SHORT COMMUNICATION

SLUG- AND SMALL MAMMAL-INDUCED SEEDLING MORTALITY IN SYCAMORE *ACER PSEUDOPLATANUS* L.

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INTRODUCTION

Throughout the British Isles sycamore (*Acer pseudoplatanus* L.) has been found to invade various habitats, including a number of forest types (Rodwell 1991; Binggeli 1992). However, the speed of the invasion is slow in comparison with sycamore's prolific seed and seedling production. As early as 1848 Bromfield noted that 'I have seen seedlings of this tree springing up by the thousands on the bare sides of our chalk downs, but they rarely are found to establish themselves in these exposed locations'. In a review of the literature, Binggeli (1992) identified seedling (<1 year old) establishment and survival and sapling (>1 year old) survival as the limiting stages in the life history of sycamore. A number of molluscs and mammals as well as environmental factors (e.g. frost, drought, pH) were thought to significantly affect survival. In particular, slugs have often been found to be responsible for the death of seedlings. For example, Urquhart (1952) investigated seedling mortality between May and October and found that stem-grazing by *Deroceras reticulatum* Müller, *Arion ater* L. and *Arion hortensis* Ferussac was the chief cause of death in the summer, particularly in July. Recently Urquhart (1993) claimed to have 'discovered that Gastropoda spend daylight hours up [sycamore] trees descending at night to gobble up seedlings'. Helliwell (1965), using artificially dispersed seeds, noted that in woodlands, within a month of seedling establishment, the majority had been killed, chiefly by slugs, and Ashby (1959) found that heavy mortality of seedlings was caused by slugs at the end of a wet summer and by rodents during the first winter.

Slugs can kill seedlings by eating their stems, but saplings suffer less slug damage because their stems are lignified and only the buds are attacked (Dethioux 1970). However, persistent consumption of leaves and leading shoots will eventually kill saplings (Urquhart 1952). In old fields, slugs and snails graze the cotyledons of seedlings and, less frequently, young leaves and growing points (Southwood *et al.* 1988), and rodents (chiefly the field vole *Microtus agrestis* L.) cause high sapling mortality.

In addition to grazing, environmental factors, mycorrhizal associations and competition are known to affect the growth of seedlings and saplings of sycamore (Binggeli 1992), but these factors as well as the impact of diseases have never been investigated under field conditions. In this present study, the causes and timing of mortality of naturally regenerated seedlings in relation to germination time and measured site factors were investigated in order to determine possible factors limiting the establishment of sycamore at a particular site in the north of Ireland.

MATERIALS AND METHODS

THE SITE

The study area is located on the north coast of Ireland at the Umbra, Co. Londonderry (Ordnance Survey Irish Grid reference C723352), in *c.* 27ha of mixed deciduous woodland. The woodland was originally used for rough grazing as part of a large country estate, which lies on a steep north-western slope of a basalt escarpment with a maximum altitude of 150m above sea-level.

The study area (approximately 200m^2) within the woodland, at an altitude of 10m, is in a well-sheltered level piece of ground at the foot of a small steep slope dominated by sycamore. The soil is moist, becoming waterlogged in an adjacent area of ash (*Fraxinus excelsior* L.) and willow (*Salix* spp). The main surrounding woody species are hazel (*Corylus avellana* L.), elm (*Ulmus* spp), cherry plum (*Prunus cerasifera* Ehrh.) and a small planted area of Norway spruce (*Picea abies* L.) to the east. The degree of cover of the ground flora is light to moderate (40–65% cover; estimated by eye in six 1m^2 quadrats), mainly consisting of lesser celandine (*Ranunculus ficaria* L.), ivy (*Hedera helix* L.), ground elder (*Aegopodium podagraria* L.) and golden saxifrage (*Chrysosplenium oppositifolium* L.).

The main fern species are hart's-tongue fern (*Phyllitis scolopendrium* L.) on the lower slopes and bracken (*Pteridium aquilinum* L.) on the upper, more exposed slopes. Salmonberry (*Rubus spectabilis* Pursh.) is rapidly invading the upper slopes of the wood and is the dominant species under sycamore.

