A Comparative Study of Late-successional Plant Strategies in the Yosemite and Wind River Forest Dynamics Plots

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Abstract

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I analyzed and compared data collected from the Yosemite Forest Dynamics Plot in Yosemite National Park and the Wind River Forest Dynamics Plot located in the Gifford Pinchot National Forest in southern Washington State to determine if there are similarities amongst the three most dominant tree species of each location. I hypothesized that *Pinus lambertiana* and *Pseudotsuga menziesii* would exhibit similar distribution and characteristics due to their dominance as the largest trees within the plot. Along those same lines I expected that *Abies concolor* and *Tsuga heterophylla* would also resemble each other considering that both are the local climax species and demonstrate rapid regeneration. *Calocedrus decurrens* and *Thuja plicata* both occupy a somewhat more minor role in the stand in part because of their slow regeneration and slow growth. Again, I was looking for similar characteristics between these two species. My results have shown that diameter distributions are very similar between comparable species for trees of the initial cohort (≥100 cm diameter at breast height). It was also shown that there is not much similarity between comparable species of the regenerating cohort (<40 cm diameter at breast height).

Acknowledgements

I would like to thank Jim Lutz for giving me the wonderful opportunity to be a part of the Big Plot Project in Yosemite and Wind River. He contributed so much to the inspiration and execution of this paper. I would also like to thank my loyal editor I. Perry Elvrum. Finally I must thank my parents and family for being so supportive throughout my college career.
Introduction

Plants occupy niches in their environment where they have successful survivorship and reproductive capabilities. People have tried to classify and sort plant species by their similar traits and common niches (Clements 1916). J. Philip Grime summarized what he believed to be plant strategies or plant functional types. Plant strategies are similar life characteristics that cause different species to appear analogous from an ecological standpoint (Grime 2001). He ascertains that plant success is controlled by three conditions: stress, competition, and disturbance (Grime 1977). His studies of herbs in the British Isles led to the development of the C-S-R Triangle, stating that all herbs fall under either the competitive, stress-tolerant, or ruderal strategies.

Figure 1. Grime’s C-S-R triangle diagram showing the relationship between plant strategies and the conditions that they are most equipped for. Competition (C) is most successful at reproduction and survival in areas of competition without much disturbance. The ruderal strategy (R) is best equipped for environments of frequent disturbance. The stress-tolerator strategy (S)
survives best in areas of high stress. Strategies are able to mix with plants showing characteristics of more than one strategy in areas of moderate competition, disturbance and stress.

Grime’s triangle has fallen under much scrutiny since its formation in the 1970’s (Silvertown et al.1992). This is largely due to the fact that his studies have been primarily done with herbs in England and not much elsewhere. Late successional forests in the Pacific Northwest provide the opportunity for many species to find their niche and develop strategies that ensure reproductive success. These strategies may be analogous to the ones that Grime named as part of the C-S-R triangle for herbaceous species despite the dramatic difference in environments for untouched forests of the Pacific Coast and herbaceous species of England. Using the data collected in the Yosemite and Wind River Forest Dynamics Plots Grime’s C-S-R triangle will be assessed to see if it can hold any relevance in the old forests of the western United States.

Grime wrote that all trees qualified only as competitors or stress-tolerators (Grime 1977). No trees are considered ruderal because of their lifespan and slowed growth compared to an herbaceous plant. For my study, the C-S-R triangle will only be interpreted using tree species and some of the species do exhibit very ruderal-type behavior. The ruderal strategy will not be limited to only herbaceous species if certain dominant characteristics can be applied to the tree species of this study.

Description of Grime’s Plant Strategies

Each of the three strategies that Grime developed display very different life characteristics. Plants following the competitive strategy have a very high potential growth rate resulting in the capacity for large diameter and increased biomass. An elevated leaf canopy is typical of this strategy as well as extensive lateral spread allowing for adequate access to sunlight (Grime 1979). Plants in this strategy are often exclusive, completely occupying a growing site. In a biologically diverse site, competitive trees are often the dominant crowns in the canopy with other strategies filling a more oppressed role. The competitive strategy is limited largely to sites with low environmental stresses and mild disturbance (Figure 1). Areas of frequent stress are primarily occupied by the stress-tolerant strategy (Figure 1). These stresses can be imposed by the environment such as in arid sites or extreme cold, imposed by other plants creating areas with severely diminished resources, or by availability of nutrients. Certain plants have evolved to be
best suited in harsh conditions. Stress-tolerators are characterized by their slow and steady nature. These plants can occupy a wide range of sites but often maintain a passive part in the race for the sky. Unlike the competitive and ruderal strategies, they have a fairly low relative growth rate, a small stature, and long living organs (Grime 1979). These plants generally process water, carbon, and nutrients more slowly and tend towards the evergreen foliage to be able to take advantage of any favorable conditions throughout the year. Because of their slow growth, young plants of the stress-tolerant category are especially vulnerable to predation and defoliation (Grime 1979). Through natural selecting many of these plants have evolved defensive qualities.

