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THE ENGLISH BEECH MASTING SURVEY 1980–2007: VARIATION IN THE FRUITING OF THE COMMON BEECH (*FAGUS SYLVATICA* L.) AND ITS EFFECTS ON WOODLAND ECOSYSTEMS

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Summary

1. Study of annual production of beech mast at twelve main sites including closed canopy beechwood, shelter belts, avenues and an isolated tree in a park, as well as intermittent observations at others, has now continued for twenty-eight years.
2. During this period beech mast was sampled from up to 100 trees by seven-minute samples collected from the ground. Aerial samples have also been collected from low-growing branches.
3. Production of full seed varies greatly from year to year, and all trees produce empty pericarps as well as full mast, especially on lower or shaded branches.
4. The proportion of full nuts consumed or damaged by the moth *Cydia fagiglandana* Z., birds and small mammals, in English sites, can become significant especially in non-mast years.
5 Good masting occurred in 1980, 1982, 1984, 1987, 1990, 1995, 1997, 2000, 2002, 2004 and 2006: after each of these good years, one year of very poor masting normally followed. The best year recorded so far was 1990. In both 1981 and 2005, no full mast was found, and singularly very little in 1991 and 2001.
6. Regional variation within England is much less than the annual variation, but over the period the northern trees have produced on average fewer full nuts but rather more empty and total nuts. In 2007, however, northern trees produced markedly less full and total nuts than their southern counterparts.
7. Over such a long period it was inevitable that site changes would occur. In some instances the substrate beneath particular trees is now less favourable for rapid nut collection. As some trees have died, additional younger trees are now being assessed. In 1996, far

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more viable seed was formed in certain Scottish sites than at those we observed in England, so it is highly desirable that Scottish and Welsh sites be monitored in the future.

Keywords: *Cydia fagiglandana*, *Fagus sylvatica*, beech mast sampling, masting, long-term ecological survey*

Introduction

The seed masting study on beech reported here has been carried out for twenty-eight consecutive seasons, thus exceeding the twenty-five years required for a long-term project. This length of time is necessary when investigating a phenomenon which of its very nature has always been so variable.

Masting is the periodic synchronous production of large seed crops (NILSSON and WASTLJUNG, 1987). The importance of this phenomenon was recognized by SALISBURY (1942), whose seminal work on the reproductive capacity of plants, with its emphasis on the role of the environment and the depredations caused by predators and parasites, is still the most important review of this subject. His introduction uses *Fagus sylvatica* as an example in a discussion of the importance of fluctuating reproduction and periodic fruiting; p. 2 also mentions the importance of hot, dry summers in promoting the fruiting of this species. The account of *F. sylvatica* given by MABEY (2007), valuable in many respects particularly with regard to its distribution and variation in growth form, and masting in general, lacks detail of the great masts of previous centuries given by HILTON and PACKHAM (2003).

LINDQUIST (1931) published studies of beechwoods in four regions of Sweden over a period of thirty-three years. He suggested an inherent natural periodicity which permitted flowering every other year, and his results showed a clear pattern of masting every two or three years, broken just once. Failure of a regular biennial pattern was shown to be caused by weather conditions: male and female flowers are destroyed by severe frosts in late April and May of what would otherwise be a mast year. It is important that temperatures are high in June and July of the year previous to masting when flower buds are initiated; a very hot summer in the year of masting also promotes a heavy crop.

General discussions of masting in forest trees are provided in PACKHAM *et al.* (1992) and THOMAS and PACKHAM (2007), while important aspects of beech masting in England are discussed in our previous publications on this subject (HILTON 1988, HILTON and PACKHAM 1986, 1997; PACKHAM and HILTON 2002, PACKHAM 2003). The pattern of masting of this species in northern Europe as a whole is described in HILTON and PACKHAM (2003). It is recognized throughout these papers that the 'seeds' collected are botanically nuts, fruits with a hard pericarp. This is important because beech frequently produces large quantities of pericarps devoid of viable seed.

Though records made by foresters are usually of viable nuts suitable for raising seedlings, the Forestry Commission Annual Report for 1975 (FORESTRY COMMISSION, 1976) mentions a very heavy beech mast disappointingly void of seed. Such empty nuts are often the result of a failure of pollination, which is by wind. Between 1942 and 1948, HYDE (1951) found a positive relationship between mean catch of pollen grains on a 5-cm square horizontal surface in Cardiff and the extent of masting in the local beech. It is also important that there be other local beech to effect cross-pollination as beech seems generally self-incompatible; indeed self-pollination produced 92% empty nuts in Danish trees investigated by NIELSEN and DE MUCKADELI (1954).

The present study gives an extensive record of masting success in England, distinguishing between full and empty nuts and also examining causes of damage to full nuts. It also discusses the difficulties of making reasonably accurate records in such widely distant sites, with varying substrates, within a relatively short time period. The value of the records is enhanced by the fact that observers are well aware of the general health of the trees surveyed, a very relevant point as common beech is a species whose establishment and success, particularly in Southern England, could be changed by global warming. In this connection it should be noted that after a period with sharp frosts early in the year, 2006 had the warmest month (July) since the Central England Temperature record (CET) first commenced at weather stations between Bristol, London and Manchester in 1659, some 347 years previously (BANNERMAN, 2006). The new UK maximum temperature record of 36.5°C was recorded in July at Wisley, near London, and the year 2006 was in the top ten warmest known to CET (CLIMATE RESEARCH UNIT, UEA, 2006).

Sites

Grid references of the twelve principal beech sampling sites are given in Table 1, together with abbreviations used in the text. The positions of the ten most important sites are shown by Figure 1; Withdean is very close to Patcham Place and Painswick only 3.3 km from Buckholt.

Most of the trees surveyed appeared to have been planted. Indeed the woods at Killerton and Woodbury were both established on ancient hillfort sites, whose ditch and bank features have been well preserved despite the presence of the tree root systems. The trees sampled from Killerton Clump formed part of a plantation created in the eighteenth century by John Veitch, who was employed by Sir Thomas Dyke Acland, 7th Baronet, to lay out the path and garden. They are in the extension area of the Dolbury Hillfort which was constructed in the period *c.*400 BC – 43 AD.

Plantings on the South Downs are extensive in places and are in some places susceptible to windthrow on shallow soils. The avenue of beech

TABLE 1. Principal beech sampling sites, giving abbreviations used in the text.

