Contrasting Regeneration Strategies in Climax and Long-Lived Pioneer Tree Species in a Subtropical Forest

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Abstract

1: This study investigated 15 coexisting dominant species in a humid subtropical evergreen broad-leaved forest in southwest China, consisting of long-lived pioneers and climax species occurring in natural and disturbed regimes. The authors hypothesized that there would be non-tradeoff scaling relationships between sprouting and seed size among species, with the aim of uncovering the ecological relationship between plant sprouting and seed characteristics in the two functional groups.

2: The sprouting variations of the species were initially examined using pairwise comparisons between natural and disturbed habitats within and across species and were noted to show a continuum in persistence niches across the forest dominants, which may underlie the maintenance of plant diversity. Second, a significantly positive, rather than tradeoff, relationship between sprout number and seed size across species within each of the two functional groups was observed, and an obvious elevational shift with a common slope among the two groups in their natural habitat was examined. The results indicate the following: 1) the relationship of seed size vs. sprouts in the natural habitat is more likely to be bet-hedging among species within a guild in a forest; 2) climax species tend to choose seeding rather than sprouting regeneration, and vice versa for the long-lived pioneers; and 3) the negative correlation between sprouting and seed dispersal under disturbed conditions may imply a tradeoff between dispersal and persistence in situ during the process of plant regeneration.

3: These findings may be of potential significance for urban greening using native species.

Citation: Wang H, Feng H, Zhang Y, Chen H (2014) Contrasting Regeneration Strategies in Climax and Long-Lived Pioneer Tree Species in a Subtropical Forest. PLoS ONE 9(11): e112385. doi:10.1371/journal.pone.0112385

Abstract

Introduction

Plant regeneration is an important ecological process for a forest ecosystem in which the sprouting and seeding of woody species is involved [1]. As a mechanism for shaping community dynamics [2], plant regeneration is important for the succession of forest communities and for the stability and restoration of vegetation in a forest ecosystem following various disturbances. As new architectural units, species sprouts [3] have been widely perceived as key functional traits [4–6] linked to plant life-history strategies [7,8], functional types [9,10] or population persistence [11,12]. Using sprouts, some damaged trees can occupy their original space niche rapidly and eventually reach the forest canopy again [13].

Furthermore, sprouts, as one of the two plant regenerative traits [4], have been reported to correlate in part to seed size. For example, sprouters would most likely be expressed in seed fecundity [14]. Moreover, it has been argued that there is a tradeoff between sprouts and seed size [15,16] due to competition for resources between vegetative and reproductive growth [14] relative to starch-tissue content [17]. Plants that sprout vigorously tend to be poorer seed recruiters than non-sprouters [8], and non-sprouters produce more seeds than congeneric sprouters growing at the same sites [8,17]. Nevertheless, others have found no correlation between the two variables (e.g., [18]). In brief, few significant associations have been reported thus far.

In contrast, because both seeding and resprouting are all ascribed to plant regeneration [4], we may infer that seed size correlates with sprouting [19,20]. In addition, in fluctuating environments, seeding shows bet-hedging [21,22], which remains correlated with seed size among community species [23–25] during the process of seed germination as an evolutionarily stable strategy to control the plant population (or ESS, e.g., [26]). With respect to resprouting, Nzunda et al. [16] recently suggested a bet-hedging model between occasional events and fixed interference in the storage reserve in good resprouting species. Based on these reports, we may hypothesize that plant sprouting may show a pattern of bet hedging in response alternating seeding, which eventually results in a positive scaling relationship, instead of a tradeoff, between plant sprout and seed size.

Moreover, interspecific and intraspecific differences in sprouting ability have been observed [2,7] that were due to various ecological factors [27–30] or the biological properties of the plants themselves [31–33]. For example, as an example of the...
latter, light-demanding species generally show enhanced resprouting abilities compared with shade-tolerant species [10], and species tends to be more widely distributed in less-productive sites [17]. It is reasonable to infer that the connections between sprouting and seed traits may be intrinsically variable in different functional plants (i.e., guilds). An examination of these properties may be vital to understand the regenerative ecology of particular species.

However, direct evidence on the relationship between sprouts and seed size in woody species remains insufficient. Furthermore, much of the existing research on regeneration following disturbances has focused on the role of pioneer species (e.g., [2,34–36]). There have been few comparative studies among long-lived pioneers (LP) and climax species (CS; however, see [37]), which may be of practical value for forestry (see the summary in [38]).

