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Seed reproduction is associated with a transient escape from parasite damage in American beech

Austin Burt and Graham Bell

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American beech (*Fagus grandifolia* Ehrh.) has two modes of reproduction, propagating both by sexual seedlings and by vegetative suckers. We compare natural levels of parasite-induced leaf damage in the two types of progeny to test the hypothesis that seed reproduction ameliorates losses to various biotic antagonists. As predicted by the parasite-escape hypothesis, we find that seedlings suffer less damage than suckers and that this advantage declines with increasing size of the young tree.

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Simple equilibrium calculations suggest that in organisms which reproduce by both sexual zygote production and asexual vegetative proliferation, the return on reproductive investment in the sexual progeny should be about twice that in the asexual progeny (Williams 1975; for relevant experimentation see Kelley et al. 1988, Kelley 1989). The source of this differential success is a central problem in evolutionary biology, the so-called 'paradox of sex', and is likely to derive from the developmental (Buss 1987), ecological (Silander 1985), or genetic (Michod and Levin 1988) differences between seeds and vegetative propagules. Much recent theory has suggested that seed reproduction may provide a transient escape from parasite attack (Hamilton 1982, Bell 1985, Silander 1985, Bierzychudek 1987); here we test these ideas by comparing natural levels of parasite-induced leaf damage in seedlings and suckers of American beech (*Fagus grandifolia*).

The hypothesized mechanisms by which seedlings may temporarily escape from parasite attack include the developmental, the ecological, and the genetic: reduced parent-offspring transmission of infections, due to developmental isolation during seed formation (Crocker 1939, Silander 1985, Bierzychudek 1987, Parker 1987); spatial or temporal escape from locally adapted para-

sites (Caten 1974, Edmunds and Alstad 1981, Wainhouse and Howell 1983, Parker 1985, Karban 1989), due to the potentially greater dispersal or longer dormancy of seeds; and increased resistance of novel recombinant progeny, due to time-lagged frequency-dependent selection favouring rare genotypes (Hamilton 1982, Rice 1983, Bell 1985). Despite the variety of proposed selective mechanisms, all predict that seedlings should have reduced levels of parasite damage compared to vegetatively produced offspring, and that this advantage should decay with time as the local parasite population evolves – by natural or habitat selection – to recolonize the host. Testing these two predictions provided the impetus for this study.

Materials and methods

American beech is a late-successional, shade-tolerant tree and a major component of the hardwood and mixed forests of east-central North America (Fowells 1965). It reproduces by both seeds and root suckers, showing considerable geographical variation in the proportion of seedlings and suckers, apparently with increased suckering in the northern end of its range (Held

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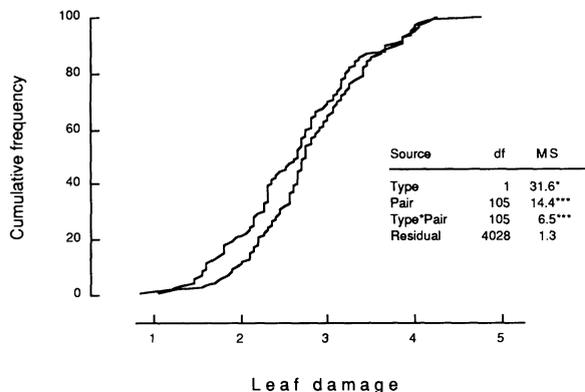


Fig. 1. Cumulative frequency distribution of leaf damage for seedlings (upper) and suckers (lower) of American beech. Damage calculated as means for 20 leaves. Also shown is the mixed-model analysis of variance for leaf damage. Data pooled across sampling dates. * - $p < 0.02$ (one-tailed); *** - $p < 0.001$ (two-tailed).

1983, Jones and Raynal 1986). Flowers are monoecious and wind-pollinated; seeds are large (~3 g), dispersed mostly by gravity and animals, and germinate the year after pollination (Rudolf and Leak 1974).