Site and grid reference	Site description
Benwell, (Be). Tyne & Wear NZ 220640	11 well spaced beech, some in a group, others in an avenue of mixed species. Benwell Dene Park, S. of A69, Newcastle upon Tyne. Trees 1 and 7 later lost. 10 trees examined in 2007.
Spennymoor, (Sp). Durham NZ 230311	7 closely planted trees in shelter belt with *Quercus petraea*. 300 m. N. of Park Head Hotel, A688, SW of Spennymoor. One tree later lost. 9 trees examined in 2007.
Ripon, (R). North Yorkshire SE 352751	12 well spaced trees in shelterbelt mainly beech. 1 km SW of A1 on A61. 12 trees examined in 2007.
Himley, (H). Staffordshire SO 888914	9 well spaced trees in avenue of lime and other species. Himley Hall Park, E. of A449 on B4176. Only 6 trees remained in 2004; all were examined in 2007.
Fish Hill, (FH). Worcestershire SP 116369	2 trees (later 4, then 5) in mature woodland by A44 east of Broadway. Two further trees in main woodland also surveyed in 2004. 10 trees examined in 2007.
Buckholt, (Bu). (Rough Park Wood) Gloucestershire SO 885133	14 closely planted trees in almost pure beechwood 3.5 km N. of Painswick on A46. 8 trees surveyed in 2007.
Painswick, (Pa). Gloucestershire SO 880130	1 (later 4 or 5) trees in group opposite drive to rear car park of 'Royal William' on A46. Four trees surveyed in 2004; 5 in 2007.
Nettlebed, (N). Oxfordshire SU 713858	2 trees (later 4) at margin of road (A423) through mature beechwood. 9 trees examined in 2007.
Patcham Place, (Pp). Brighton E. Sussex TQ 299091	9 out of a row of well spaced roadside trees along London Road until its junction with Mill Hill Road, Brighton. (No 3 lost in the great storm of 16 October 1987; others felled since, but 9 surveyed in 2007).
Withdean, (Wi). E. Sussex TQ 301077	Single isolated tree in Withdean Park east of the London Road (A23), Brighton.
Killerton, (K). Devon SS 973004	7 (later 9) spaced trees in mixed wood on hill top. Killerton Park (N.T.) on B3185. Seven trees surveyed in 2004, 8 in 2007.
Woodbury, (W). Devon. SY 032874	13 well spaced trees planted in wood on Hill Fort site. Woodbury Common, on B3180. Seven trees surveyed in 2004; 8 in 2007.

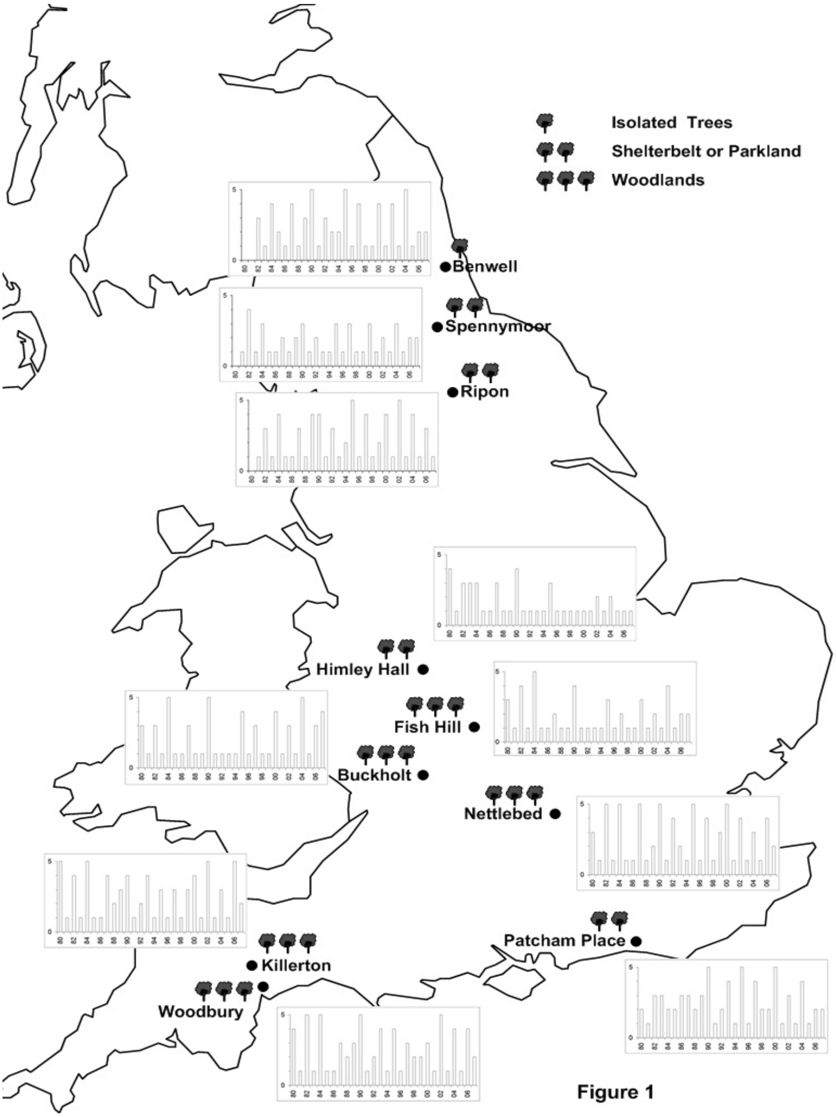

FIGURE 1. Positions of the main beech sampling sites, with mean yearly production of full nuts for each group of trees expressed on the five-point scale given in the Results section. Note that Wytham Woods are some 15 miles NW of Nettlebed.

at Patcham Place proved to be a most useful site in the extreme south. Patcham Place itself has existed as a mansion since 1558; the present house with its striking façade incorporating black mathematical tiles is the product of a rebuilding for John Paine in 1764 (RYMAN and MEAD, 1992). In the long term it was trees along the London Road, which probably date back to near the Paine period, rather than those on the adjacent hillside whose mast was assessed. Soils here appear to be quite deep in contrast to those on the hillside, where the storm of 16 October 1987 caused devastating losses. Shallow root plates were pulled completely out of the ground and the rookery established in the treetops was considerably disturbed.