The current study employed a subtropical evergreen broad-leaved forest in Mt. Jinyun Nature Reserve in China. We monitored the sprouting performance of 15 dominant species with varying seed size living in both natural and disturbed areas, and we analyzed intraspecific variations in sprouting responses to disturbances for the 15 species by examining the relationship between species individual sprout number and seed size among the two groups. Finally, we examined the associations among life-history attributes of the species, such as plant height, starch amount in current-year shoots, individual seed size, and appendages per seed carried (a parameter characterizing seed-dispersal ability that may be correlated in part with sprouting, see [39]). The primary objectives of this study were the following: 1) compare the sprouting performance within species across disturbance gradients; 2) test the expected ecological relationships between species’ sprouting behaviors and seed traits among CS and LP.

Materials and Methods

Study site and vegetation

The study area is located in the Jinyunshan National Nature Reserve (29°50’N, 106°24’E) in southwestern China, covering about 14 km² in total. The elevation within the reserve ranges from 180 to 951.5 m. The climate is of a typical subtropical monsoon type, characterized by mid-subtropical monsoons with a rainy, hot summer and a dry, warm winter. The mean annual rainfall is 1143.1 mm, which primarily falls in summer; thus leading to a relatively high mean annual relative humidity of 85%. The annual mean temperature is 17°C, with annual effective accumulated temperature (>10°C) of 6000°C, a maximum annual frost-free period of 334 d, and a mean annual sunshine time of only 1160 h. The most common soil type is acid yellow (mean pH value is 4.36) developed from Triassic quartz sandstone, carbonaceous shale and argillaceous sandstone, which contains a total content of 0.0983% nitrogen, 0.040% phosphorus, 1.413% potassium and 2.099% organic matter [40,41]. In addition, Mt. Jinyun is both a nature reserve and a famous scenic area where there are many signs of human habitation, such as roads, farmhouses, and hotels. The plants near these sites are greatly influenced by human disturbance.

With respect to zonal vegetation, there is a humid subtropical evergreen broad-leaved forest with secondary succession of vegetation in varying stages that primarily result from a forest fire (~300 years ago), mining (~50 years ago), and an abandoned tea garden (~20 years ago). The forest shows an obvious vertical structure, primarily comprising Fagaceae, Lauraceae, Theaceae, Symplocaceae, and Elaeocarpaceae [42]. The first tree layer is generally 15–20 m high with a few trees taller than 25 m. This tree layer is chiefly dominated by Fagaceae and Theaceae species that average 15 m in height and range from 25–35 cm in diameter at breast height, interspersed with large Elaeocarpaceae, Lauraceae and Symplocaceae trees that also influence the forest community. The second shrub layer is typically dominated by large shrubs or saplings that are often less than 3 m in height [40] and include species that are common in the sunny bare soil or shaded understory.

Materials and study design

Fifteen dominant or co-dominant species in the tree layer and shrub layer were selected as target species that represented, to some extent, the characteristics of the evergreen broad-leaved forest. The 15 species included three Symplocaceae species, four Theaceae species, three Elaeocarpaceae species, two Lauraceae species, two Fagaceae species, and one Rubiaceae species. They are well-layered in the forest community, and Castanopsis fargesii, Castanopsis carlesii, Elaeocarpus duchouxi, Machilus numm, Symplocos aurata and Gordonia acuminata belong to the first tree layer, Symplocos setchuanensis, Adinandra bockiana, Neolitsea aurata, Adinandra bockiana and Sloanea leptocarpa belong to the second, and Eurya boguiana, Camellia tsoufui, Adina cochininchens and Symplocos lanceolata belong to the third [41,43]. We designated these selected species as either climax species or long-lived pioneers based on their role in the forest community; the dividing approach for climax species and long-lived pioneers followed criteria used in the literature [43,44] and personal observations.

The field investigations were performed between April 2011 and May 2011 using stratified random sampling to arrange five sample plots (covering about 15 ha in total that were separated from each other by 400–600 m) in a sampling area of about 100 ha. The habitats of individual plants were divided into two types: disturbed habitat (DH; defined as a forest edge within 10 m of buildings, squares, or main roads), which was more strongly affected by human activities, and natural habitat (NH; greater than 50 m from the sources of interference), which was little influenced by human. The plots in the two types of habitats were kept as uniform as possible with respect to altitude, slope position and aspect based on target plants and plant habitat category.