The Ordnance Survey Memoirs of 1831–5 state that the townland of the Umbra contained only small patches of stunted growth, indicating that the area was 'formerly well clothed with wood'. Species found on the nearby Binevenagh included a few ash trees, hazel and thorns (Day and McWilliams 1991, 82). Around 1831–5, trees such as oak (*Quercus* spp), ash, elm and sycamore were planted along the driveway and main pathways to and from the main house on the estate to various parts of the grounds. After 1900 the surrounding pastureland was left ungrazed and the area was subsequently colonised by ash and sycamore. This resulted in a large, even-aged stand of trees, mainly dominated by sycamore.

Choice of study site was influenced by the known limited area of seed dispersal from the parent trees and the uneven dispersal of the seeds.

METHODOLOGY

Six 1m^2 quadrats were placed in the study area underneath the canopy of mature sycamore to give approximately 100 seedlings in total at the start of the study period. The location of each seedling was mapped using scaled graph paper, thus enabling the fate of each individual seedling to be studied.

The study commenced on 12 March 1994 and continued until 23 April 1994. The site was visited weekly; the seedlings were counted and any damaged or absent seedlings noted. The cause of seedling damage or death—by disease, slugs, small mammal herbivory or disturbance by animals—was ascertained. Cause of death was determined using criteria outlined by Hulme (1994), who reported that molluscs remove less than 75% of seedling tissue while rodents consumed seedlings completely.

Seedling recruitment within the study area was also recorded weekly by counting newly germinated seedlings, and the fate of these recruits was subsequently noted. The depth of the leaf litter was measured at three points within each quadrat, and at the end of the series of observations it was removed and separately bagged. The slugs and snails were removed from these litter samples by hand, counted and identified; the sycamore fruits were also counted. Litter moisture content was measured as the difference between fresh litter weight and weight after oven-drying at 80°C.

Longworth traps (five) were placed at the site over five nights to determine what small mammal species inhabited the woodland and if possible to determine population size. This proved completely unsuccessful, but evidence of digging and large numbers of caches of sycamore fruit in and around the study site indicated the presence of a mammal population. Changes in percentage cover of other ground flora within the quadrats were recorded every two weeks, as were the light levels (using two light meters simultaneously, one under the canopy and the other in an adjacent open field <100m away). One soil sample, around 5cm^3, was taken at a depth of approximately 6cm adjacent to each quadrat during the weekly visits, and these were used for determination of soil moisture based on mass differences between fresh and dry weights. Estimates of rainfall and temperature were obtained from the weather station in Coleraine, which is approximately 16km from the study site.

In order to determine the background of the seed production and success under tree species other than sycamore, saplings of sycamore found in adjacent areas of hazel stands were aged by counting the terminal bud scars.

RESULTS

On the first day's mapping the six quadrats contained a total of 109 seedlings (group 1, Table 1), which were assumed to have germinated recently owing to their early stage of development. Table 1 shows the numbers of seedlings surviving at each subsequent date and the causes of death. Subsequent germinations, i.e. groups 2 and 3 in Table 1, numbered 31 and 27 respectively. Seedlings from group 1 survived for more than five weeks; those which germinated at later dates survived for less than three weeks. None of the seedlings survived beyond the end of April.

By week 4, slugs were responsible for the greater proportion of seedling deaths in all three groups. The only snails found in the leaf litter samples were *Oxychilus alliarius* Miller, a carnivorous species, and these were uncommon (eight in total). The commonest slug species collected from the leaf litter samples were *Deroceras reticulatum* and *Arion* spp. From the litter samples, total slug density was estimated to be $11 \pm 3.9\ \text{m}^{-2}$, and this was almost certainly an underestimate because no records were taken of slugs migrating up and down the nearby trees.