Sampling methods

The intensive masting studies of GURNELL (1993), undertaken by means of seventy-five regularly monitored seed traps in a mixed oak woodland near Alice Holt, Surrey, over a period of thirteen years are unusual in being fully quantitative. The labour required to make such a survey as this over a country as large as England would be enormous. GARDNER (1977) similarly used frequently cleared litter traps in his studies of fruiting in common ash (*Fraxinus excelsior).* This is undoubtedly the best approach if time is unlimited and there is no likelihood that the traps would be interfered with, as the quality of seed varies with time during the fruiting season, more empty pericarps being shed in September with fall of full nuts occurring somewhat later. However, it is not until the seed is on the ground that the effective quality and quantity of the crop can be assessed (HARMER, 1994). An extended account of why an effort-based system of a ground search for seven minutes per tree – wherever possible in early October, but sometimes at the very end of September in the south – was adopted, is given in HILTON and PACKHAM (1997) along with a more detailed description of the various sorting processes. After a short experimental period nuts were sorted dry. When dropped onto a hard surface the noise of impact can be used to distinguish full and empty pericarps. Attempted crushing and dissection can also be employed in doubtful cases.

Where lower branches were accessible aerial samples, often of fifty cupules, were often also collected as these gave information on predation and disease. The cupules were air-dried on trays: they opened fully within two days and the nuts either fell out or could be dislodged for sorting.

From 1982 onwards, results in the tables and figures are all expressed on the basis of seven-minute samples collected from the ground. (Measurements prior to this are discussed below under *Masting patterns: numbers of full and empty nuts*.) The size and quality of the ground samples is inevitably affected by the technique of the sampler, the nature of the substrate and the removal of full nuts by animals. Amongst birds, the various tits (*Parus* species) are particularly active in this respect (WALTHER and GOSLER, 2001).

The ground search estimation method is indeed unsuitable for areas where severe predation of nuts may occur early in the season. This is certainly true of trees in the *Fagus sylvatica*/conifer woodlands in the Chilterns (MORRIS, 1997). Here nuts are consumed by populations of both the alien grey squirrel (*Sciurus carolinensis* Gmelin) and the alien edible dormouse (*Glis glis*) originally established in 1902 from a few animals released in Tring Park, Herts, by Lord Rothschild. Differences between samplers have been reduced by initially collecting with an experienced person to standardize the technique. It is particularly important to search as much of the ground beneath a tree canopy as possible, rather than staying put in a particular area, as discrete localities of viable nuts may otherwise be missed. Further consideration of this is given below under *Problems in the assessment of masting intensity over a wide area.*

Numbers of nuts handled from all sites in mast years are considerable, amounting to 14,494 total nuts and 9,597 full nuts in 2004. In this year there was 1.7kg of clean viable nuts. The weights shown in the tables are of cleaned nuts which have been air-dried in a moderately heated room.

Classification of nuts

Mast collections were sorted into six categories:

1. Nuts containing well-formed seeds likely to produce healthy seedlings, even if subsequently damaged by predators after being shed from the cupule.
2. Nuts containing a shrivelled seed unlikely to germinate.
3. Nuts attacked by the moth *Cydia* (see Figure 3) usually detected by a 1-mm hole in the pericarp (I_1).
4. Nuts gashed by birds or rodents, sometimes in search of *Cydia* larvae (I_2).
5. Mouldy nuts, which in later stages have a darkened pericarp and are sometimes found in unopened cupules.
6. Empty nuts with perfectly formed pericarps.

Masting patterns: numbers of full and empty nuts

The broad picture of the masting pattern in England during the period 1980–2004 is provided by Figure 1, which is based upon five categories of mean numbers of full nuts (whether attacked by pests or not) for each site collected in a seven-minute sample:

Grade 1. very poor <11
Grade 2. poor 11–50
Grade 3. moderate 51–100
Grade 4. good 101–150
Grade 5. very good >150

Commencement of our observations was prompted by the good mast year of 1980, when grades were awarded on ease of collection rather than the number of full nuts that could be collected in seven minutes (HILTON and PACKHAM, 1986). Figure 2 contrasts the numbers of total and full nuts in the southern and northern sites over the 28-year period the survey has run (details for the individual sites are provided in Tables 2 and 3).

Success or failure has to be measured in terms of full nuts, including those which have been attacked by *Cydia fagiglandana* (Figure 3): on this basis there is no doubt that 1990 provided the greatest mast during the survey period. In that year the mean number of full nuts for the seven southern sites (FH, N, Bu, Pa, Pp, K, W) i.e. the mean of the site means of nuts per tree, was 168, while that for all sites was 149. The value for the four northern sites in this year was 115, a little lower than the highest mean for these four sites (Be, Sp, R and H), which was 121 recorded in 1995. The second highest value for the southern sites (163) came in 1984 and this led to the second highest overall mean of 143 though that for the northern group was only 108.

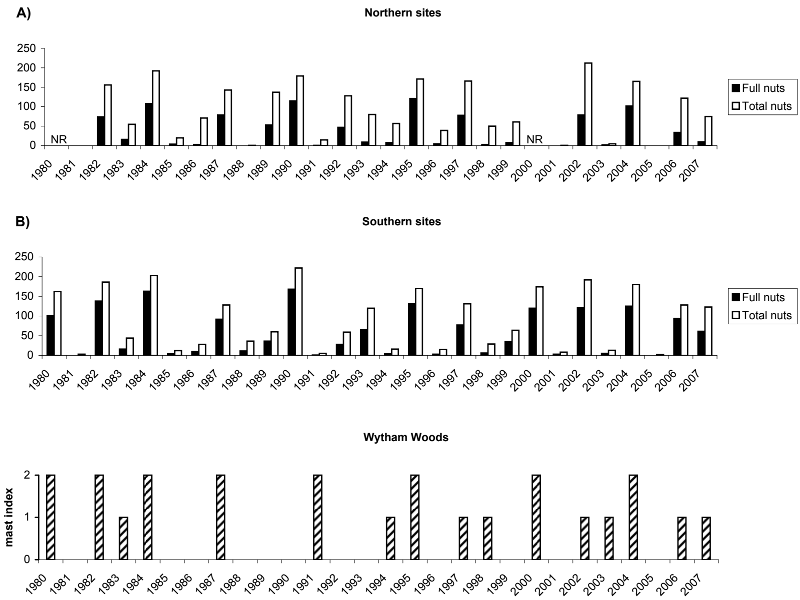

Figure 2. Mean numbers of full nuts (solid bars) and total nuts (hollow bars) collected in 7-minute samples for A) All northern sites and B) All southern sites. NR indicates no record. C) Mast indices for Wytham Woods, Oxford (1980–2007); 2 – heavy, 1 – moderate, 0 – absent (data courtesy of The Edward Grey Institute, University of Oxford).

