their Leaves for a Second Winter, While Others Lose Them?

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Abstract: In subtropical montane semi-moist forest in SW China (SMSF), a large majority of evergreen tree and tall shrub species was found to have only one cohort of old leaves in early spring. In contrast, almost all species of evergreen tree and tall shrub in warm temperate rain forest (WTRF) in Japan and sclerophylls in Mediterranean-climate forest (MSF) of the Mediterranean Basin have two or more cohorts of old leaves in early spring; they drop their oldest cohort during or soon after leaf outgrowth in spring. Japanese WTRF has no dry season and MSF a dry summer. SMSF has a dry winter. On four evergreen *Rhododendron* species from SW China with only one cohort of old leaves in spring when in cultivation in Scotland, the majority of leaves in the senescing cohort fell by the end of December. We hypothesize that with dry winters, there is an advantage to dropping older leaves in autumn, because there is a low chance of appreciable positive assimilation in winter and a high chance of desiccation, reducing the resorption of dry mass and mineral nutrients from ageing leaves. Our hypothesis may be extended to cover evergreens at high altitude or high latitude that experience cold soils in winter.

Keywords: leaf longevity; dry winters; Yunnan; subtropical montane semi-moist forest; *Rhododendron*

1. Introduction

In the extensive literature on leaf longevity, scant attention has been paid to the question of why evergreen temperate plants and subtropical montane plants drop their old leaves when they do [1]. The current understanding of the advantage of having evergreen leaves in the temperate zones goes back to the seminal paper of Small [2], which provided a rationale in terms of leaves lasting for two or more growing seasons and did not consider the function of the leaves in the coolest months. He was concerned with plants of nutrient-poor soils and argued, in effect, that the evergreenness of many woody plants of nitrogen-poor soils in the Northern Hemisphere is incidental, and their advantage lies in keeping the leaves for two or more growing seasons. That enables the evergreen leaf to fix over its life-time more carbon per unit N than is possible for a deciduous species, even though the maximum instantaneous rate of fixation per unit N is lower in longer-lived leaves. The same argument can be applied to leaves in deep shade, where the return on unit C invested may be as important as that on unit N. In the last forty years, this interpretation of the value of longer leaf-life has become generally accepted for plants on nutrient-poor soils and in deep shade and, to some extent, those of dry sites [1,3–7].

In this paper, we are concerned with the contrast in leaf persistence during winter between the evergreens in subtropical lower montane semi-moist forest (SMSF) and those in warm temperate rain forest (WTRF) and Mediterranean-climate sclerophyll forest (MSF). Evergreens in WTRF in Japan are known to suffer continual loss of leaves from a cohort [8], like trees in tropical lowland rain forest, where there is no cold or dry winter season [9]. However, as shown in Table 1, leaf fall in most species is concentrated in spring in the period during and after leaf expansion [10]; most species carry two or more cohorts of old leaves in the early-mid spring [8]. The situation is similar for sclerophylls in the Mediterranean Basin with leaf fall concentrated in the spring [4,11–15], although on some species, leaves last only one year at some sites (Table 2).

Table 1. Months of outgrowth of new leaves and of major leaf fall for species of tree and tall shrub in warm temperate rain forest (WTRF) in Japan over two years, 1994 and 1995 (from figure 4 of Nitta and Ohsawa [10]), and in Mediterranean-climate sclerophyll forest (MSF) in France from the text of Floret *et al.* [13]; the records in figure 3 of Castro-Díez and Montserrat-Martí [14] for Spain are similar to those of Floret *et al.* [13].

Species	Family	Months when new leaves grew out	Months in which leaf fall was concentrated
WTRF *Myrsine neriifolia*	Primulaceae	April–May	April–June and September–December
Neolitsea sericea	Lauraceae	April–May	May–December
Cleyera japonica	Pentaphylacaceae	April–May	July–October
Symplocos prunifolia	Symplocaceae	April–May	Continuous
Quercus salicina	Fagaceae	May	March–May
Persea thunbergii	Lauraceae	May	May–September May–October (1995)
Cinnamomum japonicum	Lauraceae	May	May–June, August– September and December–February (1994–1995)

Table 1. *Cont.*

Species	Family	Months when new leaves grew out	Months in which leaf fall was concentrated
Quercus acuta	Fagaceae	May–June	May–November
Illicium religiosum	Illiciaceae	May–June	June–December
Eurya japonica	Pentaphylacaceae	May–September and December–February	May–September and November–February
MSF			
Myrtus communis	Myrtaceae	March–June	May–June
Pistacia lentiscus	Anacardiaceae	March–June	Not recorded *
Viburnum tinus	Adoxaceae	March–June	May–June
Pinus halepensis	Pinaceae	March–July	Peaks in spring
P. pinaster	Pinaceae	March–July	July–August
Buxus sempervirens	Buxaceae	March–August	May–July
Quercus ilex	Fagaceae	April–May (+ some waves to September)	May + September to December
Arbutus unedo	Ericaceae	April–June	May–June
Quercus suber	Fagaceae	April–June	June–August
Phillyrea angustifolia	Oleaceae	April–August	April–July
Quercus coccifera	Fagaceae	May (+ some August–September)	Mostly May–July
Rhamnus alaternus	Rhamnaceae	May–August	May–August

