

# Population dynamics of *Malus sylvestris* stands in grazed and ungrazed, semi-natural grasslands and fragmented woodlands in Mols Bjerger, Denmark

Rita Merete Buttenschøn & Jon Buttenschøn

*Buttenschøn, R. M., Danish Forest and Landscape Research Institute, Kvak Møllevej 31, DK-7100 Vejle, Denmark*

*Buttenschøn, J., Molslaboratoriet, Strandkærvej 6–8, DK-8400 Ebeltoft, Denmark*

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*Malus sylvestris* (L.) Mill., is an important diversifying and structural element in semi-natural grasslands in parts of temperate Europe. Awareness of this has been growing in recent decades. Little, however, appears to be known about the dispersal of the species in nature. The field study reported here suggests that large domestic herbivores may be a major vector of dispersal, as well as providers of suitable seedbeds for germination. Of the close to 1 800 individual seedlings, the emergence and subsequent fates of which are recorded in this study, 98% have with certainty been spread through grazing by cattle or horses. The survival of the seedlings depends on a number of factors, e.g., the growth conditions due to the prevailing climate, light regimes at germination, nutrient availability, breaking of field-layer vegetation canopy and avoidance of excessive browsing. Some 20% of the seedlings may survive for longer periods if grazing ceases, while very few survive under continuous grazing. The study shows an inverse relationship between the survival rate and the grazing pressure in the early post-germination years, but it also indicates that germination density is directly related to grazing pressure. There appears to be a direct relationship between the stocking rate and level of grazing by cattle, indicating that *Malus sylvestris* may not be actively sought by the cattle for food. Accordingly, the survival expectancy of the seedlings is higher where grazing pressure is less and this may be used in a grazing strategy to establish or secure a population of *Malus sylvestris* by natural dispersal.

**Key words:** grazing, habitat management, *Malus sylvestris*, population dynamics, seed dispersal

## INTRODUCTION

*Malus sylvestris* (L.) Mill. is an indigenous tree species of the temperate, deciduous woodlands

of Europe (Henning 1947, Remmy & Gruber 1993, Wagner 1995). *Malus sylvestris* grows in a broad range of soil conditions; except for the extremely acidic soils, and has a probable optimum

at the limit of wetness for woodlands (Wagner 1995). Whereas it was found in prehistoric times in the naturally occurring light open sites of woodlands, it is now associated with many anthropogenic habitats (Schweingruber 1979, Hofmann 1993, Wagner 1995), and fragmented woodlands connected with semi-natural grasslands are now the most important growth sites.

*Malus sylvestris* is traditionally considered to be an important diversifying element of the semi-natural grassland and fragmented woodland habitats of large areas of Europe. It contributes to the spatial infrastructure of these habitats and is important for many animal species. In some parts of Central Europe it is, together with other fruit-carrying trees such as *M. domestica* Borkh., *Pyrus communis* L. and *Sorbus domestica* L., a characteristic species of the so-called "Streuobst-Wiesen" (Lucke 1989, Franke *et al.* 1990, Hofmann 1993). In this connection, there is a growing awareness concerning the conservation of the gene resources of *M. sylvestris* and the conservation of the species in its habitats (Lucke 1989, Franke *et al.* 1990, Remmy & Gruber 1993, Wagner 1995).

There is much discussion as to whether true descendants of *Malus sylvestris* exist today (Henning 1947, Remmy & Gruber 1993, Wagner 1995). One of the main difficulties in clarifying this lies in the fact that the key differentiation traits, the fine hairs of the leaves, are not conserved in recent fossil material (Wagner 1995). Schweingruber's comparison (1979) of contemporary and recent fossil apples suggests, however, that *M. sylvestris* still exists as a species, but, as he expresses it, local populations are subject to a greater or lesser degree of gene-introgression from *M. domestica*. In accordance with our two floras of reference (Hansen 1991, Rothmaler 1994), and from the literature cited above and the general traits of the *Malus* populations of this study, the authors have decided to refer to the named populations as *M. sylvestris*, regardless of the fact that the population contains some individuals of intermediate or even total identity to *M. domestica*.

The characteristics of the fruit that carries the seeds of *Malus sylvestris* suggest that one or more animal vectors could be involved in the dispersal of the seeds. Krefting and Roe (1949), reviewing

previous literature, state that birds may disperse apple seeds, and that, apart from dispersal, passage through the digestive tract is also active in breaking seed-coat induced seed dormancy. Rose and Rose (1988) implicate many birds feed on apple fruit and apple seeds, but they also state that *Malus sylvestris*, rather than being adapted to bird dispersal, is adapted to dispersal by wild pigs and deer. In examining the faeces of brown hare (*Lepus europaeus*), Turcek (1964) found evidence that apple seeds may be dispersed by this species; however, the amount of seeds (one) was small. In literature reviews and own studies, Turcek (1967) implicates no less than 26 mammals in feeding on apple fruit and apple seeds, including several herbivores (wild and domesticated), omnivores and carnivores, but provides no real evidence that feeding and subsequent faecal dispersal results in the dispersal of viable seeds. Within the long-term study, Buttenschøn and Buttenschøn (1985) have demonstrated that domestic cattle could be a main route for the dispersal of viable seeds of *M. sylvestris*. The finding of an average of 91 seeds and 15 seed coats of *M. sylvestris* per kg cattle faeces gives substantial evidence that cattle feed with high preference on apples. The germination trials on the isolated seeds suggest a viability of approximately 5%, but the subsequent findings of at least 41 seedlings in the washing residues suggest even higher viability of the seeds, germination during the experimental germination trials being suppressed by unfavourable conditions.

Together with the results reported previously (Buttenschøn & Buttenschøn 1978, 1985), this report provides information on the population dynamics of *Malus sylvestris* under grazed and ungrazed conditions in a variety of semi-natural grassland habitats containing elements of fragmented woodland. The study series includes grazing by domestic cattle, horses and sheep.

The aims of this report are to investigate factors which may determine the dynamics of the establishment phase of a *Malus sylvestris* population:

- seed dispersal routes
- conditions at sites of seedling emergence
- grazing and browsing pressures

and from this, to discuss practices in habitat management which may promote the survival of a *Malus sylvestris* population.

## MATERIALS AND METHODS

### Topography of sites

The investigation was conducted at four sites, three of which encompass an ungrazed enclosure as well as a grazed enclosure. The sites are situated in the Mols Bjerge nature reserve in eastern Jutland, Denmark. The names of the sites are Sletten, Buelund, Kirkestien and Engen.

