BETWEEN AND WITHIN GENERA COMPARISONS OF MORPHOLOGICAL PLASTICITY FOR *BETULA* AND *ACER* SEEDLINGS GROWN UNDER VARYING LIGHT CONDITIONS

David S. Ellum†, P.M.S. Ashton, and G.P. Berlyn

Introduction

The ability of genera, or species within genera, to adapt their morphology to compensate for environmental conditions (phenotypic plasticity) contributes to growth characteristics that can lead to success or failure in changing environments. The study of plasticity can give insight into the biological and physical processes that govern successful regeneration and in turn determine future forest composition. The results presented here are part of a larger project we are conducting to develop an index of morphological, anatomical and physiological plasticity for tree species in southern New England forests.

It is generally held that shade-intolerant, early colonizing species demonstrate greater phenotypic plasticity than more shade-tolerant, later successional species (Ashton and Berlyn 1992). It has also been shown that the light saturation point of many temperate broadleaf tree species is about 20% to 30% of full sunlight (Chabot and Mooney 1985). Here we test two hypotheses: 1) morphological plasticity across an experimental light gradient ranging from 3% full sun to 67% full sun will be greater for the genus *Betula* than the genus *Acer*, and 2) the maximum degree of plasticity for genera and species will be expressed in the light treatment interval where photosynthetically active radiation (PAR) of 20% to 30% full sunlight occurs.

Methods

Seedlings of two congeneric assemblages - grey birch (*Betula populifolia*), paper birch (*B. paperifera*), yellow birch (*B. alleghanensis*), striped maple (*Acer pennsylvanica*), red maple (*A. rubrum*) and sugar maple (*A. saccharum*) - were grown over their initial two growing seasons in a greenhouse at Yale-Myers Forest in Eastford, CT. Plants were grown in enclosures that represented four replications each of the following maximum PAR and Red:Far Red (R:FR) treatments respectively: 50 µmol m^{-2} sec^{-1}, 0.46; 300 µmol m^{-2} sec^{-1}, 0.97; 600 µmol m^{-2} sec^{-1}, 1.15; 1200 µmol m^{-2} sec^{-1}, 1.27 (Ashton and Berlyn, 1994). Soil moisture was held constant at field capacity. Destructive sampling was conducted at the end of the second growing season and the data was used to calculate the morphological traits presented in Table 1.

Analysis of variance was performed using PROC MIXED in SAS V8 to determine the effects of light and species, plus the interaction term of light * species on morphology. All F statistics, except light w/LWR (P = .0563), were significant at the P < .0001 level. Significance between trait values were determined using Tukey's HSD test at P < .05. Plasticity indices, φ = (maximum trait value – minimum trait value)/(maximum trait value), were calculated for each of three pairs of successive light treatments and once across the entire experimental gradient.

†Ph.D. Student (DSE), Yale University School of Forestry and Environmental Studies, New Haven, CT; Professor (PMSA), Yale FES, New Haven, CT; Professor (GPB), Yale FES, New Haven, CT. DSE is corresponding author. To contact, call (203) 432-7856 or email at david.ellum@yale.edu.

Results

Morphological Traits

Table 1.—Species mean values for morphological traits in four experimental light treatments.