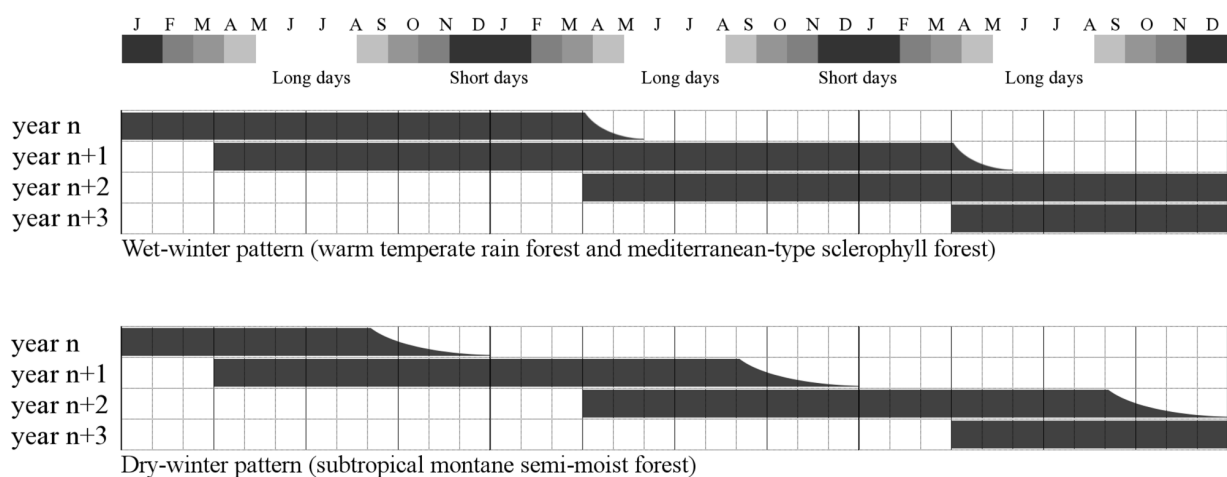* June-October according to Montserrat-Martí and Pérez-Rontomé [15].

Table 2. Mean leaf longevities recorded for sclerophyll species in Greece [12], France [13] and Spain [16]; the longevities given in months in [12] and [13] have been converted to years, and all values reduced to no more than two significant figures.

Species	Mean leaf longevity (year) determined in Greece	Mean leaf longevity (year) determined in Spain	Range of longevity (year) determined in France
Pinus halepensis		3.1	2–3, most <2.5
P. pinea		3.0	
P. pinaster		2.1	(2)–3+, mostly >3
Quercus ilex		2.0	2–3
Q. coccifera	1.1	1.3	2.1–2.3
Arbutus unedo	1.2		2 (–3)
Phillyrea angustifolia			2.1–2.2
Pistacia lentiscus	0.94		Not >2
Ceratonia siliqua	2.0		
Olea europaea	2.0		
Myrtus communis	1.9		1.1–1.2
Buxus sempervirens			1–2
Quercus suber		1.3	1.1–1.3
Arbutus andrachne	1.1		

In contrast to what has been reported for WTRF in Japan and MSF in the Mediterranean Basin, we have found for many of the evergreen trees and shrubs in SMSF that in early spring (April), there is only

one cohort of old leaves present, while or before the new leaves expand, and there is no sign of ageing leaves about to fall. It appears that leaves drop after their second summer, but before the following spring. It is possible that they lose the leaves mostly in autumn. The suggested contrasting patterns of leaf fall are shown in Figure 1.

Figure 1. Theoretical patterns of seasonal change in the numbers of leaves in successive cohorts on evergreen trees with contrasting times of leaf fall related to different amounts of rainfall in winter.

Wet-winter pattern (warm temperate rain forest and mediterranean-type sclerophyll forest)

Dry-winter pattern (subtropical montane semi-moist forest)

SMSF experiences a dry period from December to April in contrast to the WTRF of Japan and other areas where there is no strongly dry season [17], while in the Mediterranean Basin and other areas with a "Mediterranean-type" climate, the summer is dry (Figure 2). It seemed to us reasonable to relate the difference in the timing of leaf fall to the presence or absence of winter aridity.

Figure 2. Climate diagrams of the type introduced by Walter and Lieth [18] constructed for sites representative of subtropical montane semi-moist forest (Kunming, winter-dry), warm temperate rain forest (Fukuoka, no dry season) and Mediterranean-climate sclerophyll forest (Agrigento, summer-dry); for each site, altitude, mean annual temperature and mean annual rainfall are given at the top of the diagram; where mean monthly rainfall exceeds 100 mm, the amount in excess of 100 mm is given using a compressed scale (one tenth of that used for values up to 100 mm); the original data were taken from the WorldClim Global Climate Data website [19].
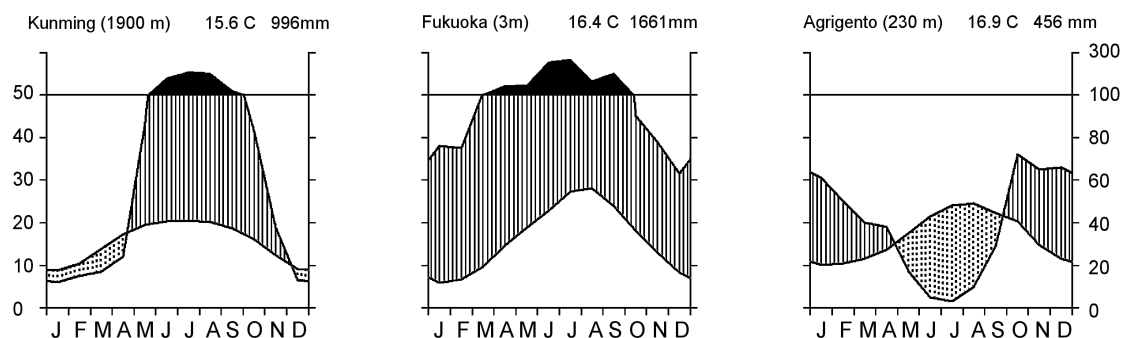
SMSF is found in Yunnan (SW China) between 23°20′ and 26°40′ N at an altitude of 1300–2650 m [20] and was widespread before a large part of it was destroyed by humans. Song [21] reported that it resembles WTRF, but the leaves of the taller trees are more scleromorphic, while, in the ground layer, ferns are less abundant and less diverse, but graminoids and geophytes are more common. There are relatively fewer species of shade-tolerant small trees, treelets, climbers and vascular epiphytes. At the level of family and genus, there is a large overlap floristically with the WTRF of eastern China and Japan, but the Fagaceae are clearly dominant over the Lauraceae, and there are very few Rubiaceae in the understorey.