### Climate

Mols Bjerge is situated in a zone characterised by a regionally warm climate, with a surplus of sunshine hours compared to the mean for Denmark, and low annual precipitation. The average annual precipitation measured at the field station, Molslaboratoriet, which lies at the centre of the study sites, was 502 mm in the period 1982–96. The annual average temperature is 8°C with monthly averages of 17°C in July and 0°C in January.

### Site description

Two of the sites, Sletten and Engen, are situated on elevated seafloor with a sandy gravelly substrate, which is high in humus content in hollows between the former beach ridges. The other two sites, Buelund and Kirkestien, are situated on sandy gravelly fluvio-glacial deposits from the Weichel Glaciation.

The soils are acidic under the grasslands (FA) and heathlands (CD), ranging from pH 3.7 under the oldest established vegetation, the FA of Sletten and the CD of Buelund and Kirkestien, to pH 4.4 under the more recently established grasslands at Buelund and Kirkestien. The soils are slightly acidic, pH 5.5, under the meadow vegetation (M) of Sletten and Engen. The humus content is relatively high under the hollows of the former seafloor (20%–30%), intermediate under the grassland of Sletten (5%–10%) and low under the vegetation types of Buelund and Kirkestien (3%). Whereas Buelund and Kirkestien are well-drained soils with subsoil water lying well below the soil surface, the soils of Sletten and Engen are water-logged during winter and spring. On average the subsoil water lies 0.2 to 0.5 m below the soil surface in the meadow, and from 0.5 to 1.5 m below, in the grassland. The seasonal fluctuation in the ground water level is within the range 1 to 1.5 m, the latter occurring under extreme summer drought.

### Site prehistory

With the exception of the M-U sub-site, Sletten has never been arable. It has a prehistory of hay cropping and grazing, later grazing, declining in the post war period until it was abandoned in 1969.

Buelund and Kirkestien have a prehistory within the heathland cropping system of the region: arable for two or three seasons, with up to three decades of grazing between arable periods. The system was maintained into the late 19th or early 20th century. The less favourable sites, now the CD of the sites, were abandoned to grazing, while the other parts, the FA-swards, remained arable until 1959 (Buelund) or 1970 (Kirkestien). Buelund was completely abandoned from 1959 to the start of the studies, whereas Kirkestien was abandoned in the early 1970s.

Engen was arable until 1970, when the M-U was abandoned, whereas the then relayed sward of the M-G was grazed until 1975. From 1976 to 1983, the M-G was used for hay cropping and late season grazing.

### Vegetation and management

The vegetation consists of four main types:

1. *Festuca-Agrostis* grassland (FA), which is dominated by *Festuca ovina* L. and *Agrostis tenuis* Sibth.
2. *Calluna-Deschampsia* heathland (CD), which is dominated by *Calluna vulgaris* (L.) Hull and *Deschampsia flexuosa* (L.) Trin.
3. Sedge-grass meadow (M), which is dominated by *Carex nigra* (L.) Reichard, *C. panicea* L., and *C. ovalis* Gooden., with variable elements and dominance of other sedges and grasses (mainly in the newly developed type of vegetation at Engen) and herbs.
4. Birch woodland (S), which is dominated by *Betula pubescens* Ehrh., but with a developing climax stage of *Quercus robur* L. dominance.

More details concerning the vegetation can be found in four papers by Buttenschøn and Buttenschøn (1982, 1985, 1991, 1992).

The densities and numbers of species are generally much higher in the grazed vegetation types than in the non-grazed, and in particular the moss stratum is dense in the grazed vegetation.

There are some structural elements in the grazed vegetation which seem to be important to the population dynamics of *Malus sylvestris*. In the FA and CD of Buelund and Kirkestien, the main element is *Calluna vulgaris*, whereas in the meadow types it is *Juncus effusus* L. tussocks. The ungrazed vegetation is generally tall, which prevents light from reaching the soil surface.

Table 1 shows details of the experimental treatment and grazing pressure at the four sites. These features have

been used as parameters for the statistical analyses.

Table 2 gives a brief description of the fragmented woodlands at the experimental sites and the number of seed sources of *Malus sylvestris* in them. The area used for the data collection is also shown in this table.

## Methods

### *Analysis plots*

The vegetation analyses were made in transects of 5 × 5-m (Sletten and Buelund) or 10 × 10-m squares (Kirkestien and Engen) aligned across the main topographical structures of the study sites. The field-layer vegetation analyses were made by annual records of this vegetation element in

1 × 1-m plots situated at the corners of every second of the 5 × 5 or 10 × 10-m squares of the transects. These analyses have been made almost continuously since the start of the studies.

### *Seed dispersal and germination*

Seed dispersal and germination are described through the data of both sets of analysis plots. It was recognised early in the studies that most *Malus sylvestris* seedlings germinated in cattle dung pats. Therefore special attention was paid to the germination sites when the seedlings were recorded. In most cases the seedlings were seen germinating directly in cattle or horse dung pats. The dung pats were washed out in all of the places where there had been flooding during win-

Table 1. Details of the experimental treatment and grazing pressure at the four sites; the sites have been divided into sub-sites, depending on the experimental treatments. The grazing pressure is expressed as the product of livestock body weight in tonnes (t) and grazing days normalised to each hectare of the experimental area. A grazing pressure of 45 t days ha<sup>-1</sup> is approximately equivalent to a dry matter take-off of 1 t ha<sup>-1</sup>.