The ruderal strategy thrives in sites with frequent disturbance. Ruderals display rapid growth and extensive seed production and distribution. Their lifespans are relatively shorter than the other strategies. A larger proportion of photosynthate is used for seed production sometimes at the expense of vegetative growth (Grime 1979). These seeds have the capacity to germinate rapidly and reach reproductive age much sooner than other strategies (Grime 1979).

The study areas utilized in this project are both late successional coniferous forests. These forests have not been actively maintained in hundreds of years. After a disturbance, a forest will naturally regenerate creating an initial cohort of trees of similar age (Franklin et al. 2002). Any seedlings that sprout after a large disturbance grow in full sun due to the lack of larger live trees in the area. As the trees mature, their dominance in the canopy creates shade competition for any juvenile trees that occur after the initial cohort has been established. All stems that began to grow after the initial cohort established itself will be called the regenerating cohort. These trees will be small in size and stature as to be expected by their age.

The intent of this study is to note whether there is similarity with the large trees of the initial cohort across the Pacific Northwest. Is there any similarity between the regenerating cohorts? Does Grime’s triangle hold any relevance in explaining life patterns of large conifers on the other side of the world from his own study sites?
Methods

Site Description

The study areas for this project were two 25.6 hectare permanent research plots in Yosemite National Park in California and the Gifford Pinchot National Forest in southern Washington State.

The Yosemite Forest Dynamics Plot is located within the park boundary near Crane Flat at an elevation of 1774.1 m and 1911.3 m. Precipitation in the Yosemite Forest Dynamics Plot is consistent with a “Mediterranean climate” with the driest months during the summer and the majority of precipitation during the winter months. Annual precipitation in this region is approximately 125 cm that falls almost entirely as snow during the months from November through April (North et al. 2002).

The primary disturbance in this region is wildfire. Low intensity wildfire returned to the forest of the Yosemite Forest Dynamics Plot every 10-13 years before fire suppression (Scholl et al. 2010). Modern fire management has greatly suppressed wildfire since the mid-19th century (North et al. 2007). The lack of regular burning has resulted in Abies concolor [Lindl. and Gord.] representing the majority of stem density and basal area in the mixed-conifer forests (North et al. 2004).

The research plot was established in 2009 as part of the Smithsonian-affiliated Center for Tropical Forest Science’s program for long-term large-scale forest research. The plot is 25.6 hectares divided into 640 20m × 20m grid cells. Every tree with 1 cm diameter at breast height (1.37 m) was tagged with a permanent number and data is recorded on species, diameter, health, and its spatial location with the grid cell. The Yosemite Forest Dynamics Plot has 34,468 recorded live trees as of the 2011 summer mortality check. The forest itself is in the Abies concolor [Mirb.] (white fir) zone but also contains an establishment of Pinus lambertiana [Dougl.] (sugar pine) and Calocedrus decurrens [Torr.] (incense cedar). The understory is fairly open with some areas of thick Cornus nuttallii [Torr. and Gray] growth, especially around the small streams that run through the plot. Deciduous species are limited but there are some Quercus kelloggii [Newb.] present. The Yosemite plot is home to the native Ursus americanus [Linn.] (Black bear), Puma concolor [Linn] (Mountain lion), and Odocoileus hemionus [Raf.] (Mule deer).
The Wind River Forest Dynamics Plot was established following the same protocol (Lutz et al. 2012, Condit R. 1998) as the Yosemite Forest Dynamics Plot in 2011. It is located in the Southern Cascade range of Washington State within the Gifford Pinchot National Forest. The plot is located at 371 m elevation on less than 10% slope (Shaw et al. 2004). The forest of the Gifford Pinchot National Forest is in the *Tsuga heterophylla* [Sarg.] (Western hemlock) zone with 288 *Pseudotsuga menziesii* [Mirb.] (Douglas-fir) trees with diameter at breast height ≥100 cm remaining from the initial cohort. Other species present are *Thuja plicata* [Donn] (western redcedar), *Acer circinatum* [Pursh] (vine maple), and *Taxus brevifolia* [Nutt.] (Pacific yew). The Wind River Plot is home to a herd of resident *Cervus canadensis roosevelti* [ErxI.] (Roosevelt elk).