Our original observations were made in Yunnan in the spring of 2008, and they were followed up in 2009–2011 on plants from SW China in cultivation outdoors in Scotland. In this paper, we provide the first-ever reports on the timing of leaf fall in a range of evergreen species from SW China growing in Scotland. We also provide a testable multi-part hypothesis as to exactly how it could be advantageous for leaves in the SMSF to be shed during their second cool season before the water shortage reaches its peak intensity and why it is worthwhile for evergreens in WTRF and MSF to keep their leaves for a second winter despite the reduced irradiance and relatively low air temperatures. Finally, we consider parallels with leaf shedding by evergreens of cold temperate regions where the winter is not lacking in precipitation, but the soil becomes so cold that the uptake of water is inhibited, and air temperatures are very low. Species nomenclature follows the new *Flora of China* [22], and assignment to families follows the APweb site [23].

2. Material and Methods

2.1. Observations in Yunnan

Observations on the numbers of cohorts of old leaves were made at two different SMSF sites (on April 12 and 14, 2008). The first was adjacent to the Bamboo Temple (Qiungzhu si) near Kunming at *ca*. 2130–2150-m altitude (Longitude 102°37′20″ E, Latitude 25°04′12″ N); the forest was mapped by Wu [20] as in his *Castanopsis orthacantha* formation. The second site was on the Jizu Shan, above the temple, at *ca*. 2300–2550 m (100°22′40″ E, 25°57′50″ N); Wu [20] also mapped this forest as in his *Castanopsis orthacantha* formation, but actually it was dominated by *C. delavayi*, which is normally absent from the *C. orthacantha* formation and is characteristic of somewhat drier areas.

We made records for all of the evergreen species we could identify, which covered around 95% of individual trees and tall shrubs. Records of the numbers of cohorts of leaves were made on a minimum of three trees or shrubs for almost all species and checked on larger numbers of trees or shrubs of the commonest species. Only a single plant of *Osmanthus yunnanensis* was found. The trees studied were chosen haphazardly while walking along paths through the forests. For almost all species (not *Cyclobalanopsis glaucoides*; see the Results), observations were confined to shoots up to 3 m above ground level. Separation of cohorts was based on ring scars on the stems, differences in the length of internodes and subtle differences in leaf colour. We report the two species that gave results that were inconsistent between the two sites and the one species on which it was impossible to separate cohorts confidently.

Observations were also made in *Rhododendron* scrub with scattered *Tsuga dumosa* on south-facing slopes on the eastern side of the Cang Shan (160°05′24″ E, 25°41′24″ N) west of Dali at about 3100–3200 m, just above the secondary pine forest, which had replaced SMSF; here, we recorded the numbers of cohorts of leaves on five species of *Rhododendron*, including *R. decorum*, which is recorded by Wu [20] in four SMSF associations. Again at least three plants per species were studied.

2.2. Initial Survey in Scotland

We studied species of *Rhododendron* from Yunnan and adjacent provinces, partly because there is a large and critically labelled collection at the Royal Botanic Garden Edinburgh (the Inverleith site in Edinburgh and the regional garden at Benmore) and partly because it is the most speciose genus of woody plants in the SMSF. Wu [20] recorded nine species in his descriptions of 12 associations. The mean values of the blade lengths recorded for the nine species [24] are 1.9 cm *R. microphyton*, 2.6 cm *R. spiciferum*, 5 cm *R. siderophyllum*, 6.8 cm *R. spinuliferum*, 8 cm *R. leptothrium*, 8.5 cm *R. moulmainense*, 10.5 cm *R. irroratum*, 11 cm *R. delavayi* and 12 cm *R. decorum* (overall mean: 7.4 cm). The blade lengths of all nine species are short relative to the total range found in the genus in southern China: 0.5–45 cm [24].

Our initial survey covered all of the evergreen species of *Rhododendron* from SW China (Yunnan and/or Xizang and Sichuan) that we could find in a healthy state at Inverleith and/or Benmore. The Inverleith garden is in Edinburgh, and that at Benmore is *ca*. 110 km west and has a much higher rainfall. The annual mean for 1959–2010 was 2358 mm (range 1807–3067) at Benmore *vs*. 626 mm (range 436–908) at Inverleith; at both sites, the rainfall is fairly evenly distributed through the year. The two sites do not differ greatly in the incidence of air frost (48 days per year in 1971–2010 at Benmore *vs*. 52 days per year in 1959–2010 at Inverleith), but the lowest recorded temperature is not as low at Benmore as at Inverleith (−10.0 °C *vs*. −15.6 °C). The higher rainfall makes it possible to grow many less drought-tolerant species at Benmore.

We studied 48 species in healthy condition at Benmore and 18 at Inverleith on June 2 and 3, 2009, respectively. Most of the species had been collected in types of forest or thicket wetter than SMSF, some having very large leaves, e.g., *R. rex*, *R. seminoides, R. magnificum* and *R. praestans* with mean lamina lengths of 25, 25, 26 and 27 cm, respectively [24].

Except for one case of special interest, we report the cohort number only for those species that gave consistent results for at least three individuals. As with our observations in China, the separation of cohorts was based on ring scars on the stems, differences in the length of internodes and subtle differences in leaf colour.

We recognized four groups of species based on the number of cohorts of old leaves present, in addition to any new leaves expanding: those with more than three, three, two or one, respectively. Studies on the North American species, *Rhododendron maximum*, have shown that the loss of leaves of a given cohort can begin and finish gradually [25,26]. Thus, on the plants of species we assigned to the groups with two or more cohorts of old leaves, there were cases where some shoots had lost some of the leaves from the oldest cohort. Similarly, in the case of plants of species assigned to the group with one cohort of old leaves, some shoots had a few leaves left from the previous cohort.