Site and sub-site	Experimental treatment	Grazing pressure
Sletten, FA, summer grazed (FA-SG)	Galloway cattle since May 1973, late April to October.	50 t days ha <sup>-1</sup>
Sletten, FA, not grazed (FA-U)	Not grazed 1973 (1969) to December 1989.	None
Sletten, FA, winter grazed (FA-UWG)	Late cattle grazing since 1989/90 in September and again in December along with FA-AWG, S-UWG and M-UWG.	40 t days ha <sup>-1</sup>
Sletten, FA, abandoned after cattle grazing (FA-A)	Cattle grazed every second year April to October 1974 and 1976, grazed as FA-SG 1977–1983. Abandoned 1983 to 1989.	None
Sletten, FA, winter grazed (FA-AWG)	As FA-UWG	40 t days ha <sup>-1</sup>
Sletten, M, summer grazed, (M-SG)	As FA-SG.	50 t days ha <sup>-1</sup>
Sletten, M, not grazed, (M-U)	As FA-U.	None
Sletten, M, winter grazed, (M-UWG)	As FA-UWG.	40 t days ha <sup>-1</sup>
Birch woodland, summer grazed (S-SG)	As FA-SG.	50 t days ha <sup>-1</sup>
Birch woodland, abandoned, (S-U)	As FA-U.	None
Birch woodland, winter grazed, (S-UWG)	As FA-UWG	40 t days ha <sup>-1</sup>
Buelund, FA, grazed (FA-G)	Galloway cattle from late April to October. Grazed along with CD-G.	25 t days ha <sup>-1</sup>
Buelund, FA, not grazed (FA-U)	Continued abandonment.	None
Buelund, CD, grazed (CD-G)	As FA-G.	25 t days ha <sup>-1</sup>
Buelund, CD, not grazed (CD-U)	Continued abandonment.	None
Kirkestien, FA, grazed (FA-G)	Icelandic horses late April to October, initiated 1984. Grazed with CD-G.	25 t days ha <sup>-1</sup>
Kirkestien, CD, grazed (CD-G)	As above.	25 t days ha <sup>-1</sup>
Engen, M, grazed (M-G)	Galloway cattle from May to November and in periods during winter and spring. Initiated may 1984.	130 t days ha <sup>-1</sup>
Engen, M, not grazed, (M-G)	Continued abandonment.	None

ter and spring. Accordingly, note was also made of any tendency of seedlings to group closely within a limited space and of whether faecal remnants, such as partly digested plant structures, were layered on the ground adjacent to the seedlings. The surroundings of seedlings which germinated without evidence of any connection with cattle or horse dung pats were examined thoroughly for any other circumstantial evidence concerning their dispersal, such as germination beneath bush or tree canopies where birds might perch.

### *On-site seedling emergence and survival*

Beside providing data for frequency and cover analysis, the field-layer analyses provide records of all of the current year's individuals of woody species and of the number of these which survive over the years. In this report, the data on *Malus sylvestris* are used to assess the life expectancy of the seedlings of this species. Further evidence concerning this can periodically be obtained through the analyses of

woody species mentioned below, although we have not used this in our report of seedling survival.

### *Population development*

The overall analysis of the development of the populations of woody species was carried out on the records of individuals of the different species in the woody-species analysis plots. These records were made annually in interrupted sequences of a number of years (4–6). An early sequence was carried out at Sletten in the mid-1970s, followed by a status analysis for a single year in 1982 (Buttenschön & Buttenschön, 1978, 1985), a second in the period 1984–1988 (Buttenschön, 1988) and the latest was initiated in 1996 or 1997. The individuals were recorded according to species and size class: current year's seedlings, saplings 0–0.5 m, saplings 0.5–1.0 m, trees 1.0–2.0 m and trees > 2.0 m, the latter class being considered to be above the reach of grazing animals. The diameters of trees > 2.0 m were meas-

Table 2. Description of the woodland element in the experimental sites and their relative populations of fruit bearing *Malus sylvestris* individuals. Furthermore, this figure presents the area of analysis used for the field-layer and woody-species vegetation analysis, expressed in square meters.

Site, area in ha	Woodland and dominating species	Fruit bearing <i>Malus sylvestris</i>	Field layer area	Woody species area
Sletten -SG 4 ha	Closed woodland at SE: <i>Betula pubescens</i> , <i>Quercus robur</i> ; dense fragmented woodland throughout: <i>Q. robur</i> , <i>Malus sylvestris</i> , <i>Betula pendula</i> , <i>Juniperus communis</i> , <i>B. pubescens</i> .	Very many	124 m <sup>2</sup>	1 500 m <sup>2</sup>
Sletten -WG 4 ha	Closed woodland at SE: <i>B. pubescens</i> , <i>Q. robur</i> ; closed woodland in meadow: <i>Salix aurita</i> , <i>S. cinerea</i> ; dense fragmented woodland throughout: <i>Q. robur</i> , <i>M. sylvestris</i> , <i>B. pendula</i> , <i>B. pubescens</i> , <i>J. communis</i> .	Very many	97 m <sup>2</sup>	1 875 m <sup>2</sup>
Buelund -G 7 ha	One ha closed woodland: <i>Q. robur</i> , <i>J. communis</i> , <i>Fagus sylvatica</i> ; small fragments of <i>J. communis</i> dominated shrub.	Very few	124 m <sup>2</sup>	3 000 m <sup>2</sup>
Buelund -U 3 ha	Mostly open; more closed fragments of woodland developing two small sites: <i>Q. robur</i> , <i>Pinus sylvestris</i> .	Very few	96 m <sup>2</sup>	1 775 m <sup>2</sup>
Kirkestien 4 ha	Dense fragments, locally closed woodland in CD-area: <i>P. sylvestris</i> , single trees to fragments in FA: <i>P. sylvestris</i> .	One plus branches of tree outside fencing	72 m <sup>2</sup>	3 500 m <sup>2</sup>
Engen -G 7 ha	Fragmented woodland on littoral cliff: <i>Q. robur</i> , <i>F. sylvatica</i> , <i>Prunus spinosa</i> , <i>Rosa canina</i> ; elevated seafloor single <i>S. aurita</i> and <i>S. cinerea</i> .	Few	92 m <sup>2</sup>	4 700 m <sup>2</sup> Not done yet
Engen -U 1.5 ha	Belts of dense woodland: <i>S. aurita</i> , <i>S. cinerea</i> , <i>B. pubescens</i> ; divided by fragmented woodland: <i>M. sylvestris</i> , <i>Q. robur</i> .	Many	36 m <sup>2</sup>	3 500 m <sup>2</sup> Not done yet



ured at a height of 1.3 m. The data concerning *Malus sylvestris* was extracted from the records in this report.

### *Abandonment and reinitiation of grazing*

In connection with the abandonment of 1.2 ha of the initially grazed area at Sletten (FA-A), all of the *Malus sylvestris* seedlings germinating in the transect were mapped and marked. Abandonment took place in October 1983 and mapping was carried out in June 1984. The fate and increase in height of each seedling was followed until 1988, when nearly all surviving seedlings had broken the canopy of the field-layer vegetation. This area was then winter-grazed from 1989/90 (FA-AWG). A new record of the remaining seedlings was made in 1997. These data are used here to describe developments in connection with the abandonment and reinitiation of grazing — factors which appeared from the initial woody-species studies to be important to the long-term establishment of a mature stand of *Malus sylvestris*.