Wind River also has a Mediterranean climate although much milder than Yosemite. Fall, winter, and spring experience the most precipitation with an average of 106 cm annually (Lutz et al. 2012). The Gifford Pinchot National Forest experiences multiple types of disturbances. The most common of which are fire, wind, insects, and disease (Franklin and Larson 2010). Before fire suppression, wildfire did burn large parcels of forest but much less frequently than Yosemite. Large wildfires only occurred at 300-650 year intervals historically (Shaw et al. 2004).
Most of the data used was collected during the summer months by university researchers and a field crew of employees and volunteers. The Yosemite Forest Dynamics Plot, being older than the Wind River Forest Dynamics Plot, had its first mortality survey done in June and July of 2011. After that data was compiled, 37,193 stems $\geq 1$ cm at breast height had been tagged and measured. Of these tagged trees, 34,468 are recorded as alive. Wind River was only just established in summer 2011 and it measures at 33,072 stems and 31,165 of those trees are tagged as alive. Within these two plots I focused upon the three most prevalent species in each. Considering that the forest type of both locations is largely coniferous, all 6 species are conifers. The three most common species in Yosemite Forest Dynamics Plot are *Pinus lambertiana*, *Abies*
concolor, and Calocedrus decurrens. For the Wind River Forest Dynamics Plot they are Pseudotsuga menziesii, Tsuga heterophylla, and Thuja plicata. The same protocol and methods were followed for data collection on both plots.

The six species were grouped together according to their life history traits. Pseudotsuga menziesii makes up the majority of the old, large diameter trees in Wind River and therefore a large part of the initial cohort. Seedlings of this species require full sunlight to grow and regenerate thickly after a disturbance (Schmidt 1957). Pseudotsuga menziesii has the capacity to live a very long time, often exceeding 500 years (McArdle et al. 1961). They are also a tall species with records showing specimens reaching 100.5 m. These characteristics follow closely what Grime had found with plants in the competitive strategy. Pinus lambertiana also displays competitive tendencies. Like Pseudotsuga menziesii, Pinus lambertiana can live up to 500 years and are the tallest and most voluminous of the pine species (Fowells and Schubert 1965). Both Pseudotsuga menziesii and Pinus lambertiana have difficulty regenerating in areas of high duff litter making it more difficult for seedlings to grow in areas of dense forestation (Fowells and Schubert 1965; Minore 1979).

Abies concolor survives with a more ruderal-like strategy. The ruderal plant’s characteristics include rapid and abundant seed production, especially in times of stress (Grime 1979). Studies on Abies concolor have shown that mature trees along clearcuts and areas of extensive disturbance produce 1.5 to 6.7 times as many cones as trees in a closed stand (Gordon 1970). This species is more shade tolerant that Pseudotsuga menziesii and pines allowing for seedling establishment in areas of dense underbrush (Minore 1979). Abies concolor has the capacity to as a suppressed member of the canopy for extended periods of time. However, as soon as there is an opening in the canopy, suppressed individuals rapidly grow to fill it (Minore 1979). Very similar to Abies concolor, Tsuga heterophylla is known for its prolific production of cones and ability to survive suppressed for long periods of time. This species is known for naturally growing at very high densities (Wiley 1976). If a disturbance occurs, Tsuga heterophylla trees experience a rapid growth release and can grow to dominate a stand. Tsuga heterophylla do not live as long as its neighbors, Pseudotsuga menziesii (Douglas-fir) and Picea sitchensis (Sitka spruce). Individuals rarely reach 500 years.

