PART OF A HIGHLIGHT ON TREE BIOLOGY

Branching habit and the allocation of reproductive resources in conifers

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- **Background and Aims** Correlated relationships between branch thickness, branch density, and twig and leaf size have been used extensively to study the evolution of plant canopy architecture, but fewer studies have explored the impact of these relationships on the allocation of reproductive resources. This study quantifies pollen cone production in conifers, which have similar basic reproductive biology but vary dramatically in branching habit, in order to test how differences in branch diameter influence pollen cone size and the density with which they are deployed in the canopy.
- **Methods** Measurements of canopy branch density, the number of cones per branch and cone size were used to estimate the amount of pollen cone tissues produced by 16 species in three major conifer clades. The number of pollen grains produced was also estimated using direct counts from individual pollen cones.
- **Key Results** The total amount of pollen cone tissues in the conifer canopy varied little among species and clades, although vegetative traits such as branch thickness, branch density and pollen cone size varied over several orders of magnitude. However, branching habit controls the way these tissues are deployed: taxa with small branches produce small pollen cones at a high density, while taxa with large branches produce large cones relatively sparsely.
- **Conclusions** Conifers appear to invest similar amounts of energy in pollen production independent of branching habit. However, similar associations between branch thickness, branch density and pollen cone size are seen across conifers, including members of living and extinct groups not directly studied here. This suggests that reproductive features relating to pollen cone size are in large part a function of the evolution of vegetative morphology and branching habit.

Key words: Corner's Rules, plant architecture, reproductive allocation, conifer, pollen cone.

INTRODUCTION

Relationships among basic features of plant architecture such as branch diameter and leaf size have been widely used to understand the evolution of plant canopy structure and the allocation of vegetative resources (see [Hallé *et al.*, 1978](#); [Wright *et al.*, 2007](#); [Olsen *et al.*, 2009](#)). In particular, many studies have explored a correlated set of traits termed 'Corner's Rules' or the 'leaf size–twig size spectrum', in which thicker branches tend to bear larger or more complicated leaves, but these thick branches occur at a relatively low density in the canopy ([Corner, 1949](#); [Halle *et al.*, 1978](#); [White, 1983a](#), [White, 1983b](#); [Ackerly and Donoghue, 1998](#); [Brouat *et al.*, 1998](#); [Westoby and Wright, 2003](#); [Olsen *et al.*, 2009](#)). These relationships probably result from the mechanical properties of stems and branches (e.g. small stems could not mechanically or hydraulically support a very large leaf) as well as selection against architectures that result in self-shading. Similar relationships should apply to reproductive structures borne on the branches as well, and therefore offer a way to understand the evolution of traits such as seed or fruit size as well as the deployment of reproductive resources within the canopy ([Primack, 1987](#); [Geber 1990](#); [Ackerly and Donoghue, 1998](#); [Preston, 1999](#); [Herrera, 2002](#)). A variety of previous studies have found strong associations between architectural features and reproductive allocation, especially within inflorescences ([Bond and Midgely, 1988](#); [Westoby and Wright,](#)

[2003](#); [Diggle and Miller, 2004](#); [Buide, 2008](#); [Chen *et al.*, 2009](#); [Ortiz *et al.*, 2009](#)). However, other studies have found only weak or complex associations between variables such as branch thickness, leaf size, and fruit or seed size ([Cornelissen 1999](#); [Wright *et al.*, 2007](#)), suggesting that branching architecture may influence only certain aspects of reproductive allocation or particular types of reproductive structures.

Investigating these relationships across a wide taxonomic sampling of plant groups may help assess their generality and their utility for understanding broader evolutionary patterns, and conifers offer several specific advantages as a study group. All conifer species are similar in growth habit (woody shrubs or trees), but their branching habit varies from highly ramified systems of tiny branches bearing small leaves to large-diameter branches bearing much larger broad leaves or needles (Fig. 1A–D). Basic reproductive biology is also directly comparable across conifers, which are all wind pollinated ([Niklas, 1982](#); [Owens *et al.*, 1998](#)), and measuring conifer reproductive investment is relatively straightforward because their pollen-producing and seed-producing organs are borne on separate, compact structures (the pollen cones and seed cones, respectively). Previous studies have used these advantages to investigate architecture and reproductive allocation in conifers, although they have generally focused on quantifying male and female investment relative to overall tree size, canopy shape and branch position in a relatively small number of species (see [Bickel and Freeman,](#)

FIG. 1. Examples of foliage morphology and branching habit in conifer species used in this study. (A) *Juniperus virginiana* with imbricate scale leaves and highly ramified small branches that terminate in small pollen cones. (B) *Cryptomeria japonica* with thicker branches bearing clusters of axillary pollen cones. (C) *Pinus resinosa* with thick branches bearing long needles and clusters of large axillary pollen cones. (D) *Cedrus atlantica* with short shoots terminating in a single large pollen cone. Scale bars = 2.0 cm.