### *Browsing pressure*

In connection with the analyses of the woody-species population development, a continuous semi-quantitative record was made of the browsing pressure on the different woody species (Buttenschøn & Buttenschøn 1978, 1985). This was made on a 4-point scale, on all individuals within the analysis plots, thus 0 = no evidence of browsing, 0.5 = evidence of browsing on a few twigs, 1.0 = evidence of browsing on many twigs and 2.0 = evidence of browsing on most twigs within the reach of browsers or the breaking-off of smaller branches, sometimes even the bending-down and browsing of the tops of certain individuals. In this report, the mean browsing pressure on *Malus sylvestris* saplings has been calculated relative to the main vegetation types. The browsing pressure on trees taller than 0.5 m is not presented, as only the analysis plots at Sletten contain this class in significant quantities and the main point of presenting the browsing pressure data is to make a comparison between the sites.

### *Statistical analyses*

The data on seedling survival were tested by non-parametric ranking tests (Log-Rank, Wilcoxon and Kruskal-Wallis, both with covariance matrices), and by SAS, for homogeneity of the survival curves over time variable against time and time constant against grazing pressure. The different statistical methods were tested for equality by the  $\chi^2$ -test.

No results are presented on statistical testing of the long-term development of saplings into a mature population of *Malus sylvestris* as there is very little development over time and almost no information on the age on this population.

The study of the abandonment and reinitiation of grazing was dealt with in the above-mentioned statistics on seedling survival; long-term survival trends were also tested by linear regression on a semi-logarithmic scale.

The browsing data were transformed to a scale of 1, 2, 3 and 4 to test the data statistically for differences between sites (Wilcoxon test) and for possible correlation between grazing and browsing pressures (Spearman correlation coefficients) on a non-parametric basis.

## RESULTS

### **Seed dispersal and germination**

A total of 1 718 seedlings were recorded at Sletten in connection with the vegetation analyses. Of these, 1 692 were definitely connected with cattle dung-dispersal and only 26 were unaccounted for. Five of the latter were found as single seedlings under larger trees, four of which were found in the ungrazed area, FA-U. Only 7 seedlings were found in ungrazed areas, apart from the 314 which were found in the first year of abandonment in the abandoned cattle-grazed area.

At Buelund, 60 seedlings in all were recorded, one of which was growing under a large *Pinus sylvestris* L. in the ungrazed area. Seven other seedlings could not definitely be associated with cattle dung pats, but they were all within the grazed enclosure.

Only four seedlings have been found at Kirkestien, all of which were found in horse dung pats in 1997. A number of saplings from 1996 were, however, found in this enclosure in 1997.

44 seedlings have been recorded at Engen, 26 of which were growing on cattle dung pats, whereas the remainder were all clustered in small groups, together with evidence of washed-out cattle dung remnants in most cases.

In summary, 1 826 seedlings were recorded at all four sites. Most (1 792) were either germinating in dung pats or showed evidence of doing so. Thirty-four seedlings showed no evidence of association with livestock dung and eight of these were found in the ungrazed area.

### **On-site seedling emergence and survival**

The emergence and survival of *Malus sylvestris* seedlings within the field-layer analysis plots at



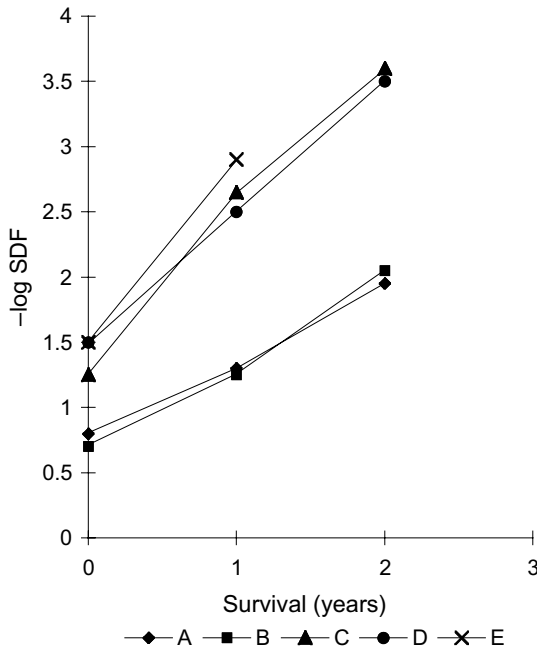


Fig. 1. Seedling survival estimates. The graphs have been redrawn from the SAS curve-fit functions of the plots of the statistical analyses carried out on the data of Table 3. Graph A represents the 0 t days ha<sup>-1</sup> grazing pressure, B that for 25, C that for 40, D that for 50 and graph E represents the 130 t day ha<sup>-1</sup> level. The graphs show an increasing slope with increasing grazing pressure and also indicate that the slope at the lower levels of grazing (A, B) is steeper in the second year as compared to the first, whereas it is less steep at the higher levels. The graphs only show the records for the first three years, as the unknown fates of the saplings surviving in 1998 could not be incorporated into the statistics in a meaningful manner and, therefore, their number (considered in relation to long-term survival) would have an unpredictable influence on estimates of further development.

the steepest slope. The figure also shows that the seedling emergence density, as expressed by the relative positions of the starting points of the graphs, is dependent on the grazing pressure, i.e. the higher the grazing pressure, the higher the seedling density. This trend is confirmed by the statistical methods used, which were intended to rank differences in survival according to grazing pressure. The test for equality between the statistical methods used yields a comfortable probability for all tests employed ( $p < 0.0005$  for all three tests).

It is apparent from Table 3 that most saplings

do not survive for very long. At the grazed part of Buelund, however, a high number of seedlings (5 of 21 germinating) have survived for more than four years. Four of these grow within the tall structure of ageing *Calluna vulgaris* bushes, which are mostly avoided during grazing.

### Population development

The development in the population structure of *Malus sylvestris* at the four sites is shown in the 12 panels of Fig. 2. As very little information, none of which is significant, was provided by the upper size classes in this species, only the data for three size classes are presented: current year's seedlings, saplings of up to 0.5 m and trees > 0.5 m.