The mammal species most likely to be responsible for the death of seedlings were the woodmouse (*Apodemus sylvaticus* L.) and the common rat (*Rattus norvegicus* Berkenhaut) owing to the lack of other likely candidates in this area of Ireland (Corbet and Harris 1991; W.L. Wilson, pers. comm.). It is estimated that these mammals were responsible for the loss of only 4% of the original 109 seedlings in the first week. These data confirm that slugs are the major factor in the death of sycamore seedlings.

Soil moisture content at the site dropped throughout the period of observations, whilst vegetation cover, excluding that due to sycamore seedlings, increased (Fig. 1). The water content of the leaf litter was 79%, which, along with an average depth of 1.5 ± 0.2cm, provided good cover for slugs. This leaf litter showed little evidence of decomposition and most of the leaves were entire. Sycamore samara in the litter were common (325 ± 225 m^{-2}), all of which lacked seeds.

Sycamore saplings at a site near the study site had a mean age of 6.9 ± 0.9 years, and none had germinated after 1989. The oldest germinated in 1986 and the largest cohort was from 1987. None of these were found under sycamore but all were found under hazel. This site was notably wetter than the study site and was in close proximity to the main stand of ash and willow.

DISCUSSION

In this coastal site all sycamore seedlings were killed before canopy trees came into full leaf. Seedling mortality was mainly caused by slugs, and to a lesser extent by small mammals. Environmental factors (e.g. variation in soil moisture, etc.) and fungal diseases did not appear to be the cause of any mortality at this site.

The maximum lifespan of seedlings was about five weeks, and no seedling managed to produce a first set of true leaves. This is in contrast with the studies of Urquhart (1952) and Helliwell (1965) (Table 2). Urquhart did not investigate spring mortality but found that 60% of the seedlings survived the summer with or without mammal grazing, and 90% were still alive by October when slugs were controlled. In Helliwell's experimental study, out of 922 seedlings 11% survived the summer and 4% were alive at the end of the winter. He also stated that much inter-site variation in mortality was observed, and that seedling mortality was lower at sites with sandy and sandy-loam soils. These sites would have been much drier than the present study site, where the ground was covered by a thick layer of sycamore leaf litter. The high water content (79%) of the leaf litter may be a factor in the low decomposition rate observed; sycamore leaves are usually thought to rapidly break up into triangular pieces and decompose in less than nine months (Mommaerts-Billiet 1971). This thick layer of leaf litter provides an ideal habitat for slugs—Philipson (1983) found that slugs (e.g. *Arion hortensis* and *Deroceras reticulatum*) were more common in areas where leaf litter was deepest and ground vegetation well developed. Russell-Hunter (1964) suggested that vegetation affects the distribution of land molluscs through modification of the microclimate. In the study area, those seedlings which germinated close to the clumps of lesser celandine appeared to be more susceptible to attack by slugs, and this was probably due to the shelter afforded to the slugs by the large leafy area of the plants. Their activity may also be affected by the close proximity of the sea (<200m) and its buffering effect on inclement weather.

The greater percentage of slug herbivory in seedlings which germinated later in the study (groups 2 and 3) could be explained by seasonal increase in temperature allowing slugs to become more active, or by slugs actively selecting the younger and perhaps more palatable seedlings, pos-

Table 1—Numbers of sycamore seedling deaths caused by slugs (S) and mammals (M) and numbers of seedlings surviving (SS) at different sample dates in the Umbra area, Northern Ireland. Samples were examined at intervals of seven days, with week 1 = 26/3/1994, 2 = 2/4/1994, 3 = 9/4/1994, 4 = 16/4/1994, and 5 = 23/4/1994. Seedlings in group 1 had germinated prior to the first recording date, i.e. before 26/3/1994. Seedlings in group 2 germinated between the first and second sample dates, and seedlings in group 3 germinated between the second and third sample dates. There was no subsequent germination.