TABLE 2. Mean numbers of full nuts in samples for each site visited for the years 1980–2007, together with means (mean[1]) for the years 1982–2007, apart from 1996 and 2002 when the data sets were incomplete. An eighteen-year mean for the years 1982–1999 (mean[2]) is also shown for all sites apart from Benwell. Equal weight was given to each site in calculating yearly means for all southern sites, all northern sites and all sites together. (NR indicates no record). Records for the isolated Withdean tree are shown separately.

	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Mean[1]	Mean[2]
Benwell	NR	NR	55	5	148	14	2	112	0	62	161	0	69	27	14	154	NR	123	10	3	NR	0	126	0	199	0	23	12	55	–
Spennymoor	NR	0	107	0	72	0	2	34	0	36	56	0	18	0	2	88	8	75	0	4	NR	0	17	0	53	0	15	19	25	28
Ripon	NR	0	71	0	115	1	1	86	0	108	130	3	97	9	14	161	4	105	1	23	NR	0	153	5	138	0	92	9	55	52
Himley	80	0	64	57	97	1	5	85	0	5	111	0	2	1	2	80	4	7	1	3	10	1	20	3	16	0	5	1	24	29
All North	–	0	74	16	108	4	3	79	0	53	115	1	47	9	8	121	5	78	3	8	–	0	79	2	102	0	34	10	40	41
Fish Hill	29	0	145	1	197	0	0	26	0	0	140	0	1	1	2	98	0	11	0	5	55	0	15	0	108	0	21	20	33	35
Buckholt	69	0	74	8	153	0	0	78	0	0	172	0	0	6	1	113	0	84	0	0	138	0	82	6	184	0	88	122	49	38
Painswick	NR	0	149	9	195	0	0	96	0	1	162	0	0	40	1	108	0	49	0	14	120	0	151	15	210	0	75	117	58	46
Nettlebed	102	0	182	0	152	0	1	184	0	16	152	0	112	23	8	176	0	126	0	92	161	0	150	0	86	0	108	49	67	68
Patcham Pl	39	0	98	92	36	27	68	90	43	97	240	0	19	126	10	215	10	113	21	29	162	3	95	2	104	0	39	38	67	74
Killerton	247	0	139	2	178	0	2	115	19	70	125	7	44	137	6	94	6	99	8	67	113	10	191	4	65	0	157	49	66	62
Woodbury	122	0	176	0	233	0	0	56	13	66	186	0	21	124	2	110	3	55	12	40	91	9	164	7	120	2	172	29	67	61
All South	101	0	138	16	163	4	10	92	11	36	168	1	28	65	4	131	3	77	6	35	120	3	121	5	125	0	94	61	58	55
All Sites	98	0	115	16	143	4	7	87	7	42	149	1	35	45	6	127	4	77	5	25	104	2	106	4	117	0	72	42	51	50
Withdean	26	0	45	27	64	6	64	35	3	9	242	0	2	18	15	112	16	9	1	12	90	16	80	41	196	0	5	64	44	38

TABLE 3. Mean total numbers of nuts in samples for each site visited for the years 1980–2007, together with means (mean[1]) for the years 1982–2007, apart from 1996 and 2002 when the data sets were incomplete. An eighteen-year mean for the years 1982–1999 (mean[2]) is also shown for all sites apart from Benwell. Equal eight was given to each site in calculating yearly means for all southern sites, all northern sites and all sites together. (NR indicates no record). Records for the isolated Withdean tree are shown separately.

	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Mean1	Mean2
Benwell	NR	NR	156	108	228	62	73	188	0	153	198	0	148	111	60	193	NR	185	92	81	NR	0	269	3	185	0	113	126	114	–
Spennymoor	NR	0	157	0	181	0	51	77	0	124	151	0	158	38	52	133	61	171	27	39	NR	0	167	0	148	0	125	80	78	79
Ripon	NR	0	161	0	153	3	42	124	1	169	159	41	154	46	56	191	9	164	8	66	NR	0	227	12	169	0	124	16	87	86
Himley	241	0	150	113	204	16	119	182	1	100	206	17	52	123	58	168	48	143	72	56	148	2	186	5	159	0	127	76	97	102
All North	–	0	156	55	192	20	71	143	1	137	179	15	128	80	57	171	39	166	50	61	–	1	212	5	165	0	122	75	94	95
Fish Hill	147	0	203	14	243	0	0	70	0	9	234	1	26	15	20	189	1	65	10	11	201	0	78	0	183	0	65	111	64	62
Buckholt	110	1	115	35	186	0	0	113	0	0	208	0	0	10	1	142	1	124	0	0	162	0	118	10	231	0	104	154	65	52
Painswick	166	0	189	20	224	0	0	129	0	1	194	0	0	51	2	128	0	105	0	19	164	0	190	30	280	0	97	182	77	59
Nettlebed	134	0	212	0	182	0	10	198	0	21	218	0	143	210	17	199	0	150	1	105	197	0	205	0	136	0	129	71	92	93
Patcham Pl	133	0	149	213	116	87	145	160	154	182	323	2	79	206	49	263	71	200	110	112	203	6	214	18	175	0	156	191	138	146
Killerton	308	10	207	24	209	0	24	149	67	110	157	32	112	187	16	124	20	155	43	128	157	31	277	8	94	0	193	83	101	98
Woodbury	133	8	227	0	258	0	14	78	28	99	220	0	52	158	9	146	14	119	36	70	133	16	259	22	160	13	150	71	92	85
All South	162	3	186	44	203	12	28	128	36	60	222	5	59	120	16	170	15	131	29	64	174	8	192	13	180	2	128	123	90	85
All Sites	172	2	175	48	199	15	43	133	23	88	206	8	84	105	31	171	23	144	36	62	171	5	199	10	175	1	126	106	91	89
Withdean	197	0	161	217	174	42	387	169	146	203	308	1	157	176	205	230	73	185	204	205	186	32	237	65	262	0	187	190	173	180

All beech trees produce a proportion of empty nuts and while the southern sites have over the period produced more full nuts per tree, the northern sites have on average had higher numbers of total and empty nuts, as is shown by both Mean[1] and Mean[2] in Tables 2 and 3. Mean[1] values for full nuts at Nettlebed, Patcham Place, Killerton and Woodbury are remarkably close.