There were some fluctuations in the seedling and sapling populations in all parts of the summer-grazed area at Sletten (FA-, M- and S-SG). These fluctuations are related to the previous year's crop of apples, to the current germination conditions of the seedling class, to the previous year's input of seedlings and to the current death of saplings, as far as the sapling class is concerned. There was no net input to the tree classes in any of the vegetation zones over the years of the study, and a decrease in number was observed in the meadow and birch/oak woodland. In grassland which was abandoned in 1983 (FA-A and -AWG), there was a very large seedling input in 1984, the year after abandonment, and again in 1997, where the area had been grazed again for some years. There was a large input of saplings in this then ungrazed, area. Over the following years, there a gradual decrease up to 1988, There was a further decrease in the sapling class from 1988 to 1997, but there was a net increase in the tree class in the same period. This input came almost exclusively from the individuals of the sapling class of 1984, as only two saplings deriving from the 1984 seedling population were taller than 0.5 m in 1997. The situation remained more or less stable from 1984 to 1988 in the ungrazed areas (FA-, M- and S-U). But there was a decrease in the sapling and tree classes in the birch/oak woodland (S-U). In 1997, there was a seedling population in all three vegetation zones of the formerly ungrazed, now winter-grazed, areas (FA-, M- and S-UWG).



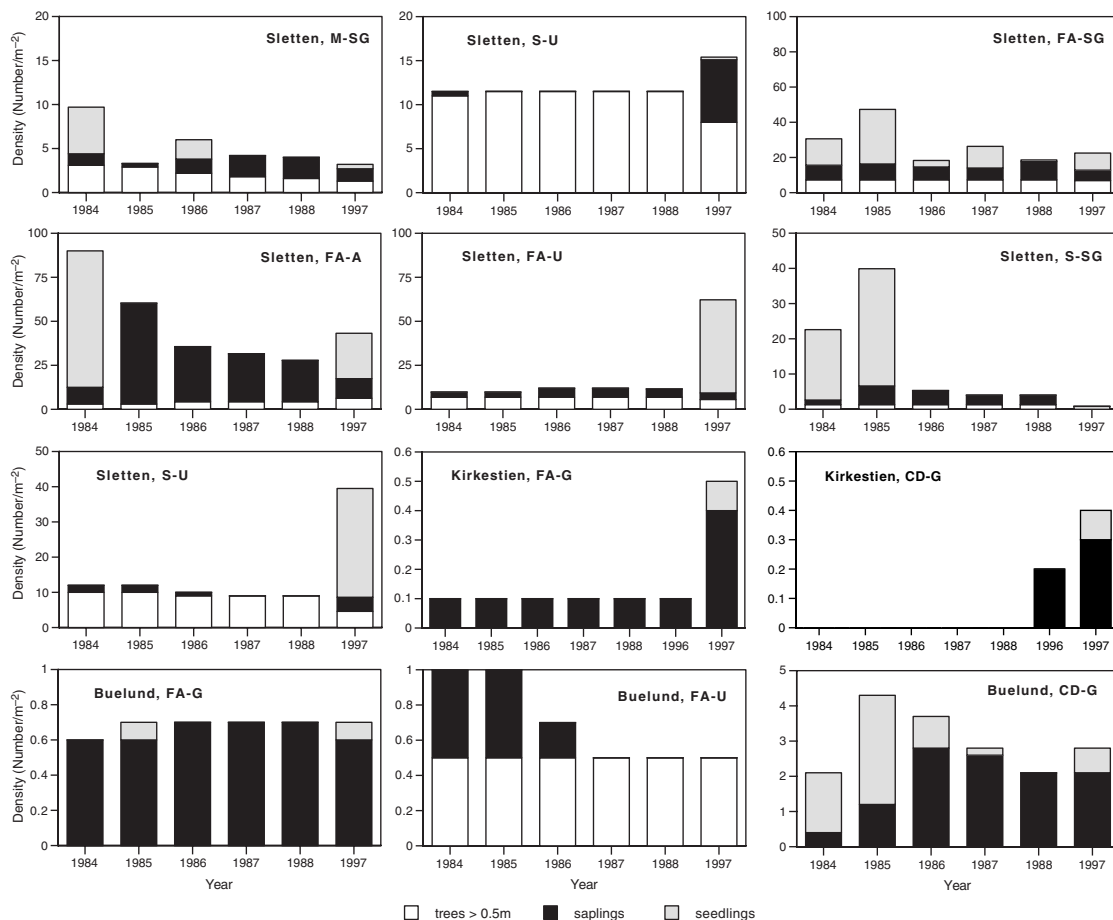


Fig. 2. The density of *Malus sylvestris* (L.) Mill. in the different vegetation types of the study sites. The population of *M. sylvestris* is divided into three classes: seedling = current year's seedlings, saplings = individuals older than seedlings and < 0.5 m in height and trees = individuals > 0.5 m in height. In the 12 panels, the comparable vegetation types of any site are placed in horizontal rows. At Sletten, the term "ungrazed" covers the management of the -U and -UWG treatments, and the term "abandoned" covers the management of the FA-A and FA-AWG. Details of the treatments are given in Table 1. The densities are expressed as the number of *M. sylvestris* individuals per 100 square metres.

The sapling class of the woodland zone was almost entirely recruited from the tree class, but in the meadow zone there was significant recruiting from the seedling and tree classes. Between 1988 and 1997, there was a decrease in the tree class in all three vegetation zones.

There were some fluctuations in the seedling and sapling classes in both types of grazed vegetation at Buelund (FA- and CD-G). The sapling class in grassland vegetation maintained its initial density, whereas it stabilised at a higher density in heathland vegetation. In the ungrazed grassland at Buelund, the sapling class had died out by 1987.

There was evidence of a slow increase in the sapling class in both vegetation types at Kirkestien, and a few seedlings were recorded in 1997. The 1996 records were made in late April, prior to the germination period of *Malus sylvestris* seeds.