This paper used sprout number to measure sprouting capability, which is the most commonly adopted method (c.f. [45,46]). Twenty to forty trees per plot were selected randomly to record sprout number per individual in the field. For the purposes of the census, we recorded “distinguished sprout” by specifically referring to the living shoots originating from the trunk [46], and the main stems branching from the trunk were not included.

Ethics statement

The field studies for each site were permitted by the staff of the Jinyunshan National Nature Reserve, and this study did not involve endangered or protected species.

Data analyses

In view of the variation in sprout data of interspecifics and intraspecifics under varying habitats, in prior to analyses of the measured traits we conducted nested ANOVAs to test variability. The results showed that both species and habitat influences sprout number markedly (F = 43.630, p<0.001 and F = 6.078, p = 0.014, respectively). Moreover, as a variable, species contributed the largest variance (87.7%) of sprouting data, following by habitat (11.5%) and the individual plant of the same species under the same habitat contributed the least to variation (0.8%). These results showed that sprout data may be compared among species, regardless of their intraspecific variations in different habitats. Data were meansed across individuals of the same species living in
Table 1. The species properties and the mean sprout number per individual (mean±SE) in natural habitat and in disturbed habitat for the 15 species studied.

| Species            | Family     | Height | Group | Abbr. | NH      | DH      | DH/NH |
|--------------------|------------|--------|-------|-------|---------|---------|-------|
| Castanopsis carlesii | Fagaceae   | Mt     | CS    | Cc    | 3.37±0.39 *** | 7.05±2.06 | 2.09   |
| Eurya loguiana     | Theaceae   | Ls     | LP    | El    | 3.61±0.75 *** | 6.11±1.89 | 1.70   |
| Neolitsea aurata   | Lauraceae  | St     | CS    | Na    | 3.24±0.41 *** | 5.44±1.08 | 1.68   |
| Elaeocarpus japonicus | Elaeocarpaceae | Mt       | CS    | Ej    | 3.00±0.46 *** | 5.00±0.92 | 1.66   |
| Aida cochinchinensis | Rubiaceae | Ls     | CS    | Ac    | 1.67±0.29 *    | 2.56±0.67 | 1.52   |
| Sloansea leptocarpa | Elaeocarpaceae | Mt     | CS    | Sc    | 2.80±0.75 *** | 4.02±3.00 | 1.43   |
| Castanopsis fargesii | Fagaceae   | Lt     | CS    | Cf    | 2.80±0.42 *** | 3.82±0.71 | 1.36   |
| Adinandra bockiana | Theaceae   | St     | LP    | Ab    | 6.35±1.54 *** | 8.57±2.72 | 1.35   |
| Symplocos lancifolia | Symplocaceae | St     | LP    | Sf    | 6.56±2.12 **   | 8.64±3.33 | 1.32   |
| Symplocos setchuanensis | Symplocaceae | Mt     | CS    | Ss    | 3.23±1.51 ns   | 4.07±1.61 | 1.26   |
| Elaeocarpus duclouxii | Elaeocarpaceae | Lt     | CS    | Ed    | 5.48±1.14 ns   | 5.29±2.33 | 0.96   |
| Camellia tsudoi     | Theaceae   | Ls     | CS    | Ct    | 3.46±0.93 ns   | 3.24±0.36 | 0.94   |
| Gordonia acuminata  | Theaceae   | Mt     | LP    | Ga    | 10.50±2.18 *** | 5.83±1.21 | 0.55   |
| Machilus nanmu      | Lauraceae  | Lt     | LP    | Mn    | 9.70±3.77 ***  | 5.17±1.89 | 0.53   |
| Symplocos laurina   | Symplocaceae | Mt     | LP    | Sl    | 9.44±2.78 ***  | 2.16±0.30 | 0.23   |

* denotes the p-level of student’s t-tests for the species in the two habitats. * = p<0.05, ** = p<0.01, *** = p<0.001, ns = non-significant. Ss = small shrub (<0.5 m), Ms = middle shrub (0.5–2 m), Ls = large shrub (2–5 m), St = small tree (5–8 m), Mt = middle tree (8–25 m), Lt = large tree (>25 m); NH & DH = sprout number in natural & disturbed habitat, respectively; Abbr. = the abbreviation of the species studied. CS denotes climax species and LP does long-lived pioneer. The species are sorted according to the column of DH/NH.

doi:10.1371/journal.pone.0112385.t001
the same habitat and log_{10}-transformed to improve normality prior to analyzing for the scaling relationships.