The highest mean for full nuts per tree in a given year is the 1990 figure of 240 for Patcham Place, where the yield is both higher and more consistent than that for the nearby Withdean tree. The isolated tree at Withdean is of particular interest; its yield and the proportion of its nuts that are full vary greatly. Only sixty-four nuts out of 387 were full in 1986 when it produced its heaviest mast. This contrasts with 242 out of 308 in 1990, and the 196 out of 262 in 2004, its next most effective year. Proof that cross-pollination occurs was provided when seed from this tree was successfully germinated. The parent tree has normal green leaves, but when saplings grown from its nuts were used in a hedge a few plants were purplish copper-coloured. It could be that the effectiveness of pollination in this tree is considerably influenced by weather conditions in its immediate vicinity at the time concerned**.** Contrasts between numbers of full and total nuts at Withdean and Patcham Place are demonstrated particularly vividly in Figure 5 of PACKHAM and HILTON (2002), in which paper the weights and condition of the full nuts are discussed in detail.

FIGURE 3. Damage inflicted by *Cydia fagiglandana*. Note the typical round penetration hole in the beech nut, whose contents have been almost totally consumed by the larva. (Photograph by Malcolm Imman).

FIGURE 4. Photograph taken on 28 September 2006 of the huge fruiting body of a Giant Polypore *Meripilus giganteus* growing on the stump of a tree, felled at some time between the 2004 and 2005 surveys, that is immediately south of Tree B, Patcham Place. This fungus is a very virulent parasite of beech and often continues to grow as a saprophyte on the stumps of trees it has killed. (Photoghraph by John R. Packham).

The domestic use of locally collected mast to grow seed for hedging in this way makes very good sense. Normally the dampened seed of common beech will not germinate unless first subjected to frost. This inhibition can be removed by storing seeds, in a medium of damp clean sand, in a domestic refrigerator for a month.

Regional relevance of the beech masting records for Wytham woods, Oxford

Records of beech masting at Wytham Woods, Oxford, have been kept continuously since 1946, and are shown in the very recent description of the developing ecology of this much studied wood (Perrins and Savill, 2008). As these records began thirty-four years before ours, we had hoped that there would be a positive correlation between the 1980–2007 records for Wytham Woods and our more detailed records for the southern sites (see Figure 2 and Table 2). Had this been the case the 1946–1979 records for Wytham Woods could have provided a guide to the south of England in general.

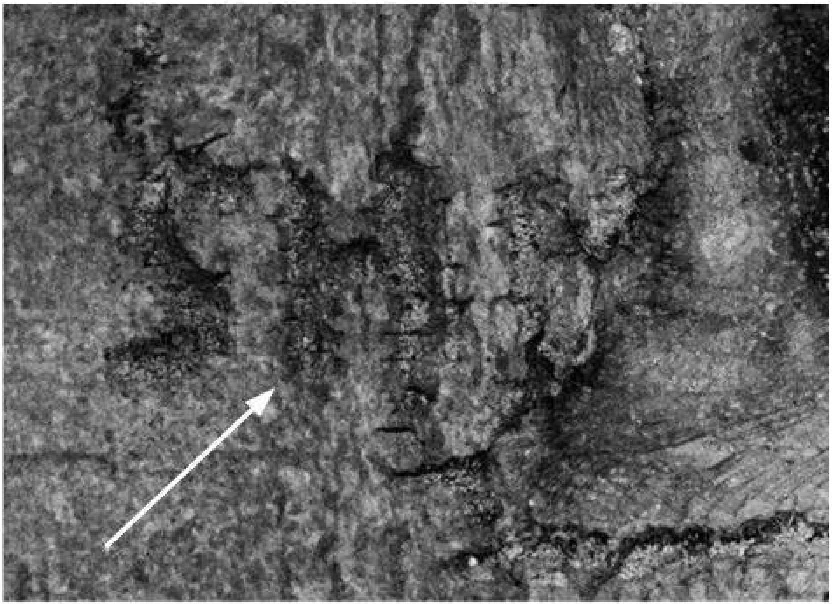

FIGURE 5. The initials SH (arrowed) cut into the trunk of Tree C, Patcham Place. (Photograph by John R. Packham).

In practice good beech masting years for our southern transect sites and Wytham Woods do correspond for 1980, 1982, 1984, 1987, 1995, 2000, and 2004. However, the good masting found in our southern transect sites for 1990, 1997 and 2002 did not occur at Wytham, where 1991 was a good masting year while almost no full nuts were found in any of our sites either north or south. The southern transect mean for 1990 of 168 full nuts was even better than that for 1984 (163), and means for the four sites nearest Wytham (Fish Hill 140; Buckholt 172; Painswick 162 and Nettlebed 152) were all high. Variation between sites did occur, however; the site mean for Fish Hill in the mast year of 2002 was only fifteen full nuts. It should also be noted that Wytham Woods data record an unusual three-year absence of mast between 1988 and 1990.

This analysis makes it clear that masting records for Wytham Woods are not a satisfactory guide to what is happening throughout the south of England. A comparison of the records for the thirty-four years from 1946 to 1979 with that for the twenty-eight years from 1980 to 2007 shows that there has also been a change of masting pattern at Wytham. During the first period there were twelve full masts (35.3%), two moderate masts (5.9%) and twenty years without mast (58.8%). This time period included a five-year span (1963–7) without mast. During 1980–2007 there were eight full masts (28.6%), eight moderate masts (28.6%) and twelve years with no mast (42.9%).

Variation in nut weights in time and space and causes of damage to nuts

Table 4 shows variation in nut weight in trees at the various sites for the years when there was adequate seed during the period 1995–2007. The remarkably high upper value for Himley (514mg) in 2004 was for a weighed sample of just nine viable full nuts. These came from Tree 9 that was not in a very healthy condition; some of its exposed roots bore fungal fruiting bodies. Variation in mean air-dry nut weights per tree is much greater in some sites than in others. In 2006, for example, the highest value amongst the ten trees assessed at Woodbury (Tree 7) was 282mg and the lowest (Tree 17) 204mg; the site mean was 252mg. The range within the nine trees assessed at Killerton was much greater, varying between 172mg (Tree 1) to 421mg (Tree 2); the site mean was 301mg.