### Abandonment and reinitiation of grazing

As mentioned above, there was a high emergence of seedlings in 1984, in the grassland where grazing had been abandoned in the late autumn of 1983 (Fig. 2). Fig. 3 shows the subsequent survival of

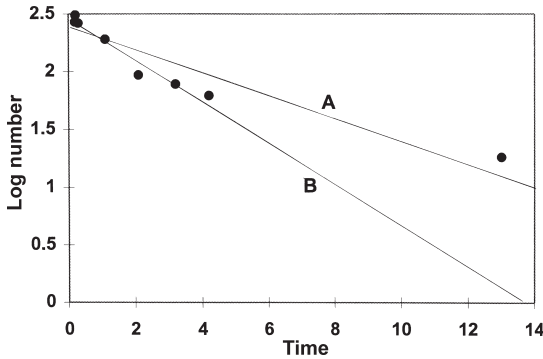


Fig. 3. Survival of the 1984 seedling generation of FA-A (1984–1988) and FA-AWG (1997). Two linear regression calculations have been carried out, one (shown as B) on FA-A only, the other (shown as A) on the complete set of data. They are expressed by  $y = -0.18x + 2.46$ ,  $r_{xy} = 0.978$ ,  $p < 0.001$  (graph B), and  $y = -0.09x + 2.35$ ,  $r_{xy} = 0.940$ ,  $p < 0.001$  (graph A).

this seedling generation plotted on a semi-logarithmic scale (log(number) against time). The survival of this seedling generation has been tested by linear regression and correlation. The SAS linear fit exhibited a slightly concave curvature, which gave a higher life expectancy than was indicated by the linear regressions, but which also ultimately suggested an increase in survival as a function of time. Linear regression was divided into two phases: first, performed on all data before the reinitiation of grazing, indicating a shorter life expectancy ( $y = -0.18x + 2.46$ ,  $r_{xy} = -0.978$ ,

$p < 0.001$ ), and second, on all data that give a shallower slope to the line, thus indicating a longer life expectancy ( $y = -0.09x + 2.35$ ,  $r_{xy} = 0.940$ ,  $p < 0.001$ ). According to the former, the saplings would die out by 1997/98, according to the latter, this would occur in 2010, 26 years after emergence.

### Browsing pressure

The browsing pressure on *Malus sylvestris* saplings at Buelund and Sletten is shown in Table 4. Earlier information concerning browsing on *Malus sylvestris* at Sletten was reported in two previous publications by Buttenschøn and Buttenschøn (1978, 1985).

The Spearman correlation coefficient was calculated for the possible link between grazing and browsing pressures:  $0.565$ ,  $p = 0.0001$ . This indicates that the grazing and browsing pressures are linked, i.e. browsing pressure increases as grazing increases. However, the authors were unable to establish a link with the same high confidence between certain regimes of grazing pressure, e.g., comparison between the summer-grazed FA at Sletten and Buelund.

Non-parametric tests on differences between treatments showed:  $p = 0.11$  for CD-G and CD-U at Buelund (only four CD-U records);

Table 4. Browsing pressure on saplings (< 0.5 m in height) of *Malus sylvestris* (L.) Mill. at study sites Buelund and Sletten. The suffixed letters of the vegetation types are defined in Table 1. The empty spaces in the table indicate that no *M. sylvestris* saplings were present

Year	1984	1985	1986	1987	1988	1997
<b>Buelund</b>						
FA-G	0.8	0.7	0.5	0.6	1.4	1.2
FA-U	1.0	0.5	0.5			
CD-G	1.2	1.2	0.8	1.6	1.0	0.9
CD-U						
<b>Sletten</b>						
FA-SG	1.2	1.1	1.3	1.3	1.1	1.6
FA-A/-AWG	1.4	0.1	0.0	0.0	0.0	1.8
FA-U/-UWG	0.4	0.3	0.2	0.2	0.2	1.2
M-SG	1.7	1.3	0.9	0.6	1.2	1.1
M-U/-UWG	1.0					1.2
S-SG	0.0	0.5	0.2	0.0	0.0	0.0
S-U/-UWG	0.0	0.0	0.0	0.0	0.0	0.8

$p = 0.05$  for FA-G and FA-U at Buelund;  
 $p = 0.02$  for FA-U at Buelund and FA-U at Sletten  
(more intensive browsing at Buelund);  
 $p = 0.0001$  for FA-U and FA-UWG at Sletten;  
 $p = 0.0001$  for FA-A and FA-AWG at Sletten;  
 $p = 0.0014$  for FA-UWG and FA-AWG at Sletten  
(less intensive browsing on FA-UWG);  
 $p = 0,20$  for FA-SG and FA-UWG at Sletten;  
 $p = 0.0001$  for M-U and M-SG at Sletten;  
 $p = 0.30$  for M-SG and M-UWG at Sletten;  
 $p = 0.0001$  for S-U and S-SG at Sletten;  
 $p = 0.48$  for S-SG and S-UWG at Sletten.

These results show that browsing depends on grazing, but they also indicate some differences in the background browsing level and the actual browsing level within the same treatment.

## DISCUSSION

Previous evidence concerning the dispersal of *Malus sylvestris* seeds is scarce (Krefting & Roe 1949, Turcek 1964, 1967, Rose & Rose 1988), and the literature in question provides circumstantial evidence for the significance of the dispersal routes, rather than consistent proof that the routes may be important. However, Buttenschön and Buttenschön (1985) have shown that domestic cattle are important to seed dispersal and that a significant proportion of the seeds thus perenterally dispersed are in fact viable, both in germination trials and in the field. The new data of the present study substantiate the previous results by showing with certainty that 98% of all germinating seedlings have been dispersed in this manner. Furthermore, the study implicates the horse as an important dispersal vector. During these studies, no evidence has been found to implicate sheep in the dispersal of *Malus sylvestris* seeds, even though sheep pasturing in conditions similar to those of the cattle-grazed areas of Sletten have been studied from 1974 to 1984 (Buttenschön & Buttenschön 1978, 1985 and this study).

One reason for this could be the relative fodder grinding efficiency of the different animal species. In this context, it can be worth considering the structure of the faeces of the animal species in question. Cattle and horse faeces have a high content of gross-structure remnants of ingested plant material, whereas this is not apparent in sheep faeces. Simi-

larly, when considering wild herbivores, the faeces of deer species has a finely structured appearance like that of sheep, whereas the hare's faeces has a coarser structure (Bang & Dahlstrøm 1972). The food processing of the omnivores, and carnivores in particular, is generally less thorough than that of the herbivores, which is evident from the faecal structure of these animal groups (Bang & Dahlstrøm 1972). Accordingly, the species groups which do eat apples (Turcek 1967) can potentially play a part in seed dispersal through dung. A number of birds feed on apples, but only relatively few of them specifically seek out the seeds (Bang & Dahlstrøm 1972, Rose & Rose 1988). Among these are the crossbill species, some tit species and the chaffinch. The latter also eats new seedlings of *Malus sylvestris* (Buttenschön & Buttenschön 1985). Rose and Rose (1988) have made a few observations showing that whole fruit or seeds are sometimes stored in the soil-litter interface of the field layer by birds. The authors assume that such storage largely takes place in shrub or woodland. This form of dispersal might enhance the emergence of seedlings more than the other two forms mentioned, i.e. feeding on fruit flesh and seeds, respectively. In the present study, a small number of the seedlings may derive from seeds dispersed by birds, e.g., the seedlings located under tree canopies. Judged from the circumstances in which the seedlings emerge, the magnitude of bird dispersal would be in the 0.5%–1% of the total observed seed dispersal.