The scaling relationships between sprout number and seed size (i.e., seed mass, referring to individual seed dry mass, as in [47]) were analyzed using a Model Type II regression method, with allometric scales of particular interest calculated as Standardized Major Axes (SMA; [48]). The heterogeneity of regression slopes and the common slopes were tested following the methods of [49], and the shifts between lines fitted to groups sharing a common slope (y-intercept) were examined using ANOVAs. The above allometric parameters were conducted using SMATR [48,50].

Although sprouting capability showed little phylogenetic conservatism [5], we nevertheless performed phylogenetic independent contrasts (PICs) analyses for the species used in the current study to determine whether a correlation between seed size and sprouts was biased by phylogenetic signal. The phylogenetic trees were constructed following Phylomatic (version 3; [51]), and PICs were conducted using the phylogenetic comparative methods of COMPARE (4.6b; [52]) for the LP and CS species.

In addition, to assess differences within species in the two habitat conditions, t-tests were conducted using Statistica 6.0 (Statsoft I 2001: Tulsa, Oklahoma). To detect broad correlations in variation among sprouting traits and plant seed traits, we performed a principal component analysis (PCA). Six statistics were employed to perform the PCA for 15 species. With the exception of two sprouting variables, the remaining four parameters were seed size (a life-history trait related to successional trade-offs), plant height (a parameter that has been shown to be strongly associated with the coexistence of pioneer and shade-tolerant tree species by [37]; sprouters are typically short plants, such as shrubs or bushes, whereas non-sprouters are commonly tall trees [11,53]), seed appendage per seed carried (taken from [39]), and starch content in shoot pith (estimated roughly using a scale of 1–5, denoting the least to the most amount based on anatomical content in shoot pith (estimated roughly using a scale of 1–5, denoting the least to the most amount based on anatomical sections of current-year shoots observed under a microscope).

DCA (detrended correspondence analysis) was performed prior to PCA to determine the ordination model (i.e., unimodal or linear) to be adopted following the requirement of [54], using Canoco for Windows 4.5 software. Because all lengths of the gradient were less than 3 (the largest being 0.863), a linear multivariate PCA approach was chosen to examine the associations among the multiple variables including sprout number in NH and DH, seed size, seed appendage per seed carried and starch content in shoot pith and plant height. Of these variables, the first two were assigned as environmental variables and the remaining as species variables for the PCA. For the PCA, the species data were log-transformed, and the focus of scaling was on inter-species correlations. The species scores were divided by the standard deviations, and sample data were centered and standardized, whereas species data were centered by species. The PCA ordination biplot was created using CanoDraw 4.0.

**Results**

**Sprouting characteristics under disturbed and natural habitats**

The mean numbers of sprouts per trunk for the 15 species in DH and in NH are summarized in Table 1. Five of the species (Gordonia acuminate, Machilus nanmu, Symlocos laurina, Camellia tsuji, Elaeocarpus duclouxii) showed more sprouts in NH than in DH; in particular, the former three were significantly different (t-test, p<0.001) and showed sprouting numbers that were 1.8-, 1.9-, and 5.9-fold greater than in the DH. The remaining 10 species showed fewer sprouts in NH than in DH.

The sprout numbers for different tree species within the same habitat were also different. The biggest sprout number in the DH was that of *Symlocos lancifolia* (8.64), followed by *Adinandra bockiana* (8.57); the lowest two were *Symlocos laurina* and *Ailurocarya* with only 1.6 and 2.56, respectively.

With the exception of 3 species (t-test, p>0.05; *Elaeocarpus duclouxii, Camellia tsuji*, and *Symlocos setchuanensis*), there were notable differences in paired sprouts for the 12 species between NH and DH (t-test, p<0.05; Table 1). Therefore, human activities affect sprouting capacity of trees in general; however, the effect of this interference differs with species.