The species of the stress-tolerator strategy are long-lived slow growing specimens. Thuja plicata (Western red-cedar) is an example of a species that has maintained its prevalence in
Pacific Northwest forests by surviving where other species cannot. *Thuja plicata* left undisturbed can reach 800 to 1000 years old. It is a short and slow growing species, often overtopped by *Pseudotsuga menziesii* or *Tsuga heterophylla* (Curran and Dunsworth 1988; Smith and DeBell 1973). It does not suffer much insect herbivory but its greatest danger when regenerating is browse by ungulates (Furniss and Carolin 1977; Curran and Dunsworth 1988). *Calocedrus decurrens* (incense cedar) was also chosen as a likely representation of a stress-tolerator due to its slow growth and long life expectancy (Schubert 1965). Seedlings are further stunted because of herbivory. *Calocedrus decurrens* in particular is extremely drought tolerant making it a staple of south facing slopes in the Sierra Nevada (Pharis 1966).

As preliminary analysis of relative abundance, I looked at the total amount of live specimens of each species within the entire plots. While this is helpful for understanding how many individuals the ecosystem can support, it still was not a good indication of similarities between two comparable species in different plots. All of the live stems in each species were partitioned into 10 cm diameter classes. The resulting age brackets were consolidated to create a constant designation for what would be considered the initial cohort (≥100 cm) and what would be considered recent establishment (<40 cm). The small trees were chosen as those with diameters ranging from 1 cm through 40 cm. At this size, these trees have a low reproductive output and contribute little to the seedling regeneration of the site (van Wagtendonk, J.W. and Moore P.E 2010). The limit of ≥100 cm diameter for the initial cohort was chosen for its congruence with other large diameter tree studies in the region (Lutz et al. 2012). For each dominant species I also calculated basal area per hectare using the recorded diameters. This provided an idea of the relative productive area that each species occupies within its environment. This information would be used to determine if similar plant strategies hold similar basal area results.

**Results**

Analysis of the data quickly began to show a large disparity between the two plots and the amount of young regeneration occurring. The plot in Yosemite National Park showed greater amounts of small diameter trees for all three of the most common species. Wind River regeneration was largely comprised of *Tsuga heterophylla*. 
Table 1. Graph showing all 6 species of the YFDP and WFDP sorted by their diameter’s at breast height in 10 cm increments. Species codes are *Pinus lambertiana* (PILA), *Pseudotsuga menziesii* (PSME), *Abies concolor* (ABCO), *Tsuga heterophylla* (TSHE), *Calocedrus decurrens* (CADE), and *Thuja plicata* (THPL).

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Family</th>
<th>Total stems</th>
<th>Stems &lt;40 cm dbh</th>
<th>Stems ≥100 cm dbh</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Yosemite Forest Dynamics Plot</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Abies concolor</em></td>
<td>Pinaceae</td>
<td>24443</td>
<td>23180</td>
<td>103</td>
</tr>
<tr>
<td><em>Calocedrus decurrens</em></td>
<td>Cupressaceae</td>
<td>1634</td>
<td>1434</td>
<td>50</td>
</tr>
<tr>
<td><em>Cornus nutalli</em></td>
<td>Cornaceae</td>
<td>2365</td>
<td>2365</td>
<td>0</td>
</tr>
<tr>
<td><em>Pinus lambertiana</em></td>
<td>Pinaceae</td>
<td>4757</td>
<td>3848</td>
<td>339</td>
</tr>
<tr>
<td><em>Prunus spp.</em></td>
<td>Rosaceae</td>
<td>127</td>
<td>127</td>
<td>0</td>
</tr>
<tr>
<td><em>Pseudotsuga menziesii</em></td>
<td>Pinaceae</td>
<td>6</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td><em>Pinus ponderosa</em></td>
<td>Pinaceae</td>
<td>2</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td><em>Quercus kellogii</em></td>
<td>Fagaceae</td>
<td>1111</td>
<td>1090</td>
<td>0</td>
</tr>
<tr>
<td><em>Rhamnus californica</em></td>
<td>Rhamnaceae</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td><em>Salix scouleriana</em></td>
<td>Salicaceae</td>
<td>10</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td><strong>Wind River Forest Dynamics Plot</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Abies amabilis</em></td>
<td>Pinaceae</td>
<td>4417</td>
<td>4315</td>
<td>1</td>
</tr>
<tr>
<td><em>Abies grandis</em></td>
<td>Pinaceae</td>
<td>46</td>
<td>29</td>
<td>0</td>
</tr>
<tr>
<td><em>Acer circinatum</em></td>
<td>Aceraeae</td>
<td>11164</td>
<td>11161</td>
<td>0</td>
</tr>
<tr>
<td><em>Cornus spp.</em></td>
<td>Cornaceae</td>
<td>823</td>
<td>823</td>
<td>0</td>
</tr>
<tr>
<td><em>Pseudotsuga menziesii</em></td>
<td>Pinaceae</td>
<td>553</td>
<td>12</td>
<td>289</td>
</tr>
<tr>
<td><em>Rhododendron macrophyllum</em></td>
<td>Ericaceae</td>
<td>457</td>
<td>457</td>
<td>0</td>
</tr>
<tr>
<td><em>Taxus brevifolia</em></td>
<td>Taxaceae</td>
<td>2094</td>
<td>2057</td>
<td>0</td>
</tr>
<tr>
<td><em>Thuja plicata</em></td>
<td>Cupressaceae</td>
<td>228</td>
<td>95</td>
<td>47</td>
</tr>
<tr>
<td><em>Tsuga heterophylla</em></td>
<td>Pinaceae</td>
<td>9991</td>
<td>7991</td>
<td>96</td>
</tr>
<tr>
<td><em>Vaccinium spp.</em></td>
<td>Ericaceae</td>
<td>1301</td>
<td>1301</td>
<td>0</td>
</tr>
<tr>
<td>Other*</td>
<td></td>
<td>80</td>
<td>67</td>
<td>2</td>
</tr>
</tbody>
</table>