The freshly shed seeds of *Malus sylvestris* are subject to seed-coat dormancy as well as embryo dormancy (Krefting & Roe 1949, Kramer & Kozłowski 1979). Both types of dormancy must be broken before germination can take place. It appears that seed-coat dormancy is induced by chemical compounds in the fruit meat (Wan & Dennis 1992). Krefting and Roe (1949) state that passage through the intestinal tract may break seed-coat dormancy. They suggest that the combination of scarification, microbial invasion of the seed coat structures and stomach acid and enzymes could facilitate this. A fermentative break-down of apple-fruit flesh would in most respects yield a similar combination of impacts. However, there would be no scarification and the bio-chemical impact would be strictly oxidative-fermentative, rather than the fermentative-reductive impact followed

by the acidic and enzymatic break-down associated with ruminant digestion, or associated in the alternate order with the horse's digestion. The seeds might also be subject to desiccation when left on the ground, which is not the case when implanted in dung pats. Desiccation may deepen embryo dormancy (Kramer & Kozłowski 1979). Embryo dormancy is normally broken by a prolonged period of cold storage (Krefting & Roe 1949, Kramer & Kozłowski 1979) and as demonstrated by the germination trials conducted on *Malus sylvestris* seeds by Buttenschøn and Buttenschøn (1985). From this we conclude that, apart from promoting the spatial dispersal of *Malus sylvestris* seeds, the perenteral dispersion route promotes the breaking of seed-coat dormancy, enhances preservation of the seeds during the cold-storage period of winter and promotes the subsequent breaking of embryo dormancy.

Apart from indicating a major dispersal route for viable *Malus sylvestris* seeds in the setting of grazing-managed, semi-natural grasslands, the study reveals some important characteristics of the germination sites that result from the different dispersal routes. This is evident from Fig. 1 and its associated data analysis. We have shown that there is a higher density of seedling emergence in the more heavily-grazed areas, e.g. a comparison of the initial level of graph B to graphs C and D. While the sward represented by graph B (Buelund) contains tall elements of *Calluna vulgaris*, the *C. vulgaris* stand at Sletten is succumbing to grazing pressure. From Fig. 1 and the description in Table 2, it appears that within certain limits seed source availability is not the limiting factor, cf. the initial level of graph E to graphs C and D. However, this point cannot be verified by comparing Sletten to Buelund (extremely high to extremely low seed source levels) through the present study. Similar elements of tall vegetation (as mentioned for Buelund) are present in all M-type vegetation, in this case connected to *Juncus effusus* tussocks. Here, however, winter and spring flooding is assumed to be detrimental to survival. These growth site characteristics are important to the survival of the seedlings, as primarily the light regimes, but also the availability of nutrients and of shelter from browsing, appear to govern seedling survival through the first critical phases.

Where bird dispersal is involved, most seeds are dropped or stored under trees. The light regimes under ungrazed tree canopies are generally insufficient for the subsequent survival of the seedlings, e.g. as indicated by the low seedling survival in the S-U at Sletten and the FA-U at Buelund (Table 3), and as clearly demonstrated by the linear regressions carried out on the abandonment study data of the FA-A/-AWG (Fig. 3), where the death rate is shown to be high in the initial phases of growth, before the field canopy is broken by the *Malus sylvestris* saplings.

Seedling survival is prolonged in the ungrazed grassland and meadow sward at Sletten, but all seedlings eventually die. In contrast to the long-term abandonment situation of the ungrazed swards, seedlings on the newly abandoned grassland at Sletten succeed very well (Figs. 2 and 3). This is due to the relatively high light regimes which prevail during the first post-abandonment years. At present (1998), the survival rate represents a sapling density of 16 per 100 m<sup>2</sup>.

During germination, and usually most of the following summer, the seedlings in the grazed enclosures are preserved from grazing by the coprophobic grazing habits of cattle and, to a lesser extent, of the horse. The cattle avoid their own dung pats for a variable period of time, which depends on the break-down rate of the dung pats. Typically, the dung pats dropped during autumn are broken down by late summer of the following year, but some structure-rich dung pats may be avoided for up to two years. This is seen in connection with herbage with a high content of *Calluna vulgaris*, e.g. autumn grazing at Buelund, or in connection with autumn and winter grazing at Sletten, where there is a high content of straw in the available vegetation. The avoidance of dung pats promotes the early survival of *Malus sylvestris* seedlings, but may also promote grazing in subsequent years, when the nutrient-rich spots constitute choice grazing. The graphs of Fig. 1 show that there are some differences in seedling survival in the initial phases of seedling establishment. In the first year, the differences in the slopes of the graphs may in part be the results of differences in desiccation exposure due to structural differences in the swards and also, late in the grazing season, of differences in the regrazing

of the dung pats in which the seedlings germinated. While graphs A and B have a steeper upward slope from year one to year two, graphs C and D have a less steep upward slope. This could be explained by greater competition for light and nutrients at A and B in the second year, due to taller vegetation on these swards, to some degree accentuated at B by the prolonged coprophobic influence of dung pats there.

Under grazing conditions, prolonged survival of the seedlings varies. Such survival attains the highest percentage where the grazing pressure is lowest, e.g., seedling survival at Buelund (Table 3, Fig. 1). A larger proportion of above-ground take-off of plant material leads to an increasingly high proportion of close, lawn-like swards with less structural diversity in the field vegetation layer. Accordingly, the number of sites with tall vegetation structure, which are safe for young seedlings, decreases with increasing relative take-off. *Calluna vulgaris* bushes constitute one of the main safe site structures at Buelund (as mentioned in the discussion of seedling emergence) and Kirkestien. At Sletten the safe sites are of a more transient character, e.g., small areas of tussocky vegetation dominated by *Nardus stricta* L. or *Juncus effusus*, swards of vegetation dominated by *Holcus mollis* L. or swards protected under open thickets of *Rubus fruticosus* L. which, depending on the current state of the vegetation in general, are grazed or remain ungrazed. The vegetation structures mentioned are the less choice types of cattle forage. As shown by the study of the abandonment and reinitiation of grazing, the survival of the saplings may be greatly enhanced by periods of less disturbed growth (Fig. 3).

