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ADAPTIVE SIGNIFICANCE OF CHANGES FROM TRUE LEAVES TO PHYLLODES IN KOA

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Paper Title: Adaptive significance of changes from true leaves to phyllodes in koa from ecophysiology to management: the significance of heteroblasty in koa

During the first months to years after germination, koa (*Acacia koa* Gray) leaves transition from bipinnately-compound and horizontally-oriented true leaves to vertically-oriented phyllodes. Previous work has elucidated the similarities and differences between the two. They are similar in gas exchange rates and plasticity of photosynthesis in response to light availability (Walters and Bartholomew, 1990; Pasquet-Kok et al, 2010), but the horizontal orientation of true leaves in the juvenile phase allows for higher amounts of light capture in partially shaded conditions. They differ in their capacity to withstand drought conditions; phyllodes exhibit more stomatal control, reducing stomatal conductance with reducing soil water potential, and are able to maintain photosynthesis at lower soil water potentials than can true leaves (Pasquet-Kok et al, 2010). These results have led to hypotheses that true leaves are adapted to partial shade and phyllodes, to drought and full sun conditions. This has been supported by unpublished data (Walters and Bartholomew) suggesting that koa would not transition at light intensities below 70% full sun. Past research, however, demonstrating differences in the rate of transition in response to light (Walters and Bartholomew, 1990) and between koa from different islands (Daehler et al, 1999) suggests that, although similarities and differences between the leaf types have been described, the adaptive significance of heteroblasty (two or more leaf forms during development) in koa has not been characterized.

In order to address these knowledge gaps, we have conducted a series of studies. First, we investigated the influence of light intensity, light quality, water availability, and population on the rate of transition. We also tested whether the transition trigger was chronological in nature (e.g. days since germination) or a function of body size (e.g. total dry biomass). Finally, we aimed to characterize effect of the treatments on the phenotype at the time of transition. In order to do this, we conducted a split-plot experiment where light was the whole-plot factor with four levels (FULLSUN, 70% FILM, 25% FILM, and 25% CLOTH; the red to far-red ratio (R:FR) and light intensity were reduced with the neutral density film (Lee Filters, Hampshire, UK) and was reverted to full sun R:FR with shade cloth) and reduced water availability, the sub-plot factor. Two populations were included in the study: Honomolino and Umikoa from a dry and wet site, respectively. At the time of transition, when at least one fully-formed phyllode was formed, the seedling was harvested measured for a host of morphological parameters expected to vary in response to light intensity and quality. We hypothesized that the rate of transition would increase with greater light intensity, an elevated R:FR (a light quality ratio reduced by photosynthetically active radiation passing through leaves and signals to plants the presence of a canopy (Tao et al., 2008)), and reduced water availability. We also hypothesized that the dry site population would transition more quickly than the wet site population. Preliminary results suggest that the rate of transition is dependent on perspective. From a chronological perspective, the rate of transition increased significantly with increasing light intensity. Water availability did not have an effect, but the dry site population transitioned more quickly than the wet site population. From the perspective of body size, however, light intensity did not affect the timing of transition. Water availability did affect timing, however, with the reduced water transition treatment resulting in trees transitioning at a smaller body size. The population effect also disappeared when looking at transition rates as a function of total biomass. We were not able to detect a significant light quality effect on the timing of transition, although this might have been because the trees outgrew the greenhouse, eliminating the potential to observe the final number of transitioning individuals in the lowest light treatments. Light quality had a significant effect on the phenotype, where the height to the first branch and slenderness (height:basal diameter) were significantly increased for the 25FILM relative to 25CLOTH. Light intensity also influenced the phenotype; reduced light intensity reduced allocation to root biomass relative to shoot and leaf biomass and had the opposite effect on shoot biomass, in which the 25FILM and 70FILM treatments were significantly different than the FULLSUN treatment, but the 25CLOTH treatment was not. These results suggest the rate of transition in plastic in response to light availability; shade-adapted true leaves can be retained with decreasing light intensity. In spite of transitioning at equal rates in response to light intensity as a function of body size, the resulting phenotype is significantly different between light treatments at the time of transition. These phenotypes are consistent with traits associated with increased adaptiveness to the light treatment conditions (Forster and Bonner, 2009; Forster et al., 2011).

We also wanted to verify whether the disparate phenotypes in response to light availability were consistent with koa responses to shade in field plantings. Moreover, we asked whether these phenotypic responses could be harnessed by silviculturalists to improve the form of koa in plantations and managed forests. Results from two plantings on Hawaiʻi Island suggest that canopy architecture interacts with the shade avoidance response (Tao et al., 2008). In one planting, where two populations were planted under a variable canopy of koa at Puʻu Waʻawaʻa, transition at one and a half years was delayed, and slenderness increased, by increased shading, but survival decreased concurrently. Survival was under 25% in the most shaded planting locations and above 85% in the most open planting sites in the absence of rust infection. These results suggest that the adaptiveness of plasticity of transition and phenotype in response to shade is limited. Our results from another study at Humuʻula on the Big Island, where koa was planted between rows of sugi pine (*Cryptomeria japonica*) with a clear path to the canopy, suggest that these plastic responses are can be adaptive to gap conditions, rather than partially shaded conditions. At Humuʻula, survival after one and a half years was not significantly affected by shade, but height increased 100 cm (39.37 in) in the most shaded planting sites when combined with fertilization. Future work at Humuʻula will assess the long-term effects on form.

The results from these three studies suggest that koa's response to partial shading is an adaptation to gap-regeneration and recruitment. The factors affecting the timing of transition, however, are not fully elucidated. Our evidence suggests an interaction between the microclimate and the provenance of the population. The factors instrumental in triggering transition, moreover, are dependent on perspective. These results have the potential to influence nursery culture of seedlings before outplanting, allowing for improved tailoring of the seedling to the planting site. They also have applications for design of koa plantations and restoration sites. Finally, further research comparing abiotic triggers of transition using populations across a range of ecoregions could improve our understanding of the adaptiveness of heteroblasty and the plasticity of phase change.

Figure 1. One-year-old *Acacia koa* seedings planted in partial shade of sugi pine (Cryptomeria japonica) at Humuʻula on Mauna Kea, Hawaiʻi Island. Seedlings increased in height when fertilized and grown in partial shade. The seeding in the foreground still has juvenile leaves while the seeding in the background has transitioned to mature leaves (phyllodes).