*Species whose total number of stems in the plot were ≤20.

The six species that were selected for the study were represented in all diameter classes (Table 1). Especially in Wind River, there were other species that had more individuals in the smaller diameter classes than the species that I selected but failed to have stems greater ≥100 cm.
It is for this reason that the species studied were the ones selected so that all diameter classes could be analyzed.

When comparing the pairs of species who share similar life strategies, greater patterns occur. There is still a large disparity between rates of regeneration but the numbers of remaining individuals from the initial cohort are very similar.

**Figure 3.** *Pseudotsuga menziesii* and *Pinus lambertiana* small diameter stems (≥1 cm dbh <40 cm). *Pseudotsuga menziesii*’s numbers are so small that it is represented as nearly zero on the graph.
Figure 4. *Pseudotsuga menziesii* and *Pinus lambertiana* large diameter stems (≥100 cm). The largest diameter *Pinus lambertiana* in the Yosemite Forest Dynamics Plot measures 204.1 cm. The largest diameter *Pseudotsuga menziesii* in the Wind River Forest Dynamics Plot measures 178.4 cm.

Figure 5. *Abies concolor* and *Tsuga heterophylla* small diameter stems (≥1 cm dbh <40 cm). *Abies concolor* >40cm stems largely outnumber *Tsuga heterophylla* small stems. For stems 1-9.9 cm in diameter, *Abies concolor* numbers 14,857 individuals. *Tsuga heterophylla* stems 1-9.9 cm in diameter number 4,875. These numbers decrease dramatically with size.
Figure 6. *Abies concolor* and *Tsuga heterophylla* large diameter stems (≥100 cm). The largest recorded *Abies concolor* was 164.9 cm diameter and the largest *Tsuga heterophylla* was 133.4 cm diameter.

Figure 7. *Calocedrus decurrens* and *Thuja plicata* small diameter stems (≥1 cm dbh <40 cm). *Calocedrus decurrens* small diameter stems greatly outnumber that of *Thuja plicata*. There is nearly no new regeneration of *Thuja plicata* in the Wind River Forests Dynamics plot evidenced by the low numbers of small trees recorded.
Figure 8. *Calocedrus decurrens* and *Thuja plicata* large diameter stems (≥100 cm). The largest recorded *Thuja plicata* measured 165.8 cm DBH and the largest diameter *Calocedrus decurrens* measured 196.2 cm.

Table 2. Basal area for all six species and their initial and regenerating cohorts. Values are in m² per hectare. Included is the total basal area for each plot including all species recorded herein.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of trees</th>
<th>Total Basal Area (m²/ha)</th>
<th>Basal Area (≤40 cm DBH)</th>
<th>Basal Area (≥100 cm DBH)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pinus lambertiana</em></td>
<td>4757</td>
<td>28.79</td>
<td>2.08</td>
<td>20.33</td>
</tr>
<tr>
<td><em>Pseudotsuga menziesii</em></td>
<td>577</td>
<td>19.25</td>
<td>0.03</td>
<td>16.28</td>
</tr>
<tr>
<td><em>Abies concolor</em></td>
<td>24482</td>
<td>29.22</td>
<td>12.06</td>
<td>5.88</td>
</tr>
<tr>
<td><em>Tsuga heterophylla</em></td>
<td>9991</td>
<td>34.48</td>
<td>5.05</td>
<td>7.16</td>
</tr>
<tr>
<td><em>Calocedrus decurrens</em></td>
<td>1588</td>
<td>4.79</td>
<td>0.75</td>
<td>2.63</td>
</tr>
<tr>
<td><em>Thuja plicata</em></td>
<td>201</td>
<td>3.82</td>
<td>0.10</td>
<td>2.77</td>
</tr>
<tr>
<td>YFDP Total Basal Area (m²/ha)</td>
<td></td>
<td>64.26</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WFDLP Total Basal Area (m²/ha)</td>
<td></td>
<td>62.67</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Discussion