1993; Arista and Talavera, 1997; Shmida *et al.*, 2000; Ne'eman *et al.*, 2011). In this study, however, I use a broad taxonomic sample of conifers to examine more general relationships between branch thickness and the deployment of reproductive resources in the plant canopy. Specifically, I test predictions based on Corner's Rules that species with larger diameter branches should bear larger cones and that these larger cones will be borne at a lower density in the canopy. I also quantify investment in pollen and pollen cone tissues in the canopy to test whether differences in branching habit influence the total allocation of reproductive resources.

This study focuses on male reproductive effort because pollen cones are simple, ephemeral structures (consisting of an axis with microsporophylls bearing the pollen-producing organs, or pollen sacs) that offer a direct measure of annual reproductive investment. In contrast, seed cones include additional investment in tissues that function in seed protection and seed dispersal (Geldenhuys, 1993; Benkman, 1995; Parchman and Benkman, 2002; Leslie, 2011). The species sampled in this study encompass the major types of foliage and branching diversity found among three large clades of conifers (Cupressaceae *sensu lato* including 'Taxodiaceae', Pinaceae and Taxaceae), as well as the smaller scale variations in branching habit found within these groups, such as planated splays of branches (e.g. in *Thuja occidentalis*) and more three-dimensional arrays (*Juniperus virginiana*). Although pollen

cone production in conifers can be influenced by many factors, including tree size and age, growth environments, annual cycles in fecundity and even interactions with pollen-feeding insects (Schoen and Stewart, 1986; Caron and Powell, 1989; McCullough, 2000; Shmida *et al.*, 2000; Ortiz *et al.*, 2002; Ne'eman *et al.*, 2011), measurements used in this study are based on lower branches of the canopy in fecund individuals where pollen cone production is typically concentrated (Lev-Yadun and Liphshitz, 1987; Shmida *et al.*, 2000). This study therefore provides an estimate of the maximum amount of pollen cone tissues and pollen production within a typical volume of the shoots and leafy twigs that fill the canopy space of each species. These estimates can then be directly compared with differences in branching habit among species.

MATERIALS AND METHODS

Branch measurements and pollen cone measurements were made immediately before or during pollen release on individual open-grown trees from five species of Cupressaceae, ten species of Pinaceae and one species of Taxaceae growing in and around the Yale University Campus in New Haven, Connecticut, the Great Mountain Forest in Norfolk, Connecticut, and the Arnold Arboretum in Jamaica Plain, Massachusetts. Counts of the number of pollen grains produced per cone were made only from cones collected prior to pollen release. Where possible, 2–4 individuals of each species were sampled, although in some cases only a single fertile individual was available. Trees were of various sizes, although most were <15 m tall (see Appendix for details). Although the species included in this study represent only a fraction of total conifer diversity, they include representatives from many of the major lineages within the Cupressaceae and Pinaceae (see Gadek *et al.*, 2000; Wang *et al.*, 2000; Mao *et al.* 2011).

Total investment in pollen cone tissues in the canopy space was calculated by multiplying three measured variables: the density of twig tips (the distalmost branch tips bearing leaves) in the canopy space; the average number of pollen cones borne on each twig; and the average pollen cone volume. Twig tips were chosen as a measured variable because pollen cones are always produced at or near tips rather than on older branches. Twig tip density was measured as the number of tips that were present inside a cubic wooden frame of known volume placed over a section of the canopy. Frames were constructed of balsa wood with an open end so as to disturb the foliage as little as possible, and different sized cubes were used to facilitate counting; for example, a smaller frame was used to count the tiny, highly ramified branches of *Juniperus* while a larger frame was used for *Pinus*. Ten separate measurements were made on different regions of the lower branches for each individual tree and averaged. Although measurements were based on the accessible lower branches of the trees, there was no visible difference in the amount or concentration of pollen cones on the upper vs. the lower branches of the trees studied here.