Nuts are frequently consumed by the larvae of *Cydia fagiglandana* Z (Figure 3); their characteristic exit holes, some of which have been enlarged by birds, and specimens of the caterpillar itself are also shown in Section 4.4.1 of THOMAS and PACKHAM (2007). The caterpillars consume the nuts so completely that only their frass remains inside the otherwise empty nut. In addition to those damaged by insects, many nuts are eaten by rodents, while others are rotted by fungi.

Discussion

Causes of the periodicity and variability of beech masting

THOMAS and PACKHAM (2007, Figure 4.10) provide a model that endeavours to account for the periodicity and variability of masting in beech, and facilitates discussion of the results obtained in the current survey. As MATTHEWS (1955) pointed out, the extent of available light and weather conditions at particular times of the year are absolutely critical to the initiation of the flowers, while the presence of adequate food reserves (carbohydrates) and also mineral nutrients is essential if the fruits are to mature. It is this latter factor that is responsible for the basic biennial pattern that is seen so often; there is a negative feedback in the year after heavy masting even if the climate is suitable. Foresters have long been aware of the importance of nutrients in beech masting, indeed Nemec (1956) discusses the role of soil improvement as a measure to increase the rate of viable seed production. He found that low levels of nutrients in the top soil layers are associated with poor, or no, masting and that seed production was improved by the addition of ground basalt to the soil. Flower buds are only initiated in summers when temperatures are high; when they are cool the buds are vegetative rather than reproductive. The extent of pollination is another vital factor; if it is inadequate many of the mature pericarps are empty.

TABLE 4. Variation in air–dry weight (mg) of beech nuts per site for nine seasons during the period 1995–2007. In 1996, 2001, 2003 and 2005 nuts were either absent or at very low levels in many sites. The values shown are the minimum and maximum values of the means for each tree sampled at the site. Only one tree was sampled at Withdean, Brighton, and in some years only one tree was masting at a particular site. (NR indicates no record; a dash a lack of sufficient viable seed).

	1995	1997	1998	1999	2000	2002	2004	2006	2007
Benwell	212–266	268–410	272–375	313	NR	211–303	195–328	115–292	242–306
Spennymoor	220	225–303	–	191	NR	165–214	174–248	84–265	172–266
Ripon	231–255	223–360	328	244–265	NR	195–331	197–270	109–278	187–348
Himley	250–273	–	286–363	–	150–301	210–330	262–514	231–308	230
Fish Hill	203–240	90	234	94–106	251–261	150–240	166–213	169–204	132–257
Buckholt	176–295	160–251	–	–	249–301	202–251	192–246	179–299	229–335
Painswick	NR	235–298	–	280–353	275–340	183–306	181–225	204–318	249–394
Nettlebed	139–281	213–258	–	221–300	208–305	202–255	104–230	174–266	140–267
Patcham Pl	199–237	177–230	149–279	231–302	174–244	156–261	139–237	148–194	160–272
Withdean	381	331	–	346	407	337	294	–	331
Killerton	211–335	319–480	136–205	257–509	258–352	212–336	184–301	172–421	217–358
Woodbury	178–261	200–367	332	213–377	241–314	184–257	219–305	204–282	245–446

A letter from Dr. A.G. Gordon, proprietor of the tree seed-supplying firm Forestart, who had read our paper concerning masting from 1980 to 1995 (HILTON and PACKHAM, 1997) made it clear that there can be considerable variation in masting behaviour within the British Isles. He remarked, "As you predicted 1996 was a near total failure in England, although in Scotland there was a bigger mast year in 1996 than in 1995, even though for many of the reasons you cite the actual set of full seed was very disappointing. After a very great deal of effort we did manage to collect nearly 200kg of pure seeds".

Correlation between extent of beech masting and reproduction of the edible dormouse

The alien edible dormouse *Glis glis* still flourishes in the Chilterns of southern England, a few animals having been released in 1902 in Tring Park, Herts, by the second Lord Rothschild. Long-term studies of this alien have been made in the Chilterns (MORRIS, 1997; MORRIS, TEMPLE and JACKSON, 1997). This animal, together with its fellow alien the grey squirrel, consumes beech nuts so heavily that the ground search estimation method for beech masting success may be compromised, though a survey of nuts still on the trees together with records of the fresh cupules remaining on the ground would afford a reasonable basis for awarding a grade. Interestingly reproductive success in this animal, at least in the beech/spruce/larch woodlands near Tring, Herts, appears to be closely related to masting success in beech. In 1995, a mast year, *Glis glis* bred well in this area but no young were found in the following non-mast year. This corresponds with similar reports from continental Europe. There was a very great production of young edible dormice in the mast year 2000. In the following year, which was Grade 1 (English Beech Mast Survey category), there was a complete absence of juveniles in nest boxes kept in the Chiltern woodlands.

Most recently there has been prolific birth of young in the mast years 2004 and 2006. The nest boxes contained no young at all in 2005. The connection between masting success in beech and breeding success in the edible dormouse is one of which the traditional dormouse hunters of Croatia and Slovenia were well aware. We have yet to ascertain the stimulus that leads these animals to have their young in the August of mast years, well before the nuts are properly developed. Heavy beech masting in the Chilterns in 2006 resulted in a tremendous population increase, so much so that a number of nest boxes had two families in them. Previous experience had led to the view that in good mast years houses were not invaded by dormice. In 2006 they were, despite the ample supply of food in the form of beech nuts (Morris *pers. comm.*). Were the individuals invading houses simply displaced by an abnormally high population pressure?

Another good breeding year followed in 2007, despite the beech crop in the Chilterns being no more than moderate. With few predators of *Glis glis*, it will be interesting to see how far they eventually spread. In the UK tawny owls occasionally take them, as do domestic cats. On the Continent, other species of owls may take a few as well, so might pine martens in certain habitats. However, dormice are strongly arboreal and suffer relatively little predation.

Consequences of masting in large natural forests

The consequences of masting on natural communities are clearly seen in the Forest of Bialowieza, Poland, whose large area is kept in as natural a condition as possible. Common beech is amongst the trees present but huge old peduculate oaks *Quercus robur*, which shed enormous weights of acorns at six- to nine-year intervals, are far more common as are hornbeams *Carpinus betulus*, that also mast heavily in synchrony with the oaks and Norway maple *Acer platanoides.* Their seeds are devoured by small rodents, notably bank voles *Clethrionomys glareolus* and yellow-necked mice *Apodemus flavicollis*, whose numbers rapidly increase, only to crash again as their food supply, including that originally cached, diminishes and their predators, including weasels, pine martens and tawny owls, devour them. This sequence of a rapid rise in small rodent populations after a heavy mast, followed by a similar rise in that of the animals preying upon them, and numbers of all the species concerned crashing or heavily diminishing in non-mast years, is described in detail by JEDRZEJEWSKA, PUCEK and JEDRZEJEWSKA (2004). There can be little doubt that similar sequences occur in beech forests also.