**Initial Cohort**

The initial cohort is comprised of those trees that occupied a site immediately after a large disturbance. These trees often have full access to sunlight without any overstory to shade
them. The competitive strategy is most effective in colonizing newly disturbed sites (Grime 1979).

The diameter distribution for *Pinus lambertiana* and *Pseudotsuga menziesii* with diameters ≥100 cm is similar (Fig. 4). These species are the foundation of the initial cohort. Competitors are recognizable by their large diameter and height and this is supported by the majority of large trees ≥100 cm being of these two species. Both species demonstrate a gradual decline in the number of large specimens up through 180+ cm diameter. These two species are the most common large diameter trees in their respective plots.

The basal area table shows that most of the basal area for the species belongs to trees >100 cm diameter. 71% of the *Pinus lambertiana* total basal area is in large stems and 85% of *Pseudotsuga menziesii*’s total basal area.

*Abies concolor* and *Tsuga heterophylla* also show a close similarity in the distribution of large stems (Fig. 6). Both species have very close numbers in all diameter classes from 100 cm to 150+ cm. Ruderal species are not known for their ability to live as long or grow as large (Grime 1979). There were no *Tsuga heterophylla* stems recorded greater than 133.4 cm and the largest *Abies concolor* stem measured 164.9 cm. These two species’ largest specimens were the smallest of the six species studied. In terms of basal area, 20% of the total basal area for *Abies concolor* trees and 21% of the total basal area for *Tsuga heterophylla* is found in large diameter trees.

Stress-tolerator species have the capacity to live for extended periods of time, expanding their girth slowly over the years. The Yosemite and Wind River plots do not contain very many large diameter *Thuja plicata* and *Calocedrus decurrens* but it is still interesting to note that while their numbers are less than other species, the diameter distributions of these two species are still very similar (Fig. 8). *Calocedrus decurrens* does seem to have to ability to grow larger than *Thuja plicata* considering that there are still *Calocedrus decurrens* stems greater than 170 cm in diameter. 55% of the total basal area for CADE and 72% of the total basal area for THPL is found in large diameter trees.

**Regenerating Cohort**

Trees growing as part of the regenerating cohort must fight for their place in an already established forest. Sunlight and water is scarcer and small trees are at a disadvantage compared
to the century old large diameter trees in the canopy (Van Pelt and Franklin 2000). Ruderals and stress-tolerators will have greater chance regenerating in this environment (Grime 1979).

Figure 9. Orthophoto of the Yosemite Forest Dynamics Plot. The surveyed plot markers are superimposed onto the image with light colored dots.

Figure 10. Orthophoto of the Wind River Forest Dynamics Plot. Surveyed plot markers are shown as green dots. The image was taken during the fall months and areas appearing yellow is the deciduous foliage of *Acer circinatum*. 
The values of young *Pinus lambertiana* and *Pseudotsuga menziesii* stems with diameters at breast height <40 cm is very different (Fig. 3). The large tree species of the Yosemite site show a greater capacity for regeneration than Wind River. This may be contributed to environmental conditions or differences in species characteristic capabilities for regeneration. Both *Pinus lambertiana* and *Pseudotsuga menziesii* thrive in full sunlight as saplings and Yosemite has much more access to sunlight because of the lack of understory and water stress. *Pinus lambertiana* saplings are able to receive the light that is needed for growth. When viewing the plots from the air Yosemite has a much less dense canopy with sunlight able to reach the forest floor (Figure 9). The Wind River plot has very little canopy gap making the understory much more competitive for sunlight (Figure 10). These conditions are not favorable for the generation of *Pseudotsuga menziesii*.