The average number of pollen cones per twig tip was recorded by tallying the total number of twig tips and pollen cones contained in branch samples cut from individual trees. Samples were cut from the first branching order proximal to the leaf-bearing twigs; in this way, the samples all contain

the same functional unit consisting of the photosynthetic twigs plus the larger non-photosynthetic branch bearing them. In most cases, five samples were cut from different parts of the lower crown of each individual tree, although for some thick-branched Pinaceae one or two large branches (typically including 20–100 twig tips) were collected instead. In total, between 25 and 8000 tips per individual were tallied depending on the species and size of the branches. Measurements of twig tip diameter were also taken from ten distal twigs in each individual of each species. Diameter measurements were made around halfway down the length of the branch proximal to the growing twig tip; they therefore record branch diameter prior to extensive secondary growth.

Volume was estimated in 5–10 pollen cones from each individual by treating cones as ellipsoids, with length and maximum width as major and minor axes, respectively. Volume was primarily used as a measure of tissue investment because this study focuses on changes in cone size in relation to branching architecture. However, dry cone mass (including the mass of pollen grains in the pollen sacs) was also measured for five cones from each species where possible, although two species of Pinaceae and one species of Cupressaceae did not include enough collected unopened pollen cones for both pollen counts and pollen cone mass measurements.

The total number of pollen grains produced by a given volume of canopy was calculated by multiplying twig tip density, the number of cones per branch and the total number of pollen grains produced per cone. This value was estimated in five pollen cones for each species by counting the number of pollen grains produced in a typical pollen sac and then multiplying this value by the number of pollen sacs produced in each cone. Pollen production per pollen sac was estimated by spreading the contents of a single pollen sac of known volume (calculated by treating it as an ellipsoid with major and minor axes corresponding to its measured dimensions) evenly across a microscope slide with a small grid placed behind it. Using a Zeiss Model SR stereomicroscope, the number of grains per grid cell was counted in each of the cells in two transects (10–20 grid cells per transect) across the total area and averaged. This number was multiplied by the number of grid squares containing pollen to arrive at the number of total pollen grains per pollen sac, which was then divided by the pollen sac volume to give the number of pollen grains per pollen sac volume. Finally, this number was multiplied by both the average volume and total number of the pollen sacs in the cone to arrive at the total pollen production. This method accounts for potential differences in pollen production due to variability in pollen sac size within the cone, but is sensitive to small errors in measured pollen sac volumes. Therefore, total pollen production per cone was also estimated simply as the number of counted grains per pollen sac multiplied by the total number of pollen sacs per cone. These different estimates of pollen production were then averaged (although they did not differ by more than 15 % in any individual).

All statistical procedures used in this study were performed with R version 2.12.1. All P -values and R^2 values shown were calculated with Standardized Major Axis regression (Reduced Major Axis regression) on log-transformed data using the R package SMATR. Because the data were not typically normally distributed, error bars in single measured variables (Figs 2A,

FIG. 2. (A) Relationship between pollen cone volume and cone dry mass in one species of Taxaceae, four species of Cupressaceae and eight species of Pinaceae, as indicated in the key. (B) Relationship between pollen grain volume and the number of pollen grains produced per volume of pollen cone tissue in one species of Taxaceae, five species of Cupressaceae and ten species of Pinaceae. Error bars represent the 95 % confidence intervals based on 10 000 resampled means (see Materials and Methods for details). In some cases, error bars are smaller than the size of the data points in these plots.

B and 3A, B) represent 95 % confidence intervals based on 10 000 means calculated from resampled data. For values derived from multiplying several measured variables (Fig. 3C–E), 95 % confidence intervals were generated through an iterative resampling procedure where the value for every species was recalculated 10 000 times, each time multiplying one randomly sampled measurement from each of the three constituent variables.

RESULTS

Cone size and pollen production

Pollen cone volume was strongly correlated with cone dry mass, including the mass of the pollen grains contained within the pollen sacs (Fig. 2A; $R^2 = 0.95$, $P < 0.001$). The number of pollen grains produced per volume of cone tissue was strongly correlated with estimated pollen grain volume, which was calculated from linear measurements of pollen grains (Fig. 2B; $R^2 = 0.95$, $P < 0.001$). Both within and among families, species with smaller grains produced more grains per cone volume.

FIG. 3. Relationships between twig diameter and twig density (A), individual pollen cone volume (B), pollen cone volume per branch (C), total pollen cone volume produced in the canopy space (D) and total pollen production in the canopy space (E) for one species of Taxaceae, five species of Cupressaceae *sensu lato* and ten species of Pinaceae (nine species in D), as indicated in the key. Error bars represent the 95 % confidence intervals generated by 10 000 resampled means (A, B) or recalculating the total values 10 000 times using a resampling procedure (C–E; see Materials and Methods for details). In some cases, error bars are smaller than the size of the data points in these plots. The position of *Cryptomeria* is indicated in (A) since it is distinct from the other Cupressaceae taxa in this study and is specifically discussed in the text.