The study population is in an undisturbed beech-maple forest at the McGill University Field Station at Mont St. Hilaire, Quebec, Canada. Seedlings and suckers can be distinguished by digging in the soil at the base of the stem and looking for a parental root. We used a paired sampling design, consisting of nearest-neighbour seedlings and suckers (mean distance $d = 0.98 \pm 0.602$ (s.d.) m). Leaves were collected from different individuals on three sampling dates: Sep 1986, Jul 1987, and Sep 1987.

Sampling proceeded by marking transects perpendicular to Lac Hertel on Mont St. Hilaire; in each transect a large tree was chosen as the focus of a search for three nearest-neighbour pairs of seedling and sucker. Twenty leaves were collected from each individual, working down from the topmost stem; only individuals less than 2 m in height with the requisite number of leaves were considered. Leaves were brought back to the lab and scored blind (arbitrarily coded, mixed together, scored for damage, and then decoded) on an approximately logarithmic integer scale from 0 (no visible damage) to 6 (over half the leaf eaten or infected). Twelve different transects were sampled on each of three dates. Data were lost for two pairs in the second sample, so the total sample sizes are 106 pairs and 4240 leaves. All leaves were scored by A.B.; the third batch was also scored by G.B. and the correlation between scorers was $r = 0.818$ at the level of leaves, $r = 0.925$ at the level of individual plants. Damage on a sample of leaves from the first batch was also measured using a digital image analyser; the line of best fit relating the proportion of leaf area damaged to our score was: $\text{Log}(\text{Proportion damaged}) = -2.825 + 0.514(\text{Score})$; $r^2 = 0.851$, $n = 213$). Arith-

metic mean damages were calculated using this equation and the mean and variance of the log estimates.

Results

The mean leaf damage for all individuals was 12.3%. On a sample of 213 leaves measured using a digital image analyser, over half of this damage (53%) was due to herbivores, recorded as gaps or holes along the edge of the leaf; another 16% was due to rust spots on the surface of the leaf, and the remaining 31% was due to a variety of blemishes and holes on the interior of the leaf. Identifying the species involved was not possible.

Pooling all the data, suckers suffered 1.1 times more damage than seedlings (12.9 and 11.8% respectively; Fig. 1). This difference between seedlings and suckers does not differ significantly between the three samples ($F_{2,103} = 0.37$, n.s.). Analysed separately, all three samples show the same trend, though the effect is statistically significant ($p < 0.05$) in only one. All three also show a significant interaction between mode of reproduction and pair, indicating that the advantage of seed reproduction differs between pairs; the next analysis deals in part with this unexplained variance.

To test whether the advantage of seed reproduction is

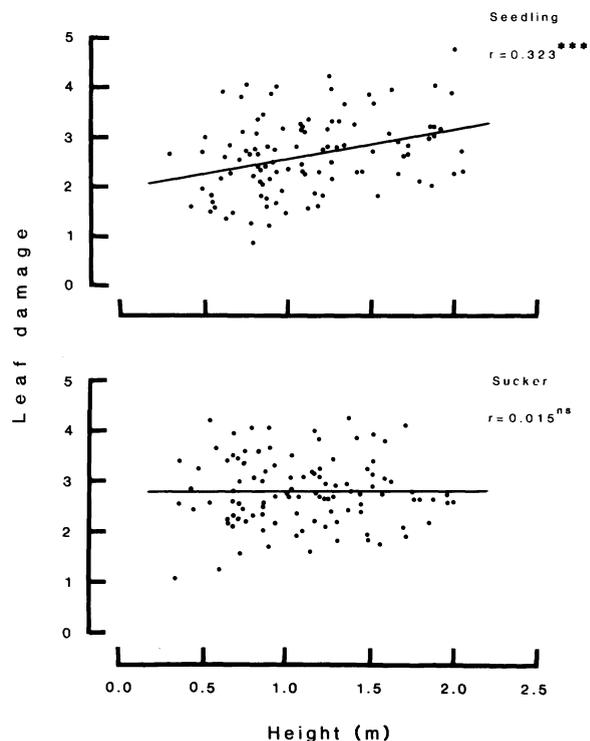


Fig. 2. Leaf damage as a function of height in seedlings and suckers of American beech. Each point is an individual, with damage scores calculated as means of 20 leaves. *** - $p < 0.001$.