PAR[1]	Grey Birch	Paper Birch	Yellow Birch	Striped Maple	Red Maple	Sugar Maple
3%						
SLA[2]	442 (16) ab	482 (20) ab	521 (19) a	448 (27) ab	403 (21) b	372 (67) b
LAR[3]	95 (12) c	152 (7) ab	171 (8) a	166 (19) a	113 (11) bc	71 (5) c
LWR[4]	22 (2) b	32 (1) a	33 (1) a	37 (3) a	28 (2) ab	21 (4) b
SWR[5]	54 (2) a	50 (1) ab	46 (1) b	36 (2) c	30 (2) c	34 (5) c
RWR[6]	25 (2)b	18 (1) b	22 (1) b	26 (2) b	42 (3) a	45 (5) a
17%						
SLA	377 (17) ab	381 (16) ab	421 (20) a	350 (17) ab	369 (16) ab	282 (13) b
LAR	94 (5) ab	103 (3) ab	130 (9) a	101 (7) ab	116 (13) a	58 (3) b
LWR	24 (2) ab	27 (1) ab	31 (1) a	29 (1) ab	31 (2) a	21 (1) b
SWR	50 (3) a	49 (2) a	43 (1) ab	36 (1) bc	30 (2) c	34 (2) c
RWR	30 (2) bcd	24 (1) d	27 (1) cd	35 (2) bc	40 (3) ab	45 (3) a
33%						
SLA	247 (8) a	228 (5) a	264 (6) a	215 (9) a	242 (10) a	204 (4) a
LAR	57 (3) a	62 (2) a	84 (4) a	62 (5) a	65 (9) a	40 (2) a
LWR	23 (1) bc	27 (1) abc	32 (1) a	29 (2) ab	26 (2) abc	20 (1) c
SWR	37 (1) a	36 (2) ab	32 (1) abc	32 (1) abc	26 (1) c	29 (2) bc
RWR	40 (2) bc	36 (2) c	36 (2) c	40 (2) bc	48 (3) ab	52 (2) a
67%						
SLA	192 (3) a	166 (5) a	179 (6) a	203 (8) a	194 (11) a	185 (5) a
LAR	49 (2) a	49 (2) a	58 (3) a	63 (6) a	48 (3) a	34 (1) a
LWR	26 (1) ab	29 (1) a	32 (1) a	31 (2) a	25 (1) ab	19 (1) b
SWR	29 (1) a	31 (2) a	27 (1) a	29 (1) a	26 (1) a	24 (1) a
RWR	45 (2) bc	40 (1) bc	41 (1) bc	40 (2) c	49 (2) ab	58 (2) a

[1]Percent photosynthetically active radiation based on 1800 μmol m^{-2} s^{-1} as full sun
[2]specific leaf area (total fresh leaf area/total dry leaf mass, cm^2 g^{-1})
[3]leaf area ratio (total fresh leaf area/total dry plant mass, cm^2 g^{-1})
[4]leaf weight ratio (total dry leaf mass/total dry plant mass, %)
[5]stem weight ratio (total dry stem mass/total dry plant mass, %)
[6]root weight ratio (total dry root mass/total dry plant mass, %).
Means within a row followed by the same letter are not significantly different according to Tukey's HSD test ($P > 0.05$). Numbers in parenthesis are ± 1 standard error.

Plasticity Indices

Table 2.-Plasticity indices[1] for morphological traits across successive light treatments and entire treatment range.

PAR Intervals[2]	GB	PB	YB	TM	RM	SM	*BETULA*[8]	*ACER*
3%/17%								
SLA[3]	0.15	0.21	0.19	0.22	0.08	0.24	0.18 a	0.17 a
LAR[4]	0.01	0.32	0.24	0.39	0.03	0.18	0.19 a	0.20 a
LWR[5]	0.08	0.16	0.06	0.22	0.10	0.00	0.10 a	0.11 a
SWR[6]	0.07	0.02	0.07	0.00	0.00	0.00	0.05 a	0.00 b
RWR[7]	0.17	0.25	0.19	0.26	0.05	0.00	0.20 a	0.10 a
17%/33%								
SLA	0.34	0.40	0.37	0.39	0.34	0.28	0.37 a	0.34 a
LAR	0.39	0.40	0.35	0.39	0.44	0.31	0.38 a	0.38 a
LWR	0.04	0.00	0.03	0.00	0.16	0.05	0.02 a	0.07 a
SWR	0.26	0.27	0.26	0.11	0.13	0.15	0.26 a	0.13 b
RWR	0.25	0.33	0.25	0.13	0.17	0.13	0.28 a	0.14 b
33%/67%								
SLA	0.22	0.27	0.32	0.06	0.20	0.09	0.27 a	0.12 b
LAR	0.14	0.21	0.31	0.02	0.26	0.15	0.22 a	0.14 a
LWR	0.12	0.07	0.00	0.06	0.04	0.05	0.06 a	0.05 a
SWR	0.22	0.14	0.16	0.09	0.00	0.17	0.17 a	0.09 a
RWR	0.11	0.10	0.12	0.00	0.02	0.10	0.11 a	0.04 a
3%/67%								
SLA	0.57	0.66	0.66	0.55	0.52	0.50	0.63 a	0.52 b
LAR	0.48	0.68	0.66	0.63	0.59	0.52	0.61 a	0.58 a
LWR	0.15	0.16	0.06	0.22	0.19	0.10	0.12 a	0.17 a
SWR	0.46	0.38	0.41	0.19	0.13	0.29	0.42 a	0.20 b
RWR	0.44	0.55	0.46	0.35	0.18	0.22	0.48 a	0.25 b