Branch and cone size

Conifer species with larger diameter twigs had fewer twig tips per cm^3 of overall canopy space (Fig. 3A; $R^2 = 0.86$, $P < 0.001$). Individual pollen cone volume was also positively associated with branch diameter across conifers in general (Fig. 3B; $R^2 = 0.80$, $P < 0.001$), although the relationship is somewhat complex within clades. Large twigs did not bear small cones, and very small twigs did not bear large cones, but there was variation among taxa between these extremes, especially in Pinaceae. However, there was a more straightforward positive relationship between the total volume of pollen cones produced per twig (individual pollen cone volume

multiplied by the number of cones per twig) and twig diameter (Fig. 3C; $R^2 = 0.91$, $P < 0.001$).

Total reproductive output

The total volume of pollen cone tissues produced per unit volume of canopy space (calculated as the product of twig density, the average number of cones per twig and the average volume of individual pollen cones) was variable across the species included in this study but did not show a trend with increasing twig diameter (Fig. 3D; $R^2 = 0.006$, $P > 0.1$). However, twig diameter does control how these tissues are deployed in the canopy. Cupressaceae species

with small diameter branches produce very small pollen cones, but the high density of fertile twig tips in the canopy space results in a total volume of pollen cone tissue that is comparable with that in other conifers (Fig. 3D; see also Fig. 1A). *Cryptomeria*, an early diverging lineage of Cupressaceae, produces thicker twigs with a corresponding decrease in twig density, but total pollen cone volume within the canopy remains similar because twigs produce clusters of cones (see Fig. 1B). Most Pinaceae have a similar arrangement, although typically pollen cones are borne on large diameter twigs at very low canopy twig densities. Pollen cones and pollen cone clusters in Pinaceae are therefore correspondingly larger (see Fig. 1C).

In contrast to the amount of pollen cone tissues, the number of pollen grains produced per unit volume of canopy space (calculated as the product of twig density, the average number of cones per twig and the number of pollen grains per cone) decreased with increasing twig diameter across the studied species (Fig. 3E; $R^2 = 0.61$, $P < 0.001$). However, this effect was primarily due to differences in pollen output between the major conifer clades; within Pinaceae and Cupressaceae the relationship between twig diameter and total canopy pollen output was not significant ($R^2 = 0.08$ and 0.03 , respectively; $P > 0.1$).

DISCUSSION

Twig size, and therefore branching density, strongly influences the way in which pollen-producing tissues are packaged and deployed in the conifer canopy and generally follows predictions based on Corner's Rules, i.e. larger branches tend to bear bigger cones but occur at lower density in the canopy. That pollen cones more closely follow these expectations than angiosperm seed or fruit investment (Cornelissen, 1991; Wright *et al.*, 2007) may result from the ecological and structural simplicity of this aspect of conifer reproduction. Unlike the biology of seeds or fruits, which show significant variation among species as a result of differences in life history strategies or propagule dispersal ecology (see Leishman *et al.*, 2002; Moles *et al.*, 2005; Moles and Westoby, 2006), the production and shedding of large quantities of pollen is a consistent feature of reproductive biology across all conifers.

This basic reproductive similarity probably underlies the similarity in total allocation to pollen and pollen-producing tissues found in this study. Although the absolute investment in male reproductive effort per tree depends on the number of fertile branches and is therefore related to overall tree size and canopy shape (Arista and Talavera, 1997; Ne'eman *et al.*, 2010), the maximum amount of resources that conifers invest in male reproductive function within the fertile portions of the canopy is similar (Fig. 3D). This is surprising given the differences in specific aspects of branching habit, reproductive biology, ecology and evolutionary history among these species. For example, both the Cupressaceae species *J. virginiana* and the Pinaceae species *Abies koreana* have similar total pollen cone production even though one is dioecious (separate individuals produce exclusively pollen or seed cones) and has highly ramified, tiny branches while the other is monoecious (individuals produce both pollen and seed cones) and has much larger branches and pollen cones. Although these types of specific differences undoubtedly contribute to the observed variation in total pollen cone

investment, this study suggests that branch size and branching habit do not play a general role in determining total reproductive allocation in the canopy, only in how these resources are arrayed within it.