Influence of winter beech mast crops on the occurrence of birds in gardens

Chamberlain *et al.* (2007) tested the assumption that woodland birds that fed on beech mast would occur significantly less often at garden feeders in mast years. In so doing they utilized the beech mast data which have been recorded annually from Wytham Woods, Oxfordshire, since 1946. They assumed that these data, recorded as low (0), medium (1) or high (2), were representative of beech mast abundance in the whole UK. They took weekly winter occurrence rates of forty bird species at garden feeders from the winter of 1970/1971 until that of 1999/2000 and compared them with beech mast abundance during that period. Seven species (great spotted woodpecker *Dendrocopos major* L., woodpigeon *Columba palumbus* L., great tit *Parus major* L., coal tit *Periparus ater* L., nuthatch *Sitta europaea* L., jay *Garrulus glandarius* L. and chaffinch *Fringilla coelebs* L.) that commonly feed on beech mast did in fact occur less commonly in gardens in years when beech mast was most abundant.

Problems in the assessment of masting intensity over a wide area

Fully quantitative masting studies, such as those mentioned in the introduction (GURNELL, 1993), are very labour-intensive, involve a great deal of equipment and cannot be used by one or two observers in public areas situated hundreds of miles apart. Under these circumstances it is not possible to devise a perfect system for such assessments; the maximum that can be claimed is that the pragmatic methods we employ give a reasonable picture of the year on year variation and enable the comparison of nut production in particular trees over long periods. Disparities in assessment can arise from a number of factors, of which the precise time at which the survey is made, any interference with the crop, and the nature of substrate from which the samples are collected are the most important.

The time of survey is most crucial. If made too early the nuts will not have been shed; if made too late seed predators, notably grey squirrels at many sites, will have consumed many of them. Timing is not easy as sites can differ considerably in speed of ripening. On 26 September 2004 a tree at 3 Ridgeway Road, Long Ashton, North Somerset, was surrounded by fallen nuts, most of which were full; a good Grade five. The situation at Killerton on the following day varied from tree to tree: K VI was Grade five and K X Grade four; overall the site grade (based on the mean number of full nuts per tree) was three. The number of full nuts gathered in seven minutes beneath K III was only fifteen, however unopened cupules taken in a canopy sample had abundant full nuts. Because site values are based on several trees this anomaly did not change the overall site grade (three).

Substrate strongly influences effort-based collections, although some seed can nearly always be collected from the upper surfaces of roots running from tree trunks. Tall grass makes sampling difficult, as with Trees 2, 5, 6, 7, and 8 at Ripon and Tree 6 at Spennymoor in 2004, while tops of walls and areas of tarmac or concrete facilitate rapid sampling. Such factors would have to be taken into account when considering the success or otherwise of masting at a particular site.

Comments on the results of the 2007 survey

The most striking feature of the 2007 mast was the poor crop in the four northern sites, with both total and full nuts being well down. Grade 4 values at both Buckholt and Painswick (see Table 2) strongly influenced the overall full nut mean for the southern sites. The weather made survey of the Fish Hill, Nettlebed and Patcham Place sites less pleasant than usual, and conditions beneath some of the trees at Fish Hill were particularly difficult. After a period of rain many nuts were extremely muddy and all had to be thoroughly cleaned and dried before assessment. It is important to ensure that only nuts of the current year are assessed: in 2007 some of the nuts picked up clearly belonged to the previous year and had to be discarded.

The pattern of empty and full seeds beneath the solitary beech at Withdean, Brighton in 2007, emphasized just how important it is to sample from as much of the ground beneath a particular tree as possible. The great majority of the seeds in the southeastern region beneath this tree were empty, while most of the seeds in the northeastern area were both large (mean air-dry weight of the sixty seeds weighed was 331mg) and in good condition. The reasons for this variation are not entirely clear, but may well be related to wind conditions during the pollination period.

Changes in the condition of sites and trees

Over a 28-year period losses of individual trees are inevitable. Where this has occurred similar sample trees have been used instead. One of us (JRP) has observed the avenue of trees at Patcham Place since 1936 and here the losses have been quite severe, all the trees used adjoining the Mill Hill Road have been felled. Observations of the tree in the woodland on the NE facing slope opposite the avenue (see Table 1) were abandoned due to difficulties of sampling on an unsuitable substrate. At Patcham Place, as elsewhere, dying beech may produce heavy crops of viable seed as did Tree D (PACKHAM, 2003).

Figure 4 shows the huge fruiting body of a Giant Polypore *Meriplus giganteus* living saprophytically on the stump of a tree that was felled at some time between the 2004 and 2005 surveys and was immediately south of Tree B. Though Tree B bore seed, it was beginning to suffer from the attentions of parasitic fungi in 2006. Several of the trees in this originally magnificent avenue have been damaged or had initials cut into them (Figure 5). This latter damage was useful in identifying some of the trees in a diminishing though formerly magnificent avenue which was probably set out in the same century as John Paine remodelled the mansion. Unfortunately Brighton Corporation is filling in its gaps with trees of the horse-chestnut *Aesculus hippocastanum*.

There have also been difficulties at other sites. Problems at Nettlebed (N), for example, arose through difficulties of access to the original sample trees when a barrier fence was erected, a problem later overcome. Over this long period considerable variations in seed size and weight have been observed many times, and a number of double cupules, such as that shown in Figure 6, have been seen. Some contained six seeds.

Masting success and regeneration success

As already stated, masting success can be defined by the total numbers of full nuts produced per tree in a particular season, regardless of whether these be damaged or not. In contrast regeneration success is obviously reduced by insect damage, consumption of nuts by vertebrates and the moulding off of damp nuts. This may explain the adaptive significance of masting. Given the large number of invertebrate and vertebrate predators of beech seeds, it is highly likely that the masting of beech fits the classic predator-satiation hypothesis of JANZEN (1971). Here the synchronized large seed crops overwhelm seed predators and some nuts survive and germinate. Certainly Salisbury (1942) observed that beech seeds escaped predation only in mast years, and TAPPER (1992), investigating ash in Sweden over six years, found increased seed survival in mast years. Masting in beech may also be a result of an adaptation to increase pollination efficiency through synchronized mass flowering, a hypothesis that finds some support for wind-pollinated trees such as beech (SORK, 1993; KELLY and SORK, 2002).