Twenty four species at Benmore, 6 at Inverleith and two studied at both sites yielded clear and consistent numbers of cohorts. The remaining species studied were too variable (from plant to plant or branch to branch) in the number of cohorts of mature leaves to be put in one of the four groups. For each of three species studied at Benmore, records were made for two subspecies; in all three species, the subspecies had different numbers of cohorts of old leaves.

2.3. Critical Observations on Leaf Fall in Scotland

Our critical study of the timing of leaf fall was confined to the Edinburgh (Inverleith) garden. Here, the winter is not lacking in rainfall as in the SMSF. As noted above, the annual mean rainfall was 626 mm in 1959–2010 (719 mm in 1981–2010), of which 32% fell in the months December–March; at the Kunming weather station at 1891-m altitude (near the mean altitude of SMSF) in 1971–2000, it was 1011 mm, of which 6% fell in December–March. The annual mean air temperature at Inverleith is much lower than at the Kunming station (8.2 *vs.* 14.6 °C), and likewise, the mean maximum air temperature of the hottest month 19.1 °C (July) *vs.* 24.6 °C (May). However, the mean minimum air temperature in the coldest month (December in both cases) is very similar at the two sites (1.3 °C Inverleith, 1.5 °C Kunming). The absolute minimum air temperature recorded at Inverleith is appreciably lower than that recorded at Kunming (−15.6 °C *vs.* −7.8 °C).

We do not know the relative importance of lower temperatures, shortened day-length and leaf desiccation in triggering the fall of old leaves in Yunnan. However, we think it likely that the first two factors have the greatest impact, because in that case the leaves can fall before any problems arise with the resorption of nutrients from dried tissues. The results of our study can be only suggestive of what happens in Yunnan, but we expect that similar results will be found in due course for plants in their native habitats.

The five species that we used are in five different subsections of *Rhododendron* and in three different subgenera, and all are native to SW China (Table 3). *Rhododendron rubiginosum* was chosen because we saw it in China and in Scotland with only one cohort of old leaves in early spring; *R. decorum* was chosen because we saw it in China and in Scotland with one cohort of old leaves in early spring on some shoots and two cohorts on others and because it was recorded by Wu [20] in SMSF.

R. pubescens was chosen because it belongs to subsection Scabrifolia, which is especially well represented in the drier parts of SW China, and because it is closely related to *R. spiciferum.* The latter was recorded by Wu [19] in two SMSF associations, and we saw it in China to have only one cohort of old leaves in the spring. *R. wallichii* and *R. wardii* were chosen because in Scotland they had only one cohort of old leaves at the time when new leaves were expanding.

Three healthy shrubs of each species were used. As shown in Table 3, for two species, all three individuals came from material collected in Yunnan, and for another two species, one came from Yunnan and the other two from an adjacent province (SW Sichuan or SE Xizang). For only one species (*R. wallichii*) did the material come from further west (Bengal and Nepal).

On June 15–17, 2009, three well-lit healthy shoots were marked with a discreet tag, and the leaves in the cohort preceding the most recent one were counted. The mean number of leaves per shoot in the study cohort varied with species from 4.88 to 9.44, and therefore, the total number of leaves per species

from 44 to 85 (Table 3). Thereafter, shoots were recorded at weekly intervals until January 5, 2011, by which time all but three of the 314 studied leaves had fallen. Two shoots on one plant of *R. decorum* died in December, 2009–January, 2010, bringing the number of study leaves for that species to 54.

Table 3. The subgenera, subsections and natural distributions of the species of *Rhododendron* growing in the Royal Botanic Garden Edinburgh at Inverleith used for monitoring the timing of leaf loss, the provenances of the three plants used per species and mean numbers of leaves studied per shoot; nomenclature and subgeneric assignments follow Fang *et al.* [24].

Species	Subgenus and subsection	Natural distribution *	Provenance	Mean number of leaves studied per shoot
R. decorum ssp. *decorum*	Hymenanthes: Fortunea	G, S, X, Y; M	2 NW Yunnan 1 W Yunnan	8.0 (reduced by shoots dying to 6.0)
R. pubescens	Pseudorhodorastrum: Scabrifolia	S, Y	3 Yunnan	9.4
R. rubiginosum var. *rubiginosum*	Rhododendron: Heliolepida	S, X, Y; M	1 NW Yunnan 2 SW Sichuan	9.4
R. wallichii	Hymenanthes: Campanulata	X; B, I, N, S	1 Bengal 2 Nepal	4.9
R. wardii var. *wardii*	Hymenanthes: Campylocarpa	S, X, Y	1 W Yunnan 2 SE Xizang	5.1

* Chinese provinces: G, Guizhou; S, Sichuan; X, Xizang; Y, Yunnan. Other countries: B, Bhutan; I, India; M, Myanmar; N, Nepal, S, Sikkim.

Regarding changes in leaf colour during senescence, a check was made at the start; only *R. wallichii* and *R. wardii* had any leaves turning from green to yellow or brown (two out of 44 and three out of 46, respectively). The number of leaves on each shoot at least partially changed from green was registered at each recording. For those species and individual shrubs on which leaves lost their green colour at least partially before dropping, we obtained an estimate of how long individual leaves remained on the plant in a partially non-green condition. We assumed that on any given shoot, no leaf fell before it ceased to be wholly green. Thus, for example, if there were four green and two no longer wholly green ones on a shoot at Time 1, then only two green and two not wholly green ones at Time 2, we assumed that the two that were not wholly green at Time 1 had fallen off, while two of the four that were green at Time 1 had turned not wholly green.

3. Results

3.1. Observations on Cohort Number in Yunnan

At the SMSF sites, thirteen species in eight families were seen with only one cohort of old leaves in mid-April, and seven of these had new leaves beginning to expand (Table 4). In contrast, only five species in four families spread over the two study sites were recorded consistently with two cohorts of

old leaves, and only one with three cohorts (Table 4); only one of these six species had new leaves expanded.