[1]Plasticity indices calculated as ψ = (max trait value – min trait value)/(max trait value).
[2]Photosynthetically Active Radiation (based on 1800 $\mu mol\ m^{-2}\ s^{-1}$ as full sun) intervals used to calculate between treatment plasticity indices.
[3]Specific leaf area (total leaf area/total dry leaf mass, $cm^2\ g^{-1}$);
[4]leaf area ratio (total leaf area/total dry plant mass, $cm^2\ g^{-1}$);
[5]leaf weight ratio (total dry leaf mass/total dry plant mass, %);
[6]stem weight ratio (total dry stem mass/total dry plant mass, %);
[7]root weight ratio (total dry root mass/total dry plant mass, %).
[8]Plasticity indices for Betula and Acer are calculated as means of the species within each genera. GB = grey birch; PB = paper birch; YB = yellow birch; TM = striped maple; RM = red maple; SM = sugar maple. Genera indices in rows followed by the same letter indicates no significant difference according to Tukey's HSD test (P > 0.05).

Conclusions

At the genus level, *Betula* demonstrated a higher degree of plasticity than *Acer* for three out of the five morphological traits across the light range of 3% to 67% full sun, and two out of five traits at the 17% to 33% interval (Table 2). This indicates that *Betula* has greater flexibility in regulating carbon allocation to below ground storage organs (RWR) and above ground support and transport tissues (SWR), and a greater ability to optimize the structure and function of photosynthetic surfaces (SLA). These traits would point to a competitive advantage for *Betula* over *Acer* in rapidly changing light environments. This supports the known ecologies of the two genera but provides greater insight into some of the adaptations and mechanisms involved.

At both the genus and species levels, morphological trait plasticity was consistently greater at the 17% to 33% light interval than the 3% to 17% or the 33% to 67% intervals (Table 2.). The exception to this trend is LWR, which is discussed below. This would indicate that while phenotypic plasticity for these genera and species is expressed across the entire experimental light continuum, there are both lower and upper limits to plasticity that coincide with the stresses of extremely low and high light levels. Given this, it should be noted that, in general, species of the genus *Betula* maintained greater rates of plasticity at the highest light interval, which would indicate a greater niche breadth along the environmental axis of light.

Plasticity for LWR remained consistently low across all light treatments both at the genus and species level when compared to SLA and LAR (Table 2). This indicates that allocation of plant resources to overall leaf mass is a relatively fixed trait, and optimization of photosynthesis is provided by morphological, anatomical and physiological trait expression. Further research, such as correlating LAR to photosynthetic rates, will provide a greater understanding of the relationships between phenotypic plasticity and forest complexity in southern New England.

Acknowledgments

This research was supported by The Andrew E. Mellon Foundation Grant, "Gauging growth responses of tree species in a southern New England Forest". We would also like to thank the Yale-Myers Forest in Eastford, CT, and Fulton Rockwell, Melissa Aikens, Melissa Smith, and Vincent Medjibe for assisting with the destructive sampling.

Literature Cited

Ashton, P.M.S., and G.P. Berlyn. 1992. **Leaf adaptations of some *Shorea* species to sun and shade.** New Phytologist 121:587-596

Ashton, P.M.S., and G.P. Berlyn. 1994. **A comparision of leaf physiology and anatomy of *Quercus* (section *Erythrobalanus-Fagaceae*) species in different light environments.** American Journal of Botany 81(5): 589-597.

Chabot, B.F., and H.A. Mooney. 1985. **Physiological ecology of North American plant communities.** Chapman and Hall, NY.