Once viable seed is on the ground subsequent seedling establishment is strongly affected by local environmental conditions including competition from neighbouring vegetation and the degree of shading. Interestingly, WIDDICOMBE (1995, 1999) found that in both Kentish and Cornish *Fagus sylvatica* and *Quercus* spp. the amount of regeneration was related to the vegetation cover rather than the number of seed trees present. *F. sylvatica* seedlings occurred most frequently in areas devoid of vegetation, usually with leaf litter but often on slopes where mineral soil was exposed. A light cover of bilberry *Vaccinium myrtillus* seemed to aid regeneration. In our own experience mown lawns provide good conditions for the germination of both beech and oak, though the lives of the resulting seedlings are inevitably short.

The initial development of seedlings into saplings and their final release and rapid growth when heavy shade is removed may take many years, so assessment of regeneration success is a long term process. The formation of gaps in the forest canopy, frequently through windthrow, is crucial to the successful development of young saplings. Failure of natural regeneration of forest trees in Britain, particularly of beech and oak, has long been a matter of concern (WATT, 1919, 1923), and is at the present time in marked contrast with the success of ash *Fraxinus excelsior*, whose seedlings and saplings occur abundantly in many woodlands. It will, in particular, be interesting to see how the changing climate alters the regional patterns of both masting and natural regeneration in beech.

Figure 7 shows vigorous saplings of *Fagus sylvatica* growing in a well-lit site at Nettlebed. Our records also include a photograph of two year old seedlings photographed at the Woodbury, Devon site in the autumn of 1987,

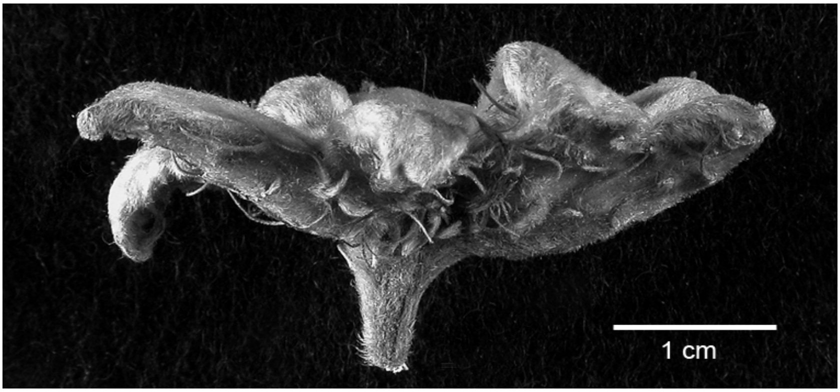

FIGURE 6a

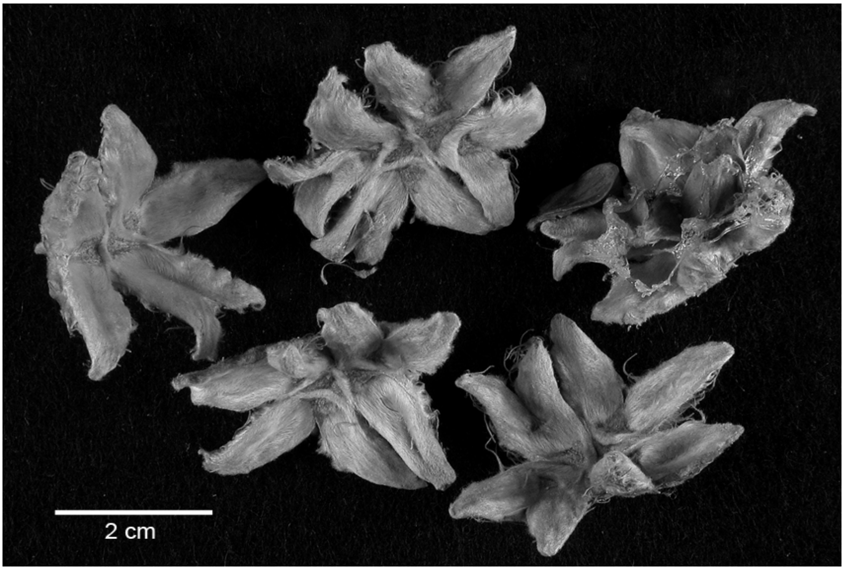

FIGURE 6b

FIGURE 6 (a) Side view of a double cupule. (b) All five of the double *Fagus sylvatica* capsules collected at the Himley, Staffordshire, site on 1 October 2007. (Photographs by Malcolm Inman).

which had been suppressed by shade. Such seedlings rapidly develop into large saplings and ultimately trees when local canopy trees are blown down or die. Figure 8 shows such a regeneration gap with vigorous young saplings of the American beech *Fagus grandifolia* that have arisen as root suckers. The ability to regenerate so effectively in this way occurs only occasionally in common beech *F. sylvatica*, which is so similar to its American cousin in other respects. In September 2006, however, Tree Y at Patcham Place, Brighton, had many young shoots growing from the exposed roots running from the base of its trunk. This may well have been related to damage incurred when the grass was mown.

Future of the survey

Monitoring of beech mast will be continued by Drs Lageard and Thomas in forthcoming years and will be supplemented by the collection of dendroecological and meteorological data sets (*cf* DITTMAR *et al*., 2003). Comparison of these and data from the long-term survey reported here will shed further light on the phenomenon of beech masting and will provide an important resource for understanding the ecological responses of beech woodland under various future climate change and woodland management scenarios (*cf* WESCHE *et al.,* 2006). That such changes are inevitable is apparent from the ring studies of the southern range-edge of *Fagus sylvatica* (PENUELAS *et al*., 2008) and drought-driven growth reduction in old beech forests of the central Appenines, Italy (PIOVESAN *et al*., 2008).

It is the intention not only to continue to investigate the masting patterns of this magnificent tree, also but to provide information which will promote

FIGURE 7. An example of the vigorous regeneration seen at the Nettlebed site in 2007. (Photograph by Jonathan G.A. Lageard).

FIGURE 8. Stand of American beech *Fagus grandifolia* that arose from root suckers. Massachusetts, U.S.A. (Photographed in 2004 by Peter A. Thomas).

its long term health and existence on these islands. We hope that the vigorous regeneration shown in Figure 7 will long occur here.

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