Table 4. Numbers of cohorts of old leaves recorded on most shoots of evergreen tree and shrub species at two sites in subtropical montane semi-moist forest and at one site in *Rhododendron* scrub in Yunnan in mid-April 2008; species that also had some very young leaves are marked with an asterisk.

Family	Species	Site
One cohort		
Araliaceae	*Metapanax delavayi**	2
Ericaceae	*Rhododendron spiciferum*	1
	R. cyanocarpum	3
	R. racemosum	3
	R. rubiginosum	3
	R. xanthostephanum	3
Fagaceae	*Castanopsis orthacantha**	3
	Lithocarpus dealbatus*	1
	Castanopsis delavayi	1
	Lithocarpus variolosus	2
Myricaceae	*Myrica nana**	2
Oleaceae	*Osmanthus yunnanensis*	1
Pentaphylacaceae	*Eurya* cf. *nitida**	2
	Ternstroemia gymnanthera*	2
Sabiaceae	*Meliosma yunnanensis*	2
Theaceae	*Schima argentea*	2
	Schima sp.*	1
Two cohorts		
Buxaceae	*Sarcococca hookeriana*	2
Ericaceae	*Craibiodendron yunnanense**	1
	Pieris formosa	1
Magnoliaceae	*Michellia yunnanensis*	1
Rosaceae	*Laurocerasus* cf. *zippeliana*	1
Three cohorts		
Theaceae	*Camellia pitardii*	2

†Sites: 1 = *Castanopsis orthacantha* formation near Kunming; 2 = *Castanopsis delavayi* formation on the Jizu Shan; 3 = *Rhododendron* scrub on the Cang Shan; for details of these sites see Materials and Methods.

For one species at Site 1, *Cyclobalanopsis glaucoides* (Fagaceae), we examined the whole crowns with binoculars; they had on some branches only newly expanded leaves and, on others, one cohort of senescing leaves plus newly expanding leaves; it seems likely that for most of the year, this species carries only one cohort of leaves.

Two common species varied in the number of cohorts of old leaves (one or two) between the two sites: *Myrsine africana* (Primulaceae) and *Viburnum cylindricum* (Adoxaceae). In *Vaccinium* cf. *sprengelii* (Ericaceae), it was not possible to separate cohorts confidently.

At the *Rhododendron* scrub site, four of the five evergreen species were found to have only one cohort of old leaves (Table 4); on the fifth, *R. decorum*, some shoots had only one cohort of old leaves, but others carried two.

3.2. Observations on Cohort Number in Scotland

Of the 35 species and subspecies for which we obtained clear results, 16 (47%) lost their oldest cohort of leaves before the new ones expanded and possibly did so months earlier (Table 5). The mean length of the leaf blade of species that had only one cohort of old leaves in spring is appreciably smaller than that of species with two such cohorts and that of those with three such cohorts: 6.1 ± 0.80 (SEM) cm *vs.* 12.9 ± 2.3 and 13.5 ± 2.9. The significance of the differences in mean length of leaf blade among the three groups was tested using ANOVA: *F* = 5.536; *p* = 0.0088. Tukey tests revealed the following probabilities for comparisons between groups: one cohort *vs.* two *p* = 0.014, one cohort *vs.* three *p* = 0.062, and two cohorts *vs.* three *p* = 0.985.

Table 5. The normal maximum longevity of leaves of *Rhododendron* species from SW China growing at Benmore (most species) and/or Inverleith, based on observations made on June 2–3, 2009, together with mean leaf blade lengths and distributions taken from Fang *et al.* [24]; (BI), studied at Benmore and Inverleith; (I), studied at Inverleith; abbreviations of provinces; G, Guizhou; S, Sichuan; X, Xizang; Y, Yunnan.

| Species, subspecies and variety	Mean length of leaf blade (cm)	Usual lower altitudinal limit (m)	Usual upper altitudinal limit (m)	Provinces where recorded
Leaves lasting >3 years				
R. strigillosum	12.0	1600	3800	S, Y
Three cohorts of old leaves present in spring				
R. faucium	8.0	2600	3400	X
R. rieri (I)	10.3	1700	1800	S
R. insigne	10.5	700	2000	S
R. arizelum	14.0	2500	4000	X, Y
R. rex ssp. *rex*	24.5	2300	3300	S, Y
Two cohorts of old leaves present in spring				
R. haematodes ssp. *haematodes*	5.1	3200	4000	Y
R. dichroanthum ssp. *apodectum*	5.5	2600	3600	Y
R. sanguineum var. *sanguineum*	5.9	2800	4300	X, Y
R. neriiflorum ssp. *neriiflorum*	6.5	2500	3600	X, Y
R. piercei	7.5	3900	4200	X
R. sperabile (I)	9.1	2600	4200	Y

Table 5. *Cont.*

Species, subspecies and variety	Mean length of leaf blade (cm)	Usual lower altitudinal limit (m)	Usual upper altitudinal limit (m)	Provinces where recorded
R. bureavi	10.0	2800	4500	S, Y
R. arboreum ssp. *arboreum*	10.5	1500	3600	X
R. argyrophyllum	10.5	1600	2300	G,S, Y
R. seminoides	20.5	3500	3900	X, Y
R. rex ssp. fictolacteum	24.5	2900	4000	S, X, Y
R. magnificum	26.0	1800	2400	X
R. praestans Only one cohort of old leaves present in spring	26.5	3100	4200	X, Y
R. pubescens (I)	2.2	2000	2600	S, Y
R. hemitrichotum (I)	2.3	2200	4000	S, Y
R. fletcherianum	3.8	3400	3400	X, Y
R. davidsonianum	4.3	1500	2800	S
R. searsiae	4.3	2300	3300	S
R. concinnum	5.0	2300	3000	G, S, Y
R. siderophyllum (I)	5.0	1800	3000	G, S, Y
R. thomsonii	5.0	3000	4000	X
R. haematodes ssp. *chaetomallum*	5.1	3100	4000	X, Y
R. rubiginosum var. *rubiginosum* (BI)	5.8	2800	3600	S, X, Y
R. cerasinum	6.5	3200	3800	X
R. wardii (I)	6.5	3000	4600	S, X, Y
R. heliolepis	8.5	3000	3700	S, X, Y
R. neriiflorum ssp. *appropinquans*	9.5	2100	3600	X, Y
R. wallichii (BI)	9.5	3000	4300	X
R. sidereum	15.0	2400	3400	Y