**Scaling relationship between sprouting capability and species seed size**

Species sprout number in NH did not generally correlate with seed size in pooled data across all 15 species (p>0.05). However, when dividing the 15 species into two groups (CS group and LP; Table 1), the sprout number closely scaled with seed mass across congeners within a group (r^2 = 0.714, p = 0.034, slope = 5.884 [2.959 11.702] for the LP group; r^2 = 0.907, p < 0.001, slope = 6.609 [5.049 8.653] for the CS group) with a significant elevation increase (y-intercept_{LP} = -4.157; y-intercept_{CS} = -1.479) fitting a common slope (r = 6.476; Figure 1).

Second, the sprout number in DH did not correlate with seed mass across species (p>0.05) even when the 15 species were divided into CS and LP (p>0.05). In addition, the above tendencies were maintained in PICs, with the exception of a weak correction in pooled data across the 15 species in DH (Table 2).

These results show that the relationship between sprouting capability and species seed size varies considerably between the two species groups in natural habitats and remained when phylogenetic signals were removed. Furthermore, the apparent difference in y-intercept (increase) between the CS and LP groups indicates that the species in the CS group produced larger seeds than those of the LP group for given sprouts.

**The broad trends among sprouting capability, stem and seed traits, and habitats**

The PCA graph summarizes the general correlations (Figure 2). The PCA revealed that the first and second PCA axes explained 58.4% and 33.2% of the variability in species data, respectively; 91.6% in total. The variability of NH sprouts paralleled the direction of seed size (Figure 2) but opposed the direction of height and starch content; however, the DH variable was orthogonal to seed size but conversely parallel to the direction of seed appendage. Thus, the NH variable was more closely and positively associated with seed size and correlated negatively with height and starch content. The DH variable correlated strongly with seed appendage per seed carried but was independent of seed size.

**Discussion**

We performed intraspecific comparisons of sprouting performance for the dominant species in a subtropical community and tested our predictions on the interspecific relationships between sprouting and seed traits for LP and CS. We observed consistently significant relationships between species sprouting and seed traits; however, the details of these relationships varied based on species and habitat type.

1) **Contrasting sprouting patterns within and across species between natural and disturbed habitats**

The species sprouting patterns differed in conspecifics in different habitat types (consistently shown using t-tests) and also...
in interspecifics. Some species sprouted vigorously in natural habitats; however, others showed enhanced sprouting in disturbed habitats. The intraspecific sprouting pattern shows that, among the species measured, the majority of species were sensitive to disturbance, indicating that disturbance affects sprouting in plants. Moreover, the differentiation among dominant species in a forest may be of particular significance due to their leader functions in a forest when considering spatial coexistence among species [55] and the dynamics of the community structure [56]. Some species sprouted more in DH whereas others performed better in NH, as mentioned above, we believe this diverse sprouting property in dominant species forms a vegetative regenerative spectrum, which lays the foundation for them to cope with various natural- or human-derived disturbances, and presumably, it also reflects a bet-hedging sprouting strategy at the species level within a community (c.f. [57]). Thus, the marked differences in sprouting performance may be critical for the dominant species to colonize gaps [58] in a complementary way and may enable maintenance of tree diversity following disturbances, based on the “alternate trait axis” argument [2].

Nevertheless, it is difficult to explain the origin of the difference in sprouting behaviors of some species that sprouted less in disturbed habitats, as observed here in this study. Further research such as investigation for underground clone structure is suggested.

2) Relationship between seed size and sprout number
Larger-sized species tend to produce more sprouts among species within a functional group in an undisturbed habitat; however, this relationship did not reach significance when all species were pooled, indicating that natural guild species may evolve the potential to reproduce vegetatively (bet-hedge rather than reproduce sexually) in response to environmental cues [57]. We believe that this result is reasonable based on two lines of reasoning. First, the observed sprouting continuum across dominant species along the disturbed gradient provided a necessity for species hedging their evolutionary bets in varying environments [59]. Second, woody plants are perennial and not annual. The sprouts on trunks were the sprouts saved for years that eventually become the biological “bet” and enable a positive relationship between seed size and sprouts; hence, there is no need