We have shown that the intensities of grazing and browsing pressures are linked, although a comparison of different levels of grazing pressure showed this not to be the whole truth as revealed by the applied method. However, the evidence provided by the seedling survival tests supports the former result rather than the latter. All in all, the results suggest that browsing on *Malus sylvestris* saplings by cattle is non-selective, i.e. it involves neither preference nor avoidance attributes, and, accordingly, that it occurs as an integral part of the grazing of the field layer in general. But it is not totally clear whether this is partly due to

structural differences in the swards in question. In other words, to what degree do tall structural elements in vegetation actually reduce the browsing pressure on the saplings? Notwithstanding this question, to which no definite answer can be given by this study, it appears that reductions or increases in grazing pressure induce similar effects in browsing on *Malus sylvestris*. This means that the survival or build-up of a stand can be enhanced by regulating the grazing pressure.

In connection with conservation efforts concerning *Malus sylvestris*, the results of these studies could be used to propagate and secure stands of this species. The abandonment and/or reduction of grazing pressure over a period should be applied to secure new recruiting of saplings in pastures where seed sources are available. When introducing *Malus sylvestris* to a site, a simple way of dispersal would be to feed the fruit to cattle and then allow them to disperse the seeds into the proven seedbeds of dung pats. This would condition the right environment for propagation. According to the grazing pressure, site productivity, etc., the survival of the emerging seedlings and saplings may then be supported by the reduction or cessation of grazing over a period of some years. Five or more years is implied by the results of the study of abandonment and initiation of grazing. Follow-up grazing over the following years should be less than or within the range of take-off used at Buelund. The development of sapling populations should be monitored to secure the development of *Malus sylvestris* stands, without excessively detrimental development of the field layer due to abandonment or semi-abandonment, which is a disadvantage of swards grazed in the long term.

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## REFERENCES

- Bang, P. & Dahlstrøm, P. 1972: Dyrespor: spor og sportegn efter pattedyr og Fugle. — G. E. D. Gads Forlag, København. 240 pp.
- Buttenschøn, J. 1988: The establishment of woody species in grassland conservation areas. — *Aspects Appl. Biol.* 16: 373–381.
- Buttenschøn, J. & Buttenschøn, R. M. 1978: The effect of browsing by cattle and sheep on trees and bushes. — *Natura Jutlandica* 20: 79–94.
- Buttenschøn, J. & Buttenschøn, R. M. 1982: Grazing experiments with cattle and sheep on nutrient poor, acidic grassland and heath: I Vegetation development. — *Natura Jutlandica* 21: 1–18.
- Buttenschøn, J. & Buttenschøn, R. M. 1985: Grazing experiments with cattle and sheep on nutrient poor acidic grassland and heath: IV Establishment of woody species. — *Natura Jutlandica* 21: 117–140.
- Buttenschøn, J. & Buttenschøn, R. M. 1991: Fra agermark til overdrev. — *Urt* 1991–3: 81–92.
- Buttenschøn, J. & Buttenschøn, R. M. 1992: Lyngpleje ved kvæggræsning. — *Flora og Fauna* 98: 53–62.
- Franke, A., Dagenbach, H. & Hauff, U. 1990: Erhaltung und Nachzucht seltener einheimischer Baumarten in Baden-Württemberg. — *AFZ* 1990 (6–7): 166–168.
- Hansen, K. 1991: Dansk feltflora, 1. udgave, 5. oplag. — Nordisk Forlag A.S., København. 757 pp.
- Henning, W. 1947: Morphologisch-systematische und genetische Untersuchungen an Arten und Artbastarden der Gattung *Malus*. — *Der Züchter* 17/18: 289–349.
- Hofmann, H. 1993: Zur Verbreitung und Ökologie der Wildbirne (*Pyrus communis* L.) in Süd-Niedersachsen und Nordhessen sowie ihrer Abgrenzung von verwilderten Kulturbirnen (*Pyrus domestica* MED.). — *Mitteil. Deutschen Dendrol. Ges.* 81: 27–69.
- Kramer, P. J. & Kozlowski, T. T. 1979: Physiology of woody plants. — Academic Press, New York. 811 pp.
- Krefting, L. W. & Roe, I. E. 1949: The role of some birds and mammals in seed germination. — *Ecol. Monogr.* 19: 269–286.
- Lucke, R. 1989: Wilde Birn- und Apflebaume für die Landschaftspflege. — *Obst und Garten* 1989 (10): 521–524.
- Remmy, K. & Gruber, F. 1993: Untersuchungen zur Verbreitung und Morphologie des Wild-Apfels (*Malus sylvestris* (L.) Mill.). — *Mitteil. Deutschen Dendrol. Ges.* 81: 71–94.
- Rose, B. & Rose, D. 1988: Birds and berries. — T. & A. D. Poyser, Carlton, England. 268 pp.
- Rothmaler 1994: Exkursionsflora von Deutschland, 15. durchgelesene Auflage, Band 2, 3 & 4. [Edition editors: R. Schubert, K. Werner & H. Meusel]. — Gustav Fischer Verlag, Jena. 2171 pp.
- Schweingruber, F. H. 1979: Wildapfel und prähistorische Äpfel. — *Archaeo-Physika* 8: 283–294.
- Turcek, F. J. 1964: Endozoische Verbreitung von Gehölzsaamen durch den mitteleuropäischen Feldhasen (*Lepus europaeus* E. Pall.). — *Biológia* (Bratislava) 19: 541–549.
- Turcek, F. J. 1967: Ökologische Beziehungen der Säugetiery und Gehölze. — *Vydavatel'stvo Slovenskej Akadémie Vied, Bratislava*. 195 pp.
- Wagner, I. 1995: Identifikation von Wildapfel (*Malus sylvestris* (L.) Mill.) und Wildbirne (*Pyrus pyrastrer* (L.) Burgsd.). Voraussetzung zur Erhaltung des einheimischen Wildobstes. — *Forstarchiv* 66: 39–47.
- Wan, C. K. & Dennis, F. G. Jr. 1992: Fruit-induced dormancy in apple seeds: role of water and inhibitors. — *J. Am. Soc. Hortic. Sci.* 117: 463–466.