3.3. Observations on the Timing of Leaf Fall and Leaf Senescence in Scotland

3.3.1. Leaf fall

The time courses of cumulative leaf fall are plotted in Figure 3. For *R. rubiginosum*, appreciable fall did not begin until October, but most leaf loss occurred by the end of December. For *R. pubescens*, the fall began earlier (July) and finished later (June), but the highest rate of fall occurred in November–December. For *R. wardii* and *R. wallichii*, there was a relatively high and rather steady rate of fall from July to November. Only a modest proportion of leaves fell from *R. decorum* in the autumn, and that loss occurred in October–November.

Figure 3. Timing of leaf fall and loss of green colour for five species of *Rhododendron* from SW China grown in Edinburgh; the numbers of leaves in marked cohorts were followed from their second summer; in each graph, the upper line is for green leaves plus non-green leaves and the lower for green leaves. (**a**) *R. rubiginosum*; (**b**) *R. pubescens*; (**c**) *R. wallichii*; (**d**) *R. wardii* and (**e**) *R. decorum*.
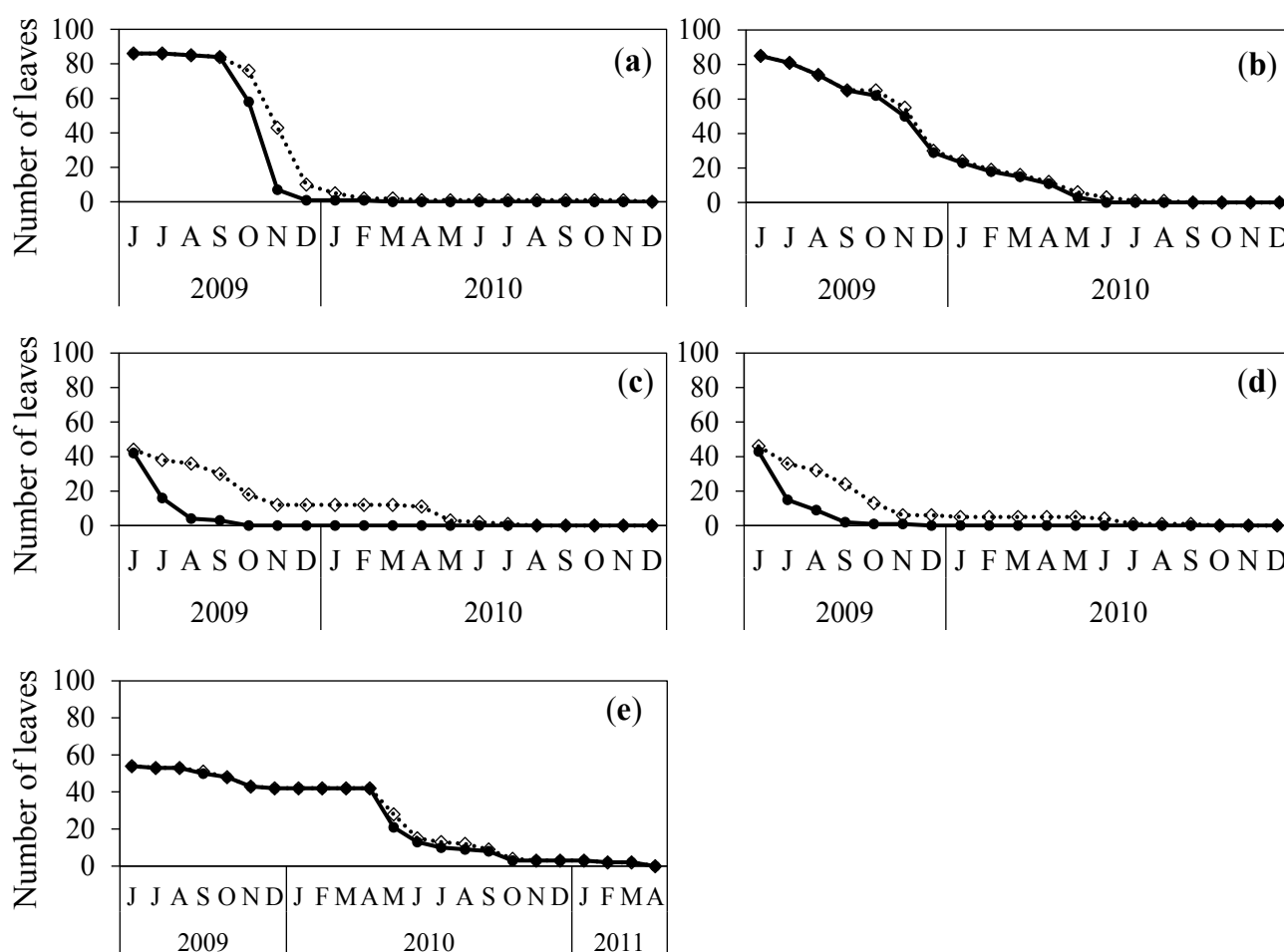
By December 30, 2009, *R. rubiginosum* had lost 76/86 leaves (88%), *R. wardii* 40/46 leaves (87%), *R. wallichii* 32/44 (73%), *R. pubescens* 55/85 (65%) and *R. decorum* 12/54 (22%). Ninety-five percent of leaves had fallen by February 3, 2010, for *R. rubiginosum*, by June 9 for *R. pubescens* and *R. wallichii*, by July 14 for *R. wardii* and by November 10 for *R. decorum*.