![Figure 1. The relationship of seed size vs. sprouts.](https://doi.org/10.1371/journal.pone.0112385.g001)

| Table 2. Summary of phylogenetically independent comparative analysis (PICs) for the relationships between sprout number and seed size of the climax species (CS) and long-lived pioneers (LP) studied, and for the pooled data (Pooled) of the two groups. |
|---|---|---|---|---|
| Habit | Group | r² | p | a | b |
| NH | CS | 0.807 | 0.002 | 6.395 | 0.057 |
| NH | LP | 0.722 | 0.002 | 3.326 | -0.284 |
| NH | Pooled | 0.702 | <0.001 | 4.508 | -0.125 |
| DH | Pooled | 0.365 | 0.029 | -2.187 | -0.670 |

Letters a and b are the regressive coefficient and the intercept of the linear regressive equation Y = ax+b, where Y and x are seed mass and sprout number, respectively. [doi:10.1371/journal.pone.0112385.t002]
which is consistent with a previous report [18].

Furthermore, based on the equal sprouting number on trunks, climax species tended to show larger individual seeds than long-lived pioneers, revealing a difference between the two species groups with respect of life history strategy under natural conditions. This tendency held true in PIC analyses, revealing its ecological significance. The CS guild may win out in a forest by evolving larger seeds, enabling seedlings to settle and establish in a darker habitat. In contrast to CS, the LP species tended to adopt a vegetative means to enable plant regeneration in brighter sites. They produce more sprouts and smaller seeds under natural conditions; thus, enhanced sprouting ability but weaker seeds.

On one hand, this result is inconsistent with authors who argue that vegetative sprouting should require a trade-off against sexual reproduction in general and consequently, that poor resprouters should show higher seed mass compared with good resprouters (e.g., [15,60]). This inconsistency may result from the differences in the type of environment studied (e.g., natural vs. disturbed habitat), the species type (the species focused upon were woody CS & LP) or the variation in seed size due to seed size/number tradeoff (e.g., [39]). On the other hand, the greater mean number of sprouts in LP compared with CS under natural conditions, as observed in our study, indicates a pattern of smaller-seeded species with more sprouts [the LP group in NH showed markedly more sprouts (\(= 7.695\)) than the CS group (\(= 3.232; t\)-test, \(t = -4.661, p < 0.001\)], which may also represent a tradeoff to some extent between seed size and sprouts. In addition, this relationship did not hold true for the species in disturbed habitats, as shown both in the PCA graph (Figure 2) and in regression analysis (\(p > 0.05\)), which is consistent with a previous report [18].

3) Associations among NH & DH sprouts, seed dispersal, carbon storage and plant height

PCA showed a clear positive correlation of sprouts in NH with seed size, further verifying the relationship between these two variables (Figure 2). NH sprouting was also negatively correlated with starch content and plant height, showing that good sprouters in natural sites may store starch less and include relatively more short species. The DH sprouts showed contrasting results, supporting some previous reports, such as [60], demonstrating that sprouters show higher starch concentrations in roots.

The DH sprouting variable was inversely correlated with seed appendage (Figure 2), suggesting that good sprouters in DH may be weak seed dispersers and vice versa. This relationship may imply a tradeoff between the space occupied by the plant between far (i.e., seed dispersal) and near (i.e., sprouting). The ecological relationship between seed dispersal and plant sprouting may be an interesting topic that deserves further discussion.

4) Ecological and practical implications of the sprouting strategy

The sprouts of dominant species in the natural ecosystem may be very useful when managing forests for products including timber, firewood, edible fruits, and landscape plants, which are some of the different uses of the species observed. Thus, our results are likely to be helpful for silvicultural treatments. For example, the difference in seed size between CS and LP implies different regeneration niches in a subtropical forest and lays a good foundation for a more resilient forest ecosystem apart from human disturbances using complementary mechanisms of responding to a more or less disturbed habitat. Still, long-lived pioneers show some excellent features, such as their fast growth and relative shade tolerance, compared with pioneers, and they have light but strong timber (characteristics proposed as part of the long-lived pioneer syndrome by [38] (pp246), which is superior not to the slow-growing climax species but to the strongly r-selected pioneer. Therefore, LP is an issue of particular concern to foresters when applying “Miyawaki’s Method” for reestablishing an urban forest [61].

