Were Mesozoic Ginkgophytes Shrubby?

W. A. Green—Department of Geology—Yale University—P. O. Box 208109, Yale Station—New Haven, Connecticut 06520—walton.green@yale.edu

The conventional view sees all ginkgophytes as arborescent, by analogy with modern Ginkgo biloba:



but there is in fact little evidence

Records of Jurassic fossil occurrences in the Compendium Index of Mesozoic and Cenozoic Type Fossils (Dorf 1940), a catalog of fossil occurrences organized by gross morphology, show a negative correlation between the presence of ginkgphytes and shrubby or herbaceous groups (pteridophytes), and little relationship with the presence of predominantly arborescent groups (other gymnosperms). Earlier examinations of evolutionary change through time, like Niklas et al. (1985) and Lidgard and Crane (1988), show no particular ginkgophyte expansion in the Middle Jurassic, but Tralau (1967, 1968) and other careful studies of ginkgophytes support the Middle Jurassic diversification shown by the Compendium Index data presented here. Since these data also include information about other major groups, it provides evidence of covariation that, if interpreted as competitive interactions, would suggest the presence of ginkgophytes of low stature and shrubbier growth form in the forest understrory or open, disturbed environments.

NUTRIENT-LIMITED

Data on leaf morphology in the Mesozoic of North America shows a proportional increase of bifurcated, ginkgo-like leaves during the middle of the Jurassic. This ginkophyte acme is correlated with a decreased proportion of the leaf forms associated with herbaceous or shrubby pteridophytes, and with no substantial change in the proportion of leaf forms associated with canopy gymnosperms. The increase in ginkgo-like foliage at the same time as fern-like forms decreased in relative abundance suggests replacement of some part of the forest understory or early-successional habitats by early ginkgophytes. That is, early ginkgophytes may not have been competing for light or water in an established gymnosperm canopy. This suggests that most Mesozoic ginkgophytes were shrubs rather than being large trees like the surviving *Ginkgo biloba*. Such a result explains the absence of Mesozoid ginkgophyte wood and supports the argument that has already been made from sedimentological data, that to a much greater extent than do individuals of *Ginkgo biloba* now cultivated around the world, many ancestral ginkgophytes pursued early-successional strategies.