3.3.2. Changes in Leaf Colour

The five study species differed in whether or not the leaves generally lost their green colour before falling. A large majority of the leaves of *R. pubescens* (66/85) were still green when they fell, and the same was true of a little under a half of those of *R. decorum* (23/54), while for both species the rest of the leaves had turned brown. On *R. rubiginosum*, most of the leaves turned yellow-brown to brown before falling (at least 73/86), while in *R. wallichii* and *R. wardii* they almost all became mottled yellow-brown to brown (at least 41/44 and 42/46, respectively).

The estimated length of time spent by leaves at least partially yellow-brown or brown before they fell differed markedly among the species. The mean number of weekly censuses at which a leaf was recorded

as no longer wholly green was 3.1 for R. *decorum*, 3.5 for *R. rubiginosum*, 4.4 for *R. pubescens*, 12.8 for *R. wardii* and 18.7 for *R. wallichii*; the median number was two for *R. decorum* and *R. rubiginosum*, four for *R. pubescens*, eight for *R. wardii* and 11 for *R. wallichii*. However, on all of the last three species, the leaves fell into two groups: those lasting in at least partially yellow-brown or brown state for <20 weekly censuses, and those lasting for 40 or more. The mean number of censuses for the shorter-lived group was 3.0 for R. *rubiginosum* (72 leaves), 7.6 for *R. wardii* (37) and 8.4 for *R. wallichii* (29). The mean for the longer-lived leaves was 40.0 for *R. rubiginosum* (one leaf), 51.6 for *R. wardii* (five) and 43.6 for *R. wallichii* (12).

4. Discussion

4.1. Leaf Behaviour Established So Far

Observations on a high proportion of the most abundant evergreen broad-leaved tree and shrub species in the SMSF of southern Yunnan found that 13/19 had only one cohort of old leaves in the spring (Table 4). To these, we can add one more genus and family on the evidence of the photograph of *Skimmia multinervia* (Rutaceae) on p. 198 of Lancaster [27] taken in the remains of SMSF on the Cang Shan. There is a marked contrast between these results and those for WTRF for which we know that the leaves of most evergreen species last two or more years [8], and in most of the 11 species in Table 1, leaf fall either began in the same month as the outgrowth of new leaves (5/11) or one month later (2/11) or two months later (1/11). In one of 11 species leaf fall began two months before outgrowth of new leaves, and in one species leaf fall was continuous throughout the year. Only in *Cleyera japonica* was there a pattern even somewhat like that found for *Rhododendron* species in cultivation in Scotland and suspected for many species in other families in SMSF in Yunnan: leaf fall not starting until July and continuing into October. None of the 12 MSF species of sclerophyll in Table 1 and none of the 14 in Table 2 has major leaf fall in late autumn-early winter. The only Mediterranean taxa reported to have that timing of leaf fall are the small shrub, *Daphne gnidium* [13] and *Pistacia* x *saportae*, the hybrid of evergreen *P. lentiscus* and deciduous *P. terebinthus* [15]. Even if a wider survey were to yield a lower proportion of species in SMSF with only one cohort of old leaves in early spring than 14/20 (70%), there would clearly be a marked difference from the situation in WTRF and MSF where such species are very few.

Our survey of a non-random sample of *Rhododendron* species from a wide range of forest and thicket types in SW China growing in Scotland also showed that many lose the oldest cohort of leaves well before new ones expand: 46% of the 35 species and subspecies that yielded clear and consistent results. The species with only one cohort of old leaves in the spring had significantly smaller leaves than those with two or more cohorts. The mean blade length was 6.1 cm (Table 5), close to the mean for the nine species of *Rhododendron* reported by Wu [20] in SMSF (7.4 cm). These observations suggest that both small leaf size and leaf fall before winter are characteristic of winter-dry areas. There is huge variation in climate and vegetation type in SW China, and the larger-leaved species of *Rhododendron,* found to have more than one cohort in early spring when growing in Scotland, are found at sites not subject to winter drought [20] or protected by the topographic effects from it [27].

Our detailed observations on leaf fall of *Rhododendron* species in Scotland for more than a year are particularly significant because, for two of the five species, the number of cohorts in early spring was as

we had recorded in China. Our records for four of the species studied in Scotland have provided the first-ever precise information on the timing of leaf fall among evergreen species that lose all or almost all of their oldest leaves before new ones expand, as seen in the second pattern in Figure 1.

The only other studies of leaf phenology in *Rhododendron* that we have found are those for *R. maximum* [25,26], which grows in eastern North America. Leaf fall was concentrated in July–August one year and more spread out in the following year: June–July and September–November when records ceased. There was no obvious explanation in terms of weather; there was a dry spell in the first year, but that came after most leaf fall had occurred. The year-to-year variation thus revealed should make us cautious, but at least it is clear that in both years the leaves of the oldest cohort fell after the expansion of new leaves had occurred.

We have found that there is not only a wide range of leaf behaviour in evergreen species of the genus *Rhododendron* in SW China (the number of cohorts of old leaves in the spring varying from one to >3), but also a continuum. This was shown by the species on which the numbers of cohorts of old leaves in the spring varied between individual plants and/or between branches on individual plants and by the differences between species in the timing of leaf loss (Figure 3). Our studies were all made on well-lit individuals, and it may well be that in at least some species, leaves remain longer on shaded plants than on well-lit ones, as found in WTRF in Japan [8,10] and for *Rhododendron maximum* in eastern North America [25,26].

Despite the continuum, it is striking that so many species of evergreen in SW China do lose their oldest leaves before the expansion of new leaves, and, if our limited study of the timing of leaf fall in Scotland is a true guide, they lose them before leaf desiccation resulting from winter drought being likely to become severe. Obviously, new work on the timing of leaf fall in SMSF in China is needed, preferably linked to studies on changes in leaf water content, leaf colour and nutrient resorption. Meanwhile, we set out a multi-part hypothesis to explain how the early leaf fall could be advantageous.