Conclusions

We tested and confirmed our hypothesis on the ecological correlation of sprout vs. seed size. Dominant forest species differ in their sprouting capability, build divergent sprouting patterns along disturbed gradients and display contrasting relationships of sprouts vs. seed size among guilds, manifesting in diverse sprouting strategies across woody plants and suggesting a strong selection for species life-histories under varying conditions. These results provide evidence for the evolutionary mechanism and consequences of variations in plant sprouting behavior, which may contribute to the ecology of regeneration in a forest community.

Acknowledgments

We thank Yanfang Liu for analysis of the anatomy of plant shoots in the laboratory and Danrong Wang for preparing the images used in this paper. We also appreciate the two anonymous reviewers for their constructive comments on early versions of this manuscript.

Author Contributions

Conceived and designed the experiments: HW. Performed the experiments: HF HW. Analyzed the data: HC. Contributed reagents/materials/analysis tools: HC. Wrote the paper: HC YZ.
References

1. Pratt RR, Jacobsen AL, Hernandez J, Ewers FW, North GB, et al. (2012) Allocation tradeoffs among chaparral shrub seedlings with different life history types. Oikos 121: 1464–1476.

2. Dietz MC, Clark JN (2000) Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. Ecological Monographs 70: 331–347.

3. Turnbull CG (2005) Plant architecture and its manipulation: Blackwell.

4. Cornelissen J, Lurovso, Garnier E, Diaz S, Buchmann N, et al. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51: 355–380.

5. Proctor PA, Westoby M (2004) Sprouting ability across diverse disturbances and vegetation types worldwide. Journal of Ecology 92: 310–320.

6. Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, et al. (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Physiologist 197: 19–35.

7. Bellingham PJ, Sparrow AD (2006) Resprouting as a life history strategy in woody plant communities. Oikos 90: 409–416.

8. Bond WJ, Midgley JJ (2003) The evolutionary ecology of sprouting in woody plants. International Journal of Plant Sciences 164: S103–S114.

9. Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, et al. (2012) Biomass allocation to leaves, stems and roots: meta-analysis of interspecific variation and environmental control. New Phytologist 193: 30–50.

10. Weisser W, Wetz J, Rotherick M, Garnier E, et al. (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. Journal of Vegetation Science 10: 609–620.

11. Hodgkinson KC (1998) Sprouting success of shrubs after fire: height dependent variation for different strategies. Oecologia 115: 64–72.

12. Houssard C, Escarré J (1995) Variation and covariation among life-history traits in iteroparous species. Oecologia 102: 590–593.

13. Bellingham PJ, Kohyama T, Aiba S (1996) The effects of a typhoon on Japanese warm temperate rainforests. Ecological Research 11: 229–247.

14. Lamont BB, Wiers D (2003) Are seed set and speciation rates always low among species that resprout after fire, and why?. Evolutionary Ecology 17: 277–292.

15. Nishiyama E, Lawes M (2013) Costs of resprouting are traded off against reproduction in subtropical coastal dune forest trees. Plant Ecology 212: 1991–2001.

16. Nuzen ED, Griffiths ME, Lawes MJ (2014) Resource allocation and storage relative to resprouting ability in wind disturbed coastal forest trees. Evolutionary Ecology 28: 735–749.

17. Bond WJ, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology & Evolution 16: 45–51.

18. Shibata R, Shibata M, Tanaka H, Iida S, Masaki T, et al. (2014) Interspecific variation in resprouting. Oikos 123: 477–492.

19. Cohen D (1966) Optimizing reproduction in a randomly varying environment. Journal of Mathematical Biology 2: 60–62.

20. Lohier T, Jabot F, Meziane D, Shipley B, Reich PB, et al. (2014) Explaining variation in the size-dependent resprouting ability of temperate woody species and its adaptive significance. Journal of Ecology 102: 209–220.

21. West GB, Brown JH, Enquist BJ (1999) The fourth dimension of life: fractal geometry and allometric scaling of organisms. Science 284: 1677–1679.

22. Kohyama T, Jokouchi D, Shipley B, Reich PB, et al. (2014) Explaining symbiotic shifts in root-shoot scaling with transient dynamics. Annals of Botany 114: 513–521.

23. Cole D (1966) Optimizing reproduction in a randomly varying environment. Journal of theoretical biology 12: 119–129.

24. Philipp T (1993) Bet-hedging germination of desert annuals: variation among populations and maternal effects in Lepidium lasiocarpum. American Naturalist 142: 565–567.