When looking at the basal area for each species depending on their diameters as shown in Table 1 young *Pinus lambertiana* stems <40 cm in diameter still comprise 7% of the total basal area for the species in the whole plot. *Pseudotsuga menziesii* stems <40 cm only make up less than 1% of total basal area for the species. It is evident that nearly 100% of the basal area of *Pseudotsuga menziesii* in the entire plot consists of large, more reproductive trees.

*Abies concolor* and *Tsuga heterophylla* thrive in the understory of established forests (Fig. 5). These two species show the most similar diameter distribution for small stems of all 3 pairs. The Yosemite Forest Dynamics Plot still has greater rates of regeneration than Wind River but it is evident that small *Tsuga heterophylla* stems occupy a large percent of the understory vegetation for Wind River. Even though the numbers of small stems of *Tsuga heterophylla* is less than *Abies concolor*, it still represents the second most common species in the understory after *Acer circinatum*. Wind River has a much more diverse and crowded understory than Yosemite (Table 1). Unlike Yosemite, there are many species in Wind River that exist only in the understory with the diameter at breast height rarely going above 40 cm. This leads to a much more competitive environment for young seedlings in the understory. This may contribute to the large discrepancy between the numbers in the small diameter classes for *Tsuga heterophylla* and *Abies concolor*.

Looking at the basal area table *Abies concolor* the total basal area for stems <40 cm is 41% of the total basal area for the species. Only 16% of *Abies concolor’s* total basal area for the plot is held by trees <40 cm in diameter.
The stress-tolerators play a much more minor role in the forest ecosystem than the competitors and ruderals. There are more small *Calocedrus decurrens* trees than *Thuja plicata* (Fig. 7). Only 3% of the total basal area for *Thuja plicata* throughout the plot is attributed to <40 cm stems. *Calocedrus decurrens* shows good rates of regeneration with its small stems comprising 16% of the species basal area for the whole Yosemite Forest Dynamics Plot. The large difference in numbers between species could be attributed to browse. Wind River Forest Dynamics plot is home to an active herd of Roosevelt Elk. Few *Thuja plicata* saplings are able to overcome the amount of damage that they receive by browse. Yosemite Forest Dynamics Plot does maintain some seasonal deer activity but not to the same degree. Nonetheless there is still a large discrepancy between the small stems of the stress-tolerators as well.

**Effects of Stress**

The primary stress in the Yosemite Forest Dynamics Plot is lack of water (North et al. 2004). The lack of moisture in the plot results in more spacing between the trees and a sparse, low lying understory. The extra spacing between trees is responsible for the regeneration of *Pinus lambertiana* that requires sunlight to establish. Wind River does not experience an annual water deficit like Yosemite. It was measured that Wind River had three times the amount of water than Teakettle Experimental Forest (located in the Sierra Nevada) in the top 15 cm of soil in October (North et al. 2004).
Figure 11. Diagram showing the water supply to the Yosemite Forest Dynamics Plot. The water deficit occurs annually from May through October. Snow pack occurs from November to April and contributes the majority of the water supply to the site.

![Diagram showing the water supply to the Yosemite Forest Dynamics Plot.](image)

Figure 12. The water balance for the Wind River Forest Dynamics Plot. The climatic water deficit here is much smaller than the Yosemite Forest Dynamics Plot. Not only is the deficit less in amount but it only occurs from June through September. The supply of water between the two plots occurs at similar times during the year but the supply is much greater in Wind River.

Wind River’s greatest stress for understory trees is the availability of light (North et al. 2004). The canopy is much denser in this plot and most species cannot tolerate the lack of light on the forest floor thus leading to the large difference in the regenerating cohort of the two plots.

When studying the behaviors of the forests of the west coast of the United States, definite patterns begin to arise. There seems to be a model that is followed from early colonization of a disturbed site to the regeneration of new trees centuries later. There are those species that are quick to occupy an open site, grows to enormous heights, and lives for hundreds of years. Grime would call these competitors. There are also those species that are not the first to establish a site but occur afterwards, waiting and multiplying until an opening of the canopy occurs and they shoot upwards eventually dominating the canopy. Grime has named this strategy ruderal. Finally, there are the species that grow slowly and live in places that are too difficult for other species to be successful. They experience slow rates of growth but can grow for centuries. This is the stress-tolerator strategy. Grime mainly studied herbaceous species of Britain but it would seem like his models are applicable to the forest of the Pacific Northwest and Sierra Nevada.
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