Sample date	*Group 1 (total 109)*						*Group 2 (total 31)*						*Group 3 (total 27)*						*Overall total (167)*			
	SS	%	S	%	M	%	SS	%	S	%	M	%	SS	%	S	%	M	%	S	%	M	%
Week 1	64	59	41	38	4	3													41	25	4	2
Week 2	39	61	23	36	2	3	22	71	7	23	2	6							30	18	4	2
Week 3	28	72	8	20	3	8	12	55	10	45	0	0	15	55	11	41	1	4	29	17	4	2
Week 4	4	5	20	71	4	14	0	0	12	100	0	0	0	0	14	95	1	5	46	28	5	4
Week 5	0	0	4	100	0	0			0		0				0		0		4	2	0	0
Totals			96	54	13	14			29		2				25		2		150	90	17	10

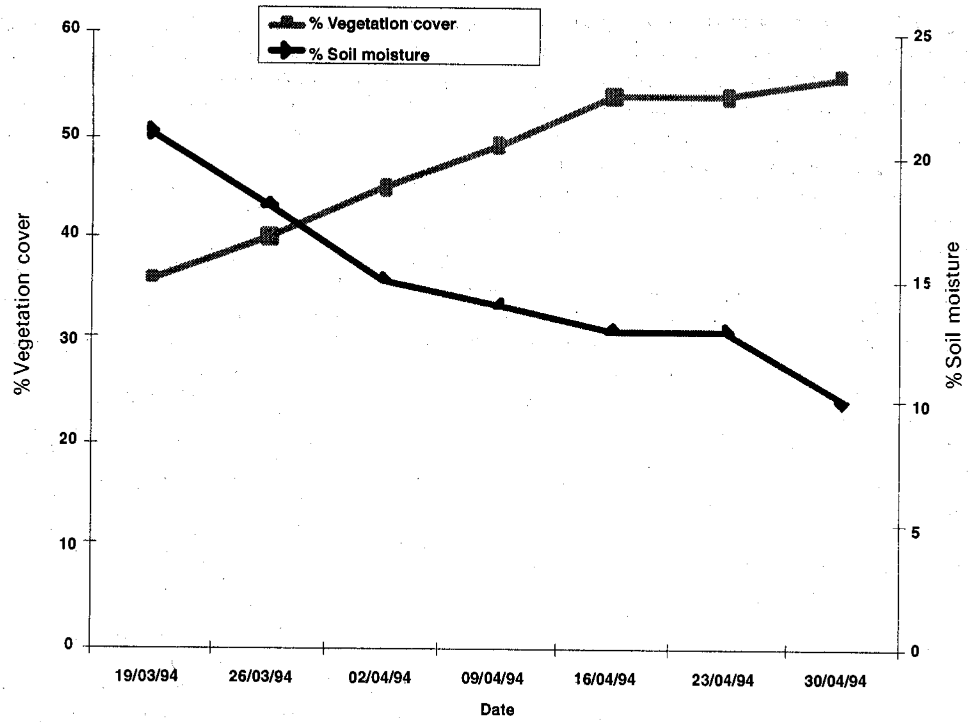

Fig. 1—Soil moisture content and vegetation cover (excluding sycamore seedlings) within the quadrats during the course of the observations.

sibly owing to their lower levels of tannins. This may explain why some seedlings from the first group survived longer than those in subsequent groups. There is obviously a clear need for further research into the grazing pressures of molluscs and mammals on sycamore seedlings in a woodland setting, possibly adapting the exclosure methods used by Hulme (1994).

Waters and Savill (1992) have shown that sycamore and ash are less likely to regenerate under their own canopy but can do so under the canopy of the other species. Sycamore and ash, being ecologically similar (they share many life history traits and site requirements), should remain in a cyclical equilibrium in ash woodlands presently dominated by ash and invaded by sycamore (Waters and Savill 1992). The reasons for the observed patterns of regeneration are as yet unknown. A number of factors may be responsible, including microsite requirements, allelopathy and herbivory. This study suggests that in coastal areas, such as the Umbra, slug herbivory prevents sycamore regeneration under sycamore. Ash leaf litter under ash appeared to be thinner and is known to decompose more rapidly than that of sycamore (e.g. Mommaerts-Billiet 1971), which would probably

Table 2—Percentage survival of sycamore seedlings recorded from a number of studies (n = total number of seedlings).