25. Pake CE, Venable DI (1996) Seed banks in desert annuals: implications for persistence niche. Trends in Ecology & Evolution 11: 101–105.

26. Falster DS, Warton DI, Wright IJ (2006) SMATR: standardised major axis tests of comparative data, 4.6b. Computer program and documentation distributed by the author; Available: http://compare.bio.indiana.edu Accessed 2014 Aug 1.

27. Martins EP (2004) COMPARE: Computer programs for the statistical analysis of comparative data, 4.6b. Computer program and documentation distributed by the author; Available: http://compare.bio.indiana.edu Accessed 2014 Aug 1.

28. Martens JP (2004) COMPAR: Computer programs for the statistical analysis of comparative data, 4.6b. Computer program and documentation distributed by the author; Available: http://compare.bio.indiana.edu Accessed 2014 Aug 1.

29. Stebbins RL, Cronquist A (1997) Resprouters vs. reseeders in South African forest trees; a model based on forest canopy height. Functional Ecology 11: 101–105.

30. Lept J, Sinhaaer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge university press.

31. Shen H, Nakis KJ, Yang D, Sun S (2009) The effect of twig architecture and seed number on seed size variation in subtropical woody species. New Phytologist 183: 1212–1221.

32. Wagner DT, Wright IF, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. Biological Reviews 81: 259–291.

33. Falster DS, Warton DI, Wright IJ (2006) SMATR: standardised major axis tests and routines ver 2.0 ed. Available: http://www.hbro.du.edu.au/ecology/ SMATR/Accessed 2014 Aug 1.

34. Webb CO, Dowogne MJ (2005) Phylomatic tree assembly for applied phylogenetics. Molecular Ecology Notes 5: 101–103. Available: http:// phyloinformatics.net/phylomatic/Version 5.4.2.e. Accessed 2014 Aug 1.

35. Martens JP (2004) COMPAR: Computer programs for the statistical analysis of comparative data, 4.6b. Computer program and documentation distributed by the author; Available: http://compare.bio.indiana.edu Accessed 2014 Aug 1.

36. Kruger L, Midgley J, Cowling R (1997) Resprouters vs. reseeders in South African forest trees; a model based on forest canopy height. Functional Ecology 11: 101–105.

37. Lept J, Sinhaaer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge university press.

38. Amarasekara P (2003) Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6: 1109–1122.

39. Wang X, Kent M, Fang X (2007) Evergreen broad-leaved forest in Eastern China: its ecology and conservation and the importance of resprouting in forest restoration. Forest Ecology and Management 245: 76–87.

40. Venable DL (2007) Bet-hedging in a guild of desert annuals. Ecology 88: 1086–1090.

41. Bullock JM (2000) Gap size and seedling colonization. In: Fenner M, editor. Seed: the ecology of regeneration in plant communities: CABI Publishing.

42. Fenner M, Thompson K (2005) The ecology of seeds: Cambridge University Press.

43. Claus M, Venable D (2000) Seed germination in desert annuals: an empirical test of adaptive bet hedging. American Naturalist 155: 168–186.

44. Sait CF, McMahon SM (2011) Ecological and environmental factors constrain sprouting ability in tropical trees. Oecologia 166: 485–492.

45. Van Bloem SJ, Murphy PG, Lago AE (2007) A link between hurricane-induced tree sprouting, high stem density and short canopy in tropical dry forest. Tree Physiology 27: 475–480.

46. Zhu W, Xiang J, Wang N, Li M (2012) Resprouting ability and mobilization of carbohydrate reserves in an oak shrubland tree with increasing elevation on the eastern edge of the Qinhai Tibet Plateau. Forest Ecology and Management 278: 118–126.

47. Moreira B, Tomo J, Pausas JG (2012) To resprout or not to resprout: factors driving intraspecific diversity and correlations. Biological Reviews 87: 742–753.

48. Knox KJE, Clarke PJ (2005) Nutrient availability induces contrasting allocation and st anch formation in resprouting and obligate seedling shrubs. Functional Ecology 19: 690–698.

49. Sayavedra A (1999) Theoretical ecology: restoration of native forests by native trees. Plant Biotechnology 16: 13–25.