transient, we estimated the correlation between damage and height separately for both seedlings and suckers. The results are as predicted by the parasite-escape hypothesis: the slope of the relation in the seedlings is both significantly greater than zero and significantly greater than in the suckers (0.57 ± 0.163 (s.e.) vs 0.03 ± 0.160 , $p < 0.01$ (one-tailed); Fig. 2). The seedling intercept is also significantly lower than the sucker intercept (1.99 ± 0.196 vs 2.77 ± 0.189 $p < 0.01$). One gets the same results by controlling for main-effect differences between samples: damage is significantly correlated with height in seedlings ($p < 0.001$), but not in suckers ($p > 0.5$) and the common slopes of seedlings and suckers differ significantly ($p < 0.01$). Again, the three samples analysed separately show the same trends: seedling damage is positively correlated with height in all three samples, significantly so in two of them, and the slope of damage on height is greater among the seedlings than the suckers in all three samples, significantly so in one of them. Only two of the three correlations between sucker damage and height are positive, and none is significant.

Note that this difference in slopes indicates that the magnitude (and statistical significance) of the difference between seedling and sucker damage depends on the height of the trees concerned. For example, at 0.5 m, the lower end of our sampled range, suckers have 1.7 times more damage than seedlings (12.7 vs 7.4%; $p < 0.0025$, one-tailed). At 2 m, the upper end of our range, the difference is no longer significant.

Discussion

The two major predictions of the parasite-escape hypothesis are supported: seedlings suffer less damage than vegetatively produced individuals, and this advantage decays with time. Though our study was not specifically designed to distinguish the potential selective mechanisms underlying the escape from parasitism, two in particular seem unlikely to account for our observations. First, most of the observed damage was due to herbivores, we did not find any evidence in the remainder of a systemic disease, and there is no mention of systemic foliage diseases in a review of beech pathology (Hepting 1971); this suggests that the developmental hypothesis is perhaps an unlikely explanation. Second, beech trees have no extended dormant period or seed bank; thus temporal escape is not possible. We are not aware of any similar reasons for discounting the other two proposed mechanisms, that seeds allow escape in space from locally adapted parasites, or genetic escape from parasites adapted to previous generations.

It is not possible to relate the observed differences in leaf damage to the predicted two-fold difference in return on reproductive investment, both because sexual and asexual reproduction involve quite different costs

(flowers and seeds versus roots and nutrients) and because the relationship between leaf damage and individual fitness is unknown. Two points seem worth making. First, while leaf damage may be the most visible and the most easily measured form of damage, stem and root parasites may be equally important determinants of host fitness. If seedlings also suffer less from these sources, then the advantage of seed reproduction will be compounded. Second, even if all else were equal, the mean annual survival of seedlings need only be 1.017 times greater than that of suckers in order to result in a two-fold difference at the end of a 40-yr juvenile period (Fowells 1965). Such a difference would be all but impossible to observe directly. Fortunately, the data presented here suggest that much of this difference may be concentrated in the first metre of life.

This study was specifically designed to test two predictions of the parasite-escape hypothesis; negative results would have required modifying or rejecting the hypothesis, and so the positive results observed constitute support for it. However, as is often the case, it is possible to construct post hoc an alternative explanation. For example, it is possible that the pattern of investment by seedlings and suckers in chemical defenses is exactly that required to produce the observed results: high initial investment by seedlings, gradually decreasing with increasing size, and low investment by suckers which does not change with size. We are not aware of any evidence supporting this alternative explanation, but neither are we aware of any rejecting it. Thus, future work will want to have two objectives: first, to see if these results apply to the many other plant (and animal) species with these two modes of reproduction, and second, to investigate the mechanism responsible for any observed difference using manipulative experiments.