4.2. Hypothesis Proposed

We hypothesize that in areas with dry winters, there is a net advantage to dropping the oldest cohort of leaves in autumn because: (1) there is a low chance of appreciable positive net assimilation in winter, and the loss of water by older leaves would outweigh the value of any positive net assimilation; and (2) there is a high chance of desiccation, reducing the effectiveness of the resorption of dry mass and mineral nutrients from ageing leaves. In contrast, where the winter is moist, there is a net advantage to retaining the oldest cohort of leaves, because there will be, in most years, a significant chance of positive net assimilation with no concurrent risk of leaf desiccation and, in almost all years, little risk of resorption being inhibited by leaf-desiccation.

With a single exception (see below), there has been no relevant observational or experimental work on SMSF species, but there have been several relevant studies on species in WTRF, MSF and related vegetation types.

For evergreen broad-leaved species in WTRF [28,29] and MSF [30,31], there is evidence from short-term observations that net assimilation during daylight is positive in winter. For sclerophylls, corroboration that net assimilation over the 24-hour cycle is positive, when it is too cool for extension growth, comes from the finding that the concentrations of non-structural carbohydrates in the leaves and

branch wood increase during the winter [32,33]. This longer-term positive net assimilation occurs despite short-term damage to the photosynthetic system on the rare days with temperatures just below 0 °C [34,35].

Studies on various vegetation-types have found that drought often reduces respiration less than it reduces photosynthesis [36], and some have found that the respiration rate is not reduced by drought in all species [37]. Indeed, there is mounting evidence of increases in respiration as a result of drought [38,39], so that the possibility of negative net assimilation during dry periods has to be taken seriously. It may also be of value to a tree to reduce its leaf mass in such a way that it is easier to maintain a favourable water status (and, as a result, a favourable carbon balance) in the remaining leaves.

The value of the transfer of both dry mass and nitrogen from senescing leaves to newly expanding leaves has been documented for evergreen trees and shrubs in Japanese WTRF [40,41]. In *Ternstroemia gymnanthera*, a species also widespread in SMSF in Yunnan, the foliar concentration of N decreased during senescence by about 40% [40]. Regarding sclerophylls in MSF, resorption of N can reach 48% in *Quercus suber* [4]. Clearly, we need measurements for the dominant oaks (species of *Castanopsis* and *Lithocarpus*) in SMSF in Yunnan. We have not found work on the inhibition of resorption by desiccation during dry spells for species of WTRF or MSF, but in the North American deciduous shrub, *Viburnum acerifolium* [42], the decrease in P per unit leaf area during senescence can be 50%–100% inhibited by drought and that of N per unit area up to 60%.

Our finding that on some *Rhododendron* species in cultivation many of the leaves fell while wholly green suggests that in them, resorption of major nutrients was minimal in extent. We need to know if these species behave in the same way in the field. If they do, then for them, our hypothesis simplifies to a concern for carbon balance.

Testing our hypothesis is not straightforward, because no test can be made in late winter on leaves that have fallen in the autumn. We suggest that a reasonable test would be to find out in a field experiment whether appropriate levels of leaf desiccation do reduce net assimilation to zero or negative values in (1) leaves between one and two years old in early to mid-autumn before they fall; and (2) leaves in their first year in late winter. The sensitivity of the resorption of nutrients would have to be tested on the leaves between one and two years old in early to mid-autumn. Only when these experiments have been made can we assess the likelihood that our hypothesis has identified the major selection pressures for early leaf fall. The observations and experiments should be made on species that keep their leaves until the third summer, as well as species that drop them after the second summer.

4.3. Wider Application of the Hypothesis

Our concern so far has been with evergreens subject to water shortage in winter, because of a paucity of rainfall, but other evergreens are subject to water shortage in winter, because the soil is so cold, that uptake becomes difficult, partly as a result of the viscosity of water being increased substantially and partly because the permeability of the root cell membranes is reduced a great deal [43]. We have in mind low to medium-height evergreen shrubs with small or very small leaves and evergreen conifers, growing in high latitudes or at high altitudes. For such plants, a further reason for

dropping leaves soon after their second or third summer is that temperatures in winter may be so low that there is negligible net assimilation.

Karlsson [44] found that the mean expected leaf life length for five shrubby Ericaceae in Scandinavia was 1.5–1.6 years, *i.e.*, most second-year leaves did fall off before winter. Other Ericaceae had means nearer to 2.0 or 3.0 years, just as we found that some tree species in SMSF had two or three leaf cohorts in spring (Table 1). For heathland shrubs, as for broad-leaved forest trees, a full interpretation will involve an understanding of the physiology of both the species that lose their leaves before winter and those that keep them until the following spring.

Leopold [45] noted that around his home in Wisconsin, most needles of jack pine (*Pinus banksiana*), red pine (*P. resinosa*) and white pine (*P. strobus*) fall in November, those of the first species being 1.5 years old and those of the other two 2.5 years old. However, for the last two species, Gower *et al.* [46] reported that in their study area in another part of Wisconsin, the mean longevities equate to an exact number of years or close to one: 36 months for *Pinus strobus* and 46 for *P. resinosa*. There is clearly a need to understand not only variation between species in a vegetation type, but also variation within species.

5. Conclusions

More attention should be paid to the seasonal timing of leaf fall from evergreen trees and shrubs that experience water shortage resulting from a lack of rain or prolonged cold weather in winter. The available evidence suggests that many of the leaves of such species fall soon after their second summer before conditions become significantly unfavourable, but observations on more species are needed, coupled with critical physiological measurements and experiments.

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Author Contributions

Peter J. Grubb made the observations in China and the study of the numbers of cohorts of old leaves in spring on plants in cultivation in Scotland. Christine L. Thompson and Geoffrey H. Harper made the longer-term observations on leaf fall from five *Rhododendron* species in cultivation in Scotland. The three authors are jointly responsible for the analysis and presentation of the results and the discussion.

Conflict of interest

The authors declare no conflict of interest.

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