	Year	*n*	*% of seedlings surviving until*		
			Summer	*Autumn*	*Spring*
This study	1994	167	0	—	—
Helliwell (1965)	1964	922	—	11	4
Urquhart (1952)*	1948a	30	—	63	—
	1948b	42	—	60	—
	1949a	27	—	66	—
	1949b	31	—	90	—

* Urquhart's treatments were: a = control (no treatment) and b = treatment (i.e. rabbit control in 1948, slug control in 1949); — = no data.

result in smaller slug populations; some sycamore seedlings should hence escape slug herbivory. At present there is little evidence to explain why ash seedlings/saplings survive under sycamore but not under their own canopy. Sydes and Grime (1981) noted that young ash seedlings were most abundant in areas with a deep accumulation of tree leaf litter, suggesting that a deep sycamore litter may be ideal for ash seedling establishment. Future studies should focus on the seed germination of both species under contrasting litter depths and composition, as well as on seedling and sapling mortality under differing environmental conditions and tree canopies.

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REFERENCES

Ashby, K.R. 1959 Prevention of regeneration of woodland by field mice (*Apodemus sylvaticus* L.) and voles (*Clethrionomys glareolus* Schreber and *Microtus agrestis* L.). *Quarterly Journal of Forestry* **53**, 228–36.

Binggeli, P. 1992 Patterns of invasion of sycamore (*Acer pseudoplatanus* L.) in relation to species and ecosystem attributes. Unpublished D.Phil. thesis, University of Ulster.

Bromfield, W.A. 1848 Notes and occasional observations on some of the rarer British plants growing wild in Hampshire. *Phytologist* **3**, 205–91.

Corbet, G.B. and Harris, S. (eds) 1991 *Handbook of British mammals* (3rd edn). Oxford. Blackwell.

Day, A. and McWilliams, P. 1991 *Ordnance Survey Memoirs of Ireland. Parishes of Co. Londonderry III, 1831–1835. Roe Valley Lower.* Queen's University, Belfast.

Dethioux, M. 1970 Les semis d'érable sycomore. *Notes Techniques du Centre d'Écologie Forestière et Rurale* **11**, 1–11.

Helliwell, D.R. 1965 Factors influencing the growth of seedlings of sycamore and Norway maple. *Quarterly Journal of Forestry* **59**, 327–37.

Hulme, P.E. 1994 Seedling herbivory in grassland: relative impact of vertebrate and invertebrate herbivores. *Journal of Ecology* **82**, 873–80.

Mommaerts-Billiet, F. 1971 Aspects dynamiques de la disparition de la litière de feuilles. *Bulletin de la Société Royale de Botanique de Belgique* **104**, 181–95.

Philipson, J. 1983 Slug numbers, biomass and respiratory metabolism in a beech woodland—Wytham Woods, Oxford. *Oecologia* **60**, 38–45.

Rodwell, J.S. (ed.) 1991 *British plant communities, vol. 1. Woodlands and scrub.* Cambridge University Press.

Russell-Hunter, W.D. 1964 Physiological aspects of ecology in non-marine Mollusca. In K.M. Wilbur and C.M. Yonge (eds), *Physiology of Mollusca*, vol. 1, 83–126. New York. Academic Press.

Southwood, T.R.E., Brown, V.K., Reader, P.M. and Mason, E. 1988 Some ecological characteristics of the primary trophic level of a secondary succession. *Proceedings of the Royal Society* B **234**, 11–44.

Sydes, C. and Grime, J.P. 1981 Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. 1. Field investigations. *Journal of Ecology* **69**, 237–48.

Urquhart, B.P. 1952 Slugs and natural regeneration. *Quarterly Journal of Forestry* **46**, 110–12.

Urquhart, B.P. 1993 Sycamore. *Scottish Forestry* **47**, 4.

Waters, T.L. and Savill, P.S. 1992 Ash and sycamore regeneration and the phenomenon of their alternation. *Forestry* **65**, 417–33.