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References

- Bell, G. 1985. Two theories of sex and variation. – *Experientia* 10: 1235–1245.
- Bierzychudek, P. 1987. Resolving the paradox of sexual reproduction: a review of experimental tests. – In: Stearns, S. C. (ed.), *The evolution of sex and its consequences*. Birkhäuser, Basel, pp. 163–174.
- Buss, L. W. 1987. *The evolution of individuality*. – Princeton Univ. Press, Princeton, NJ.
- Caten, C. E. 1974. Intra-racial variation in *Phytophthora infestans* and adaptation to field resistance for potato blight. – *Ann. Appl. Biol.* 77: 259–270.
- Crocker, W. 1939. Ageing in plants. – In: Cowdry, E. V. (ed.), *Problems of ageing*. Williams and Wilkins, Baltimore, pp. 1–31.
- Edmunds, G. F. Jr. and Alstad, D. N. 1981. Responses of black pineleaf scales to host plant variability. – In: Denno, R. F. and Dingle, H. (eds), *Insect life history patterns:*

- Habitat and geographic variation. Springer, N.Y., pp. 29–38.
- Fowells, H. A. 1965. Silvics of forest trees of the United States. – U.S. Dept. Agric. Forest Service, Washington.
- Hamilton, W. D. 1982. Pathogens as causes of genetic diversity in their host populations. – In: Anderson, R. M. and May, R. M. (eds), Population biology of infectious diseases. Springer, Berlin, pp. 269–296.
- Held, M. E. 1983. Pattern of beech regeneration in the east-central United States. – Bull. Torrey Bot. Club 110: 55–62.
- Hepting, G. H. 1971. Diseases of forest and shade trees of the United States. – U.S. Dept. Agric. Forest Service, Washington.
- Jones, R. H. and Raynal, D. J. 1986. Spatial distribution and development of root sprouts in *Fagus grandifolia* (Fagaceae). – Am. J. Bot. 73: 1723–1731.
- Karban, R. 1989. Fine-scale adaptation of herbivorous thrips to individual host plants. – Nature, Lond. 340: 60–61.
- Kelley, S. E. 1989. Experimental studies of the evolutionary significance of sexual reproduction. V. A field test of the sib-competition lottery hypothesis. – Evolution 43: 1054–1065.
- , Antonovics, J. and Schmitt, J. 1988. A test of the short-term advantage of sexual reproduction. – Nature, Lond. 331: 714–716.
- Michod, R. E. and Levin, B. R. (eds). 1988. The evolution of sex: an examination of current ideas. – Sinauer, Sunderland, MA.
- Parker, M. A. 1985. Local population differentiation for compatibility in an annual legume and its host-specific fungal pathogen. – Evolution 39: 713–723.
- 1987. Pathogen impact on sexual vs asexual reproductive success in *Arisaema triphyllum*. – Am. J. Bot. 74: 1758–1763.
- Rice, W. R. 1983. Parent-offspring pathogen transmission: a selective agent promoting sexual reproduction. – Am. Nat. 121: 187–203.
- Rudolf, P. O. and Leak, W. B. 1974. *Fagus* L. Beech. – In: Schopmeyer, C. S. (ed.), Seeds of woody plants in the United States. U.S. Dept. Agric. Forest Service, Washington, pp. 401–405.
- Silander, J. A. Jr. 1985. Microevolution in clonal plants. – In: Jackson, J. B. C., Buss, L. W. and Cook, R. E. (eds), Population biology and evolution of clonal organisms. Yale Univ. Press, New Haven, CT, pp. 107–152.
- Wainhouse, D. and Howell, R. S. 1983. Intraspecific variation in beech scale populations and in susceptibility of their host *Fagus sylvatica*. – Ecol. Ent. 8: 351–359.
- Williams, G. C. 1975. Sex and evolution. – Princeton Univ. Press, Princeton, NJ.

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