ords quares v

1: Competitive displacement

Pt

Gi

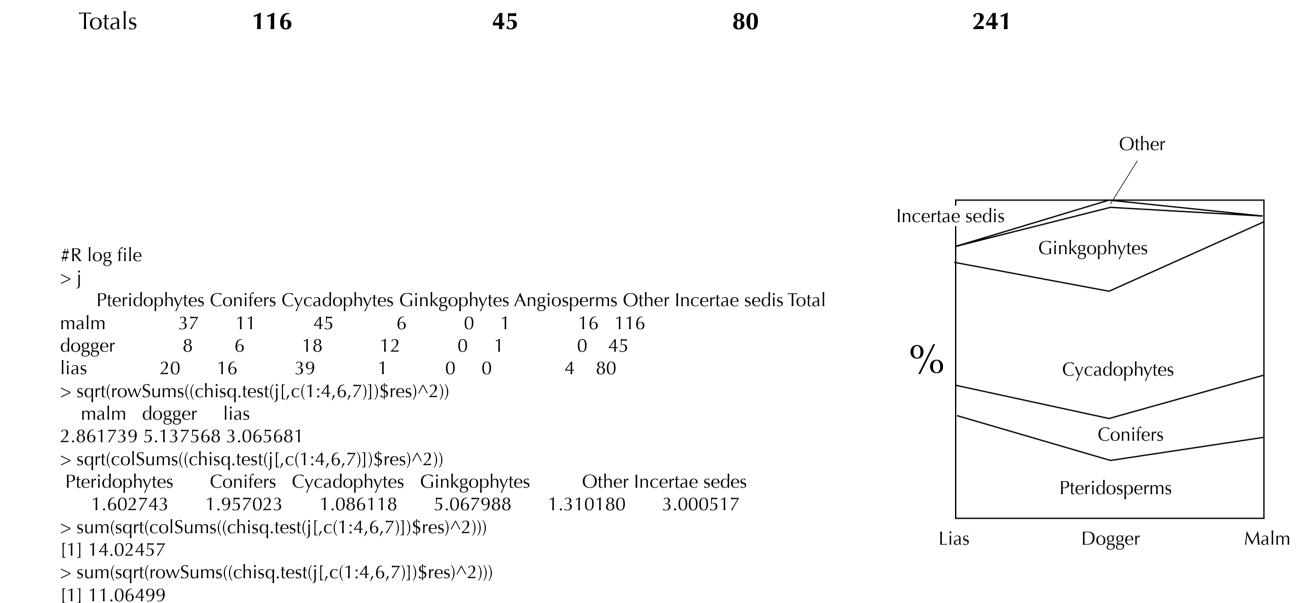
Ot

In

Jurassic Records from the Compendium Index			Total Naroinal root-sum-set ()	
	Early (Lias)	Middle (Dogger)	Late (Malm)	to. Mrs. t.
teridophytes	37, 32%, $\chi^2 = -0.34$	8, 18%, $\chi^2 = -1.2$	20, 25%, χ ² = 1.0	65 1.6
onifers	11, 9%, $\chi^2 = 1.5$	6, 13%, $\chi^2 = -0.07$	16, 20%, $\chi^2 = -1.2$	33 2.0
ycadophytes	45, 39%, $\chi^2 = 0.88$	18, 40%, χ ² = <mark>-0.24</mark>	39, 49%, $\chi^2 = -0.58$	102 1.1
inkgophytes	6, 5%, $\chi^2 = -2.1$	12, 27%, $\chi^2 = 4.5$	1, 1%, $\chi^2 = -1.0$	19 <mark>5.1</mark>
Other	1, 1%, χ ² = -0.81	1, 2%, χ ² = 1.0	0, 0%, χ ² = 0.04	2 1.3
ncertae Sedis	16, 14%, χ ² = -1.0	0, 0%, $\chi^2 = -1.9$	4, 5%, $\chi^2 = 2.0$	20 3.0
Totals	116	45	0 0	241

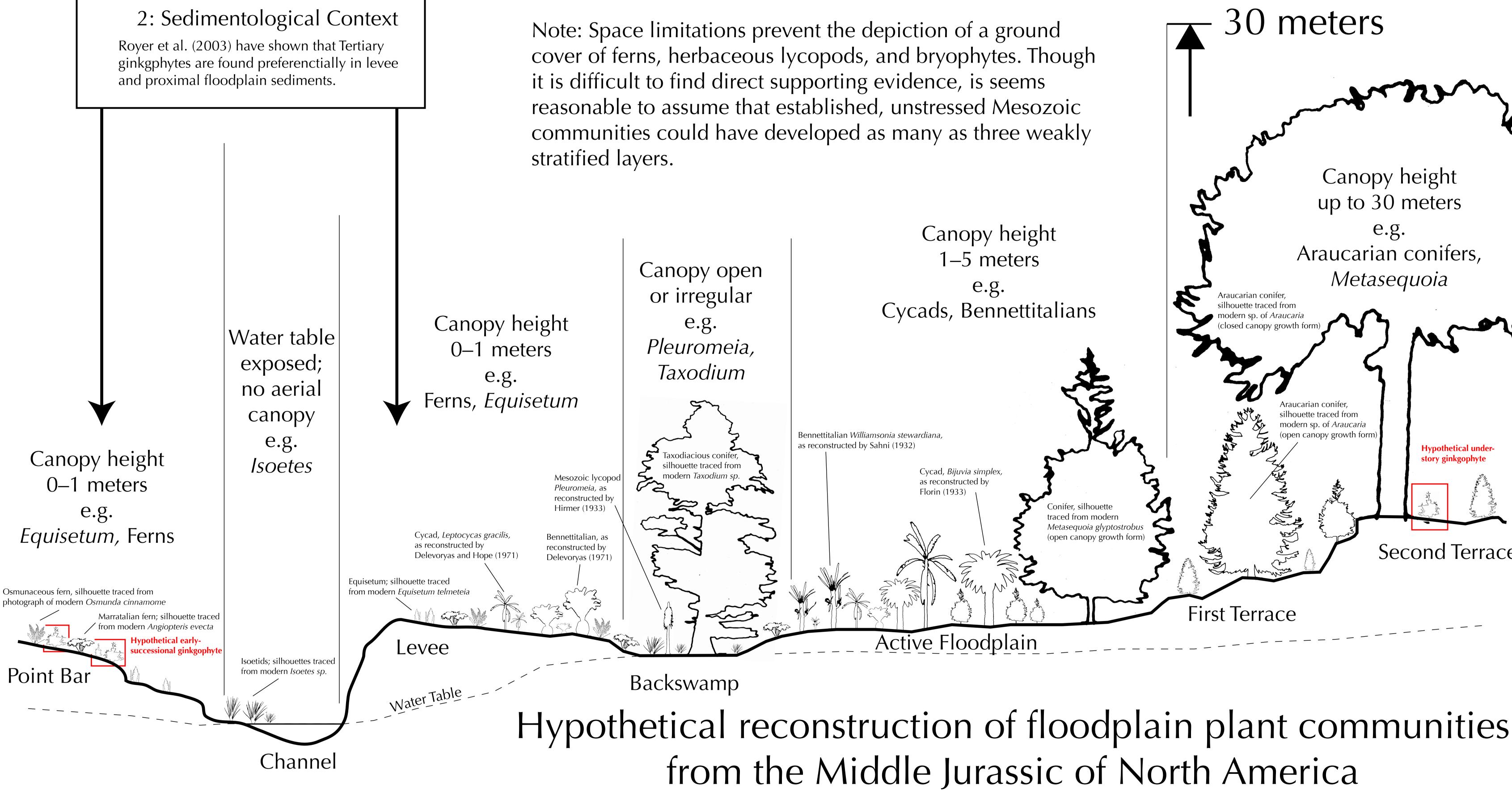
for arborescent ginkgophytes before the Tertiary. On the contrary, a number of indications seem to suggest the possibility that many early gingkophytes were small shrubs:

2 meters



COMPETITION-LIMITED

DISTURBENCE-LIMITED



Proximal floodplain;

disturbance frequent compared with generation

time, canopy poorly developed, species likely to be short-lived, low of

stature, and *r*-selected, investment in reproduction and vegetative growth comparatively low. Clonal

reproduction and ast initial growth likely. Fossils found in coarse or well-sorted sediments showing evidence of alluvial deposition and

lacking extensive soil formation. Note that the common occurrence in the fossil record of allochthonous (transported) ginkgophyte foliage in proximal facies must be discounted.

3: Absence of wood

Scott et al. (1962) could verify no occurrences of clear ginkgophyte wood earlier than the Eocene: "in marked contrast to the abundant leaf remains of the order, fossil woods of the Ginkgoales are rare" (Scott et al. 1962:1095). No other convincing candidates for Mesozoic ginkgophyte wood have been found, which is surprising given the amount of other well-preserved Mesozoic gymnosperm wood.

4: Atypical characters

Distal floodplain; disturbance less frequent, canopy better developed, species longer lived, higher in stature and with greater investment in disseminules and non-photosynthetic

vegetative growth. Fossils found in fine sediments, often with ped structures or identifiable soil stratification. Note that the gradiant depicted

above is frequently compressed into relatively short distances when flood disturbance is low. This representation

Ginkgo biloba has polymorphic foliage, an early bolting growth phase, and poor shade tolerance, all characteristics that are rare or absent in habitually canopy-forming trees. See Royer et al. (2003) for further discussion.

Works Cited

Delevoryas, T. (1971) Investigations of North American Cycadeoids: Weltrichia and Williamsonia from the Jurassic of Oaxaca, Mexico. American Journal of Botany 78:177–182. Delevoryas, T. and R. C. Hope (1971) A new Triassic cycad and its phyletic implications. *Postilla* 150:1–14. Dorf, E. (1940) An illustrated catalogue of Mesozoic and Early Cenozoic plants of North America. Science 91(2368):1–2. Florin, R. (1933) Studien über die Cycadales des Mesozoikums. Kungl. Svenska Vetenskapsakademiens Handlinger III 12:1–134. Hirmer, M. (1933) Rekonstruktion von Pleuromeia sternbergi Corda nebst bemerkungen zur Morphologie der Lycopodiales. Paleontographica B 78:47–56. Knoll, A. H., K. Niklas, and B. H. Tiffney (1979) Phanerozoic land plant diversity in North America. Science 206:1400–1402. Lidgard, S. and P. R. Crane (1988) Quantitative analysis of early angiosperm radiation. *Nature* 331:344–346. Royer, D. L., L. J. Hickey, and S. L. Wing (2003) Ecological conservatism in the "living fossil" Ginkgo. Paleobiology 29(1):84–104. Scott, R. A., E. S. Barghoorn, and U. Prakash (1962) Wood of Ginkgo in the Tertiary of western North America. *American Journal of Botany* 49(10):1095–1101. Sahni, B. (1932) A petrified Williamsonia (W. sewardiana, sp. nov.) from the Rajmahal hills, India. Palaeontologia Indica 20(N.S.):1–19. Tralau, H. (1967) The phytogeographic evolution of the genus *Ginkgo L. Botaniska Notiser* 120:409–422. Tralau, H. (1968) Evolutionary trends in the genus *Ginkgo*. *Lethaia* 1:63–101.

Summary of Indications

is intended to show all the possible habitats and communities any of which

may be missing in a given situation.

1. Ginkgophytes seem to replace (negatively co-vary with) herbaceous or shrubby rather than arborescent groups.

2. Fossil ginkgophytes are found predominantly in high-energy facies that are less likely to have supported an established complex canopy.

3. Firmly identifiable ginkgophyte wood does not seem to appear in the fossil record until the late Cretaceous or Tertiary.

4. Modern *Ginkgo biloba* has a suite of characters that are not typical of canopy trees including polymorphic foliage, an early bolting growth phase, and poor shade tolerance.