While the size of pollen cones and their canopy density appear to be primarily determined by vegetative branching habit rather than phylogenetic relationships, traits shared by particular clades can influence how reproductive resources are deployed in other ways. For example, pollen cones of Cupressaceae and Taxaceae produce more pollen grains per cone volume than those of Pinaceae (Fig. 2B) because their pollen grains are smaller ($26\ \mu\text{m}$ in diameter compared with $57\ \mu\text{m}$ in diameter for Pinaceae not including sacci). These small grains are a feature shared by a larger clade composed of Cupressaceae, Taxaceae and the monotypic genus *Sciadopitys* (Gadek *et al.*, 2002; Rai *et al.*, 2008). Because pollen cone density is roughly constant (see Fig. 2A), variation in pollen grain size among conifer species represents another important difference in how reproductive resources are deployed, leading to the production of either large numbers of small grains or a small number of large grains from the same amount of tissue. In this case, these different inherited strategies have important implications for reproductive biology, since species producing a greater number of pollen grains may be capable of pollinating more ovules.

In a broader evolutionary sense, the associations between branch thickness and pollen cone size demonstrated in this study are pervasive across living and extinct conifers. For example, extant Podocarpaceae genera such as *Dacrydium*, *Halocarpus* and *Microcachrys* are similar to many unrelated Cupressaceae species in having small scale-leaves and small terminal pollen cones borne on highly ramified twigs (pers. obs.; see also Biffin *et al.*, 2012). Similar morphology also occurs in Jurassic and Cretaceous representatives of the Araucariaceae, Cupressaceae and Podocarpaceae clades, as well as members of the extinct Cheirolepidiaceae (Harris, 1979; Archangelsky and Del Fueyo, 1989; Del Fueyo, 1991; Axsmith *et al.*, 2004). These associations probably result from convergence in vegetative morphology, since both living and extinct conifers exhibit a similar suite of foliage types reflecting the shared hydraulic constraints that govern morphology in the single-veined leaves common to most members of the group (Zwieniecki *et al.*, 2004; Brodribb *et al.*, 2010). These foliage types are strongly associated with different branch thicknesses, and so are therefore related to the size of the cones borne by the branches. The limited suite of conifer leaf morphologies leads to repeated patterns of correlated vegetative and reproductive morphology, where cone size evolution appears to be largely controlled by changes in vegetative morphology. For example, extant Araucariaceae species tend to have large branches bearing large pollen cones, while many Mesozoic fossil representatives had small, highly ramified branches bearing small pollen cones (Leslie *et al.*, 2009). Corner's Rules therefore offer a way to understand and interpret important macroevolutionary patterns in conifer reproductive biology, particularly cone size evolution. However, we might also expect to find similar patterns and size relationships expressed in a much wider variety of vascular plant groups in which reproductive organs are borne in cones or strobili, such as in extinct and extant lycopsids and horsetails.

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APPENDIX

Tree species used in this study. Diameter at breast height (DBH) provides information on the size of the trees studied, although it was not recorded for all individuals since this study did not focus on variation in reproductive allocation as a function of tree size. Native species are those that occur naturally in the New England area. Locations are the areas where each species was sampled; Arnold = Arnold Arboretum, Jamaica Plain, Massachusetts; GMF = Great Mountain Forest, Norfolk, Connecticut; Yale = Yale Campus, New Haven, Connecticut.

Taxon	Family	Individuals studied	DBH (cm)	Native species?	Location
<i>Abies chensiensis</i>	Pinaceae	1	20.6	No	GMF
<i>Abies koreana</i>	Pinaceae	2	25.1–32.7	No	GMF
<i>Abies nordmanniana</i>	Pinaceae	1	–	No	GMF
<i>Cedrus atlantica</i>	Pinaceae	4	22.6–76.6	No	Yale/ Arnold
<i>Picea abies</i>	Pinaceae	1	–	No	GMF
<i>Picea glauca</i>	Pinaceae	2	28.3	No	GMF
<i>Pinus resinosa</i>	Pinaceae	2	24.5–44.9	Yes	Yale
<i>Pinus rigida</i>	Pinaceae	2	–	Yes	GMF
<i>Pinus strobus</i>	Pinaceae	2	34.4–64.9	Yes	Yale/GMF
<i>Tsuga canadensis</i>	Pinaceae	3	58.9	Yes	Yale/GMF
<i>Cryptomeria japonica</i>	Cupressaceae	2	14–18.5	No	Yale
<i>Callitropsis nootkatensis</i>	Cupressaceae	1	–	No	Arnold
<i>Chamaecyparis pisifera</i>	Cupressaceae	2	43.7–59.0	No	Yale
<i>Juniperus virginiana</i>	Cupressaceae	4	27.9–55.0	Yes	Yale
<i>Thuja occidentalis</i>	Cupressaceae	2	20.7–21.0	Yes	Yale
<i>Taxus cuspidata</i>	Taxaceae	2	25.1